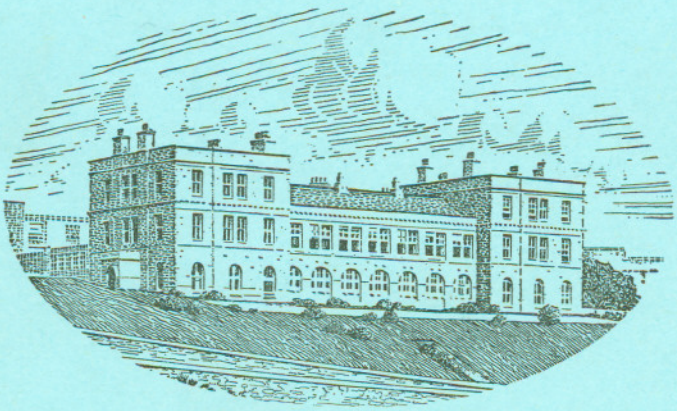
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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February 1959

(*Frontispiece*)

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OBITUARY

Dr G. A. Steven, F.R.S.E.

George Alexander Steven was born at Freshwick, Caithness, on 13 April 1901. His boyhood was spent among crofter fisherfolk, and fishing and boats were part of his youthful environment. During 1924–28 he studied Zoology in the University of Edinburgh, being Vans Dunlop Scholar in 1926. After graduation he came to Plymouth, first as student probationer and then, a year later in 1929, he was appointed to the permanent staff of the laboratory. In 1931 he was elected a Fellow of the Royal Society of Edinburgh, and in 1952 was awarded the Doctor of Science degree of the University of Edinburgh. After a long illness he died on 7 April 1958 at his home in Yelverton, Devon, leaving a widow and two sons.

The bulk of Steven's scientific work at Plymouth was closely concerned with the commercial fisheries of Devon and Cornwall, but many of his findings have wider application, both in the field of biology and of economics. The work is grouped around the following four major subjects: (1) rays and skates, (2) shags and cormorants, (3) seals, (4) mackerel. He had early realized the importance in the south-west of the ray and skate fishery and the prevailing general ignorance concerning the biology of the fishes on which it is based. His researches established that rays tend to congregate in unispecific and unisexual shoals, that they are slow-growing and that, at any rate in the Thornback Ray, juveniles stay for years on the same ground with little tendency to move away. A result of this habit is the depletion of stocks in areas of intense trawling unless care be taken to return all young rays to the water at once. Investigations into the food of shags and cormorants followed a request from the Cornwall Sea Fisheries Committee. In the belief that these birds menaced the inshore fisheries, especially flatfishes, the Committee had paid away hundreds of pounds for thousands of their heads. Steven was able to show that shags, by far the most numerous of the two birds, eat largely non-marketable fishes and flatfishes scarcely at all. The latter do form an appreciable element in the food of cormorants but these birds are too few to have any marked effect on the fishery. His studies of the seal population of Cornwall similarly arose from complaints of fishermen that seals gravely menaced their livelihood. While making his census Steven visited, often by swimming into them under uncomfortable and risky circumstances, all the caves along the north Cornish coast. He concluded that there were (in 1935) between 300 and 500 Grey Seals in the area. Steven's work on the biology of the mackerel undoubtedly ranks as his major contribution to fishery science.

Through a fog of earlier pre-conceived ideas and conflicting statements he made his way to a rational interpretation of the annual movements of the mackerel shoals, showing that they winter in dense congregations near banks and gulleys on the bottom, rising in the spring to the surface to migrate to a common spawning ground near the 100-fathom contour, which in the western region lies west of the Isles of Scilly. After spawning they migrate into shallow water inshore during the summer, later returning to winter quarters. He also made important observations on spawning, feeding, age and growth.

Steven's scientific work at Plymouth suffered interruption during the war years. He had served in the Army in France during the 1914–18 war, and during the first years of the Second World War he saw active service with the Royal Navy. During 1942–45 he was seconded from the Navy to develop the fisheries of Sierra Leone under the Colonial Office. From his base in Freetown, despite many difficulties and much discouragement, he played a leading part in preparing the groundwork for the post-war fisheries of that region, in so doing producing two comprehensive Reports for the Colony of Sierra Leone.

Just prior to the outbreak of war in 1939 he had accepted the post of Director of the Newfoundland Fisheries Research Laboratory at St Johns. Within a few days a disastrous fire destroyed the St Johns Laboratory and the war intervening before other arrangements could be made he never took up this post.

The research vessel 'Sarsia', the finest ever owned by the Association, owes much in her design and equipment to Steven's practical knowledge of work at sea. He was much interested in net-making, and a useful small handbook he wrote on the subject has been very favourably received.

From 1930 to 1948, exclusive of the war years, Steven took an active part in the Courses in Marine Biology for university students, held at the Plymouth Laboratory each year during the Easter Vacation. There are many zoologists who to-day remember with gratitude his care for them while on their first dredging and trawling expeditions, and the excellence and stimulating manner of his teaching. His many friends and colleagues at the Laboratory and elsewhere will sorely miss him.

D.P.WILSON

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THE BIOLOGY OF *NICOTHOË ASTACI* AUDOUIN AND MILNE EDWARDS

By JAMES MASON
Marine Laboratory, Aberdeen

(Text-figs. 1–4)

Nicothoë astaci is a choniostomatid copepod (Gurney, 1929) parasitic on the gills of the lobster, *Homarus vulgaris* Milne Edwards. In view of the possible effect of *Nicothoë* on the lobster, which is of considerable commercial importance in Scotland, a programme of work was instituted on the biology of the parasite.

Nicothoë attaches itself by means of its suctorial mouth to a gill filament of the lobster, and the wall of the filament is pierced by the sharp, styliform mandibles. The host's blood is sucked by means of a muscular gullet leading to the stomach. *Nicothoë* often occurs in groups, especially near the bases of the gills. The adult parasite is incapable of any movement except a slight lateral displacement of the abdomen and, once attached, probably remains in the same position throughout its life. Little is known of the life cycle, and all individuals so far definitely recognized have been females.

MATERIAL AND METHODS

Specimens of *Nicothoë astaci* were collected from six samples of preserved Orkney lobsters between September 1954 and November 1955, and, in order more adequately to cover the annual cycle of *Nicothoë*, nine further samples were obtained from Bernera, Lewis, between October 1955 and November 1956. Lobsters arriving in poor condition at two merchants' premises were preserved in formalin and sent to the Marine Laboratory, Aberdeen, for examination. Living parasites were also examined, and stained sections and whole mounts prepared.

THE ADULT FEMALE

The adult female (Figs. 1 and 2) is made up of three parts: (i) cephalothorax; (ii) thorax, which bears two large lateral expansions or wings; and (iii) abdomen, which carries two oval egg-sacs. The length to the tip of the abdomen is some 1·2 to 1·7 mm; each wing, measured from its tip to the junction of its anterior edge with the trunk, is up to some 4 mm long; the egg-sacs measure up to 3 mm.

The segmentation is set out in Table 1 and shown in Fig. 2. The appendages

are not figured in detail as this has been done by previous workers (Leigh-Sharpe, 1926; Gurney, 1929).

The first two thoracic segments are fused to the head, and the next three, which are distinguishable dorsally by three rings, are concerned in the formation of the wings. Articulation is between the posterior edge of the wings and the sixth thoracic segment, the latter being fused to the first abdominal segment.

The adult female of *Nicothoë* has the full complement of segments and limbs, and is to be regarded as a modification of, rather than a degeneration from, the typical copepod form.

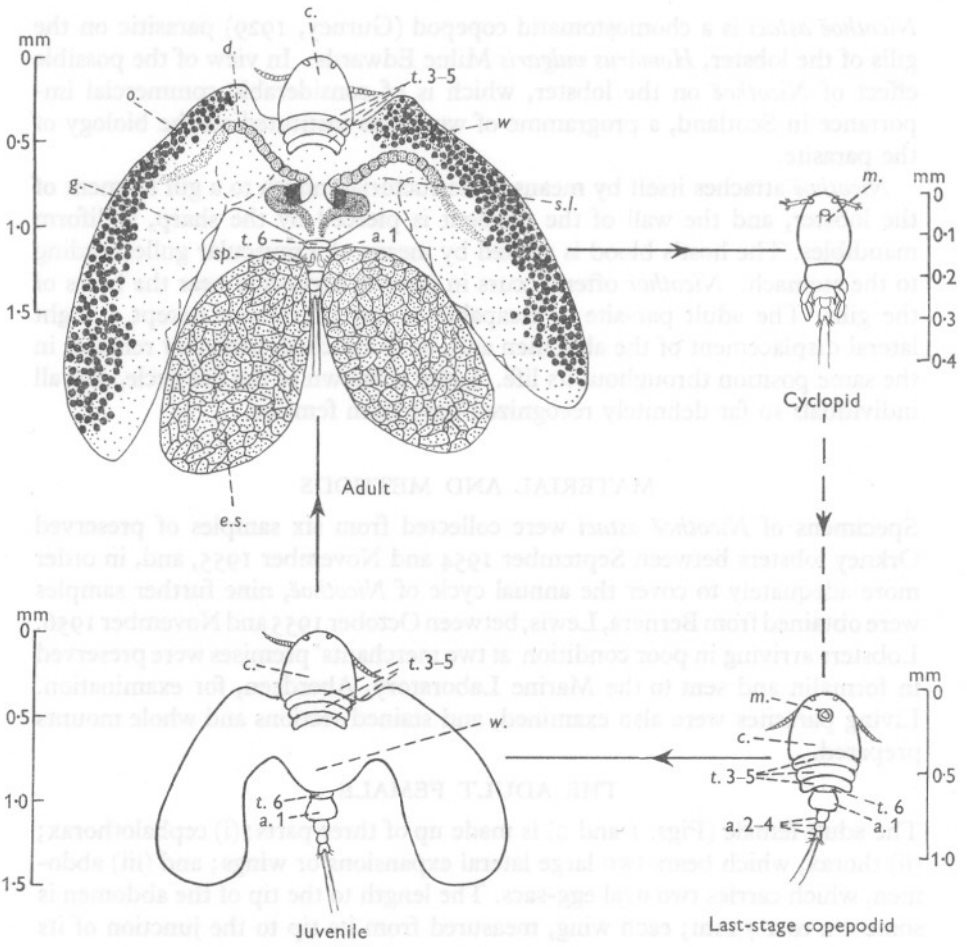

Fig. 1. Dorsal views of stages in the life cycle of *Nicothoë*. *a.* 1–4, abdominal segments; *c.*, cephalothorax; *d.*, duct; *e.s.*, egg-sac; *g.*, cement gland; *m.*, mouth showing through from ventral surface; *o.*, ovary; *s.l.*, stomach lobe; *sp.*, spermathecae; *t.* 3–6, thoracic segments; *w.*, wings.

TABLE 1. SEGMENTATION IN *NICOTHOË*

Body region	Segment	Appendages: Name	Appendages: Form
Cephalothorax	1. 1st cephalic	—	—
	2. 2nd cephalic	1st antennae	Long, 11-jointed, setigerous
	3. 3rd cephalic	2nd antennae	4-jointed, flexed on themselves
	4. 4th cephalic	Mandibles	Styliform, passing into mouth tube
	5. 5th cephalic	1st maxillae	2-jointed, anterior joint tripartite
	6. 6th cephalic	2nd maxillae	2-jointed, with a pair of lappets distally
	7. 1st thoracic	Maxillipeds	4-jointed, terminal joint small
	8. 2nd thoracic	Biramous limbs	Basal joint and two 3-jointed rami, setigerous
Thorax (wings)	9. 3rd thoracic (dorsal ring)	Biramous limbs	Basal joint and two 3-jointed rami, setigerous
	10. 4th thoracic (dorsal ring)	Biramous limbs	Basal joint and two 3-jointed rami, setigerous
	11. 5th thoracic (dorsal ring)	Biramous limbs	Basal joint and two 3-jointed rami, setigerous
Abdomen	12. 6th thoracic	Uniramous limbs	Vestigial, setigerous
	13. 1st abdominal. Genital	(Egg-sacs)	
	14. 2nd abdominal		
	15. 3rd abdominal		
	16. 4th abdominal. Bilobed	(Each lobe has a caudal style and 4 setae)	

THE BREEDING CYCLE

The paired ovaries are situated one in each wing, where they cover the stomach lobes anteriorly (Fig. 1). Posteriorly each lobe is covered by a cement gland. A dorsal genital duct, which serves both ovary and cement gland, passes proximally in each wing to open on the 1st abdominal segment. The contents of the ducts, thought by Van Beneden (1850) to be eggs, are, in fact, glandular in nature. Near the looped bases of the ducts are dark bodies, thought to be concerned in the secretion of the egg-sacs. In the 1st abdominal segment, near the openings of the oviducts, is a pair of curved spermathecae.

Individuals of *Nicothoë* with small wings but without egg-sacs (juveniles, Fig. 1) are found almost entirely on lobsters which have recently cast their shells (see p. 13). As the wings grow the ovaries begin to develop; they first appear when the wings are some 1·5 mm long, and soon become ripe, generally when the wings have attained a length of 2·0–2·2 mm. The eggs are extruded with the secretion of the duct and cement glands, to form the egg-sacs. The parasites have then become adults, and have empty gonads and egg-sacs full of eggs. Development of the eggs into embryos commences at

once, fertilization by sperm from the spermathecae (see p. 11), presumably having occurred before they entered the egg-sacs. The ovaries recover at the same time, and concurrent series of changes take place in the ovaries and

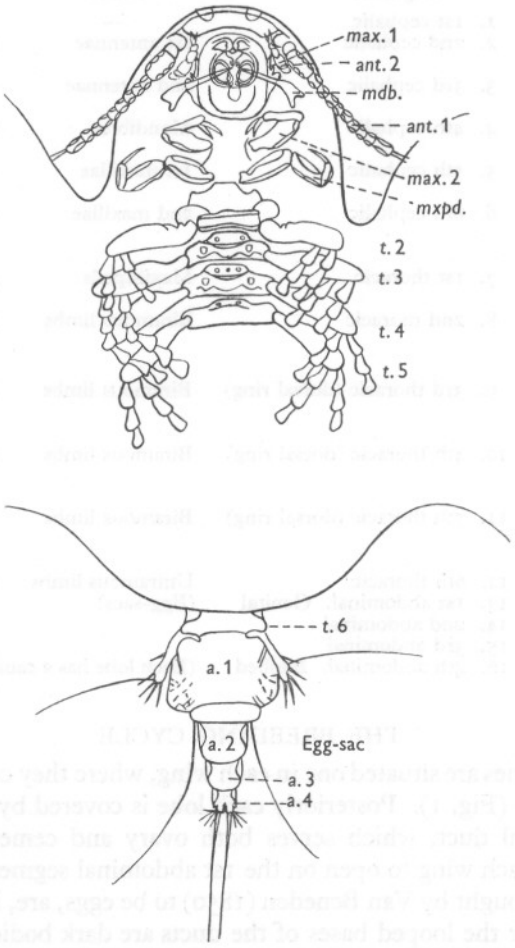

Fig. 2. Ventral view of adult female, showing segmentation (simplified for clarity). *a.* 1–4, abdominal segments; *ant.* 1, 1st antenna; *ant.* 2, 2nd antenna; *max.* 1, 1st maxilla; *max.* 2, 2nd maxilla; *mdb.*, mandible; *mxpd.*, maxilliped; *t.* 2–6, thoracic segments and appendages.

egg-sacs, so that when the egg-sacs are full of active larvae ready to be released, the gonads are again full of ripe eggs. The egg-sacs burst, releasing the larvae, the gonad spawns and new egg-sacs are extruded, and the cycle is repeated.

The series of changes in the reproductive system of the juvenile and adult *Nicothoë*, and the corresponding changes in the egg-sacs of the adult, have been divided into six stages, as follows.

Immature (juvenile) or *Spent* (adult). Stomach lobes occupy almost whole of wings. No sign of development of ovaries visible externally in juvenile; adult ovary appears empty or contains a few residual eggs; sections show many young oocytes, 10–12 μ, each with a spherical, vesicular nucleus. Cement glands small, appear translucent externally; contain a little granular secretion, staining pale blue in haematoxylin and eosin, from glandular cells near outer wall of gland. Ducts, 75 μ wide, tapering slightly distally, appear empty, or contents sparse, but sections show that they are composed of a glandular tissue similar to that of cement glands and contain a little granular secretion. Egg-sacs contain spherical eggs, 120–150 μ, or eggs which have just commenced division.

Developing. Ovaries become visible externally as granular, greyish bodies, but with no definite oocytes visible; sections show strings of young oocytes, 10–12 μ, with a few larger ones, up to 30 μ, between. A group of actively dividing oogonia on anterior edge of each wing. Cement glands larger, pale, containing more granular secretion. Glandular tissue in ducts assumes a segmented appearance, being divided up into well-defined packets, some 80 μ long, which also contain granular secretion. Larvae in egg-sacs 150–200 μ.

Half-full. Ovaries darker, definite rounded oocytes up to 75 μ visible externally; strings of young oocytes and groups of actively dividing oogonia seen in sections. Cement glands and ducts appear darker and have similar granular contents, staining pink in haematoxylin and eosin; at centre of cement gland granules are coalescing to form small droplets of a clear fluid which stains pale pink. Larvae in egg-sacs 200–230 μ, showing signs of segmentation.

Full. Ovaries large, full of spherical oocytes up to 95 μ in diameter, each with germinal vesicle 17 μ and nucleolus 4 μ; few young oocytes; patches of oogonia present. Cement glands large, appear opaque externally, but sections show further coalescence of granules to form clear fluid which stains pale pink. Ducts darker, contents granular. Larvae in egg-sacs 230–270 μ, showing rudimentary limbs.

Ripe. Ovaries densely coloured, pink. Eggs up to 110 μ, polygonal in sections, closely packed together; some have undergone, or are undergoing, maturation, germinal vesicles break down and spindles often visible in sections. Patches of active oogonia still present, but few young oocytes. Cement glands now full of clear fluid after coalescence of granules, staining pink. Ducts also now contain clear pink-staining secretion, though some granules may persist; glandular tissue in duct now reduced to a narrow strip along one side. Dark bodies near bases of ducts also contain clear fluid, which stains pink. Egg-sacs full of active cyclopid larvae, 270–290 μ, with suctorial mouth and two pairs of swimming legs. Each sac contains several hundred cyclopids. Egg-sacs of some ripe individuals have burst, releasing cyclopids, prior to spawning and extrusion of new egg-sacs.

Spawning. Old egg-sacs have been lost and larvae released. New egg-sacs formed and in process of being filled with spherical eggs. Outer wall of egg-sac probably composed of secretion from dark bodies which will be first secretion extruded. Ovaries patchy; matured eggs pass slowly down ducts in clear, sticky secretion from cement glands, and into egg-sacs, causing them to swell. Eggs in ducts compressed, cylindrical. Spawning results in the production of the spent individual, and the next generation of oocytes arise from the oogonia. Few individuals were seen at this stage.

The development of the larvae in the egg-sacs was described by Rathke (1843) and Van Beneden (1850), and is not given here in detail.

THE LIFE CYCLE AND GROWTH OF *NICOTHOË*

The cyclopid larva of *Nicothoë* (Figs. 1, 3), which is released from the egg-sac into the surrounding water, has been described by Gurney (1929). It is some 0·27–0·29 mm long, with a full complement of mouthparts, two pairs of legs and a rudimentary third pair. It has a suctorial mouth tube. The cephalothorax is as long as the rest of the body, and includes the segment of leg 1. The segments of legs 2 and 3 are free, and are followed by two legless segments and a pair of furcal rami.

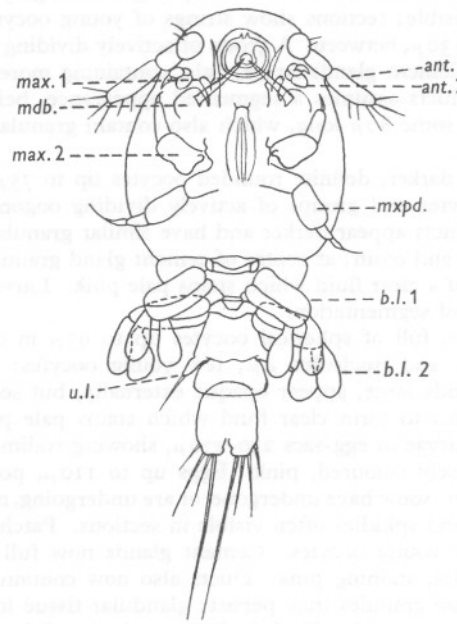

Fig. 3. Ventral view of cyclopid larva (appendages simplified). *b.l.*, biramous limb; *u.l.*, uniramous limb; other lettering as in Fig. 2.

The earliest stage of *Nicothoë* seen on lobster gills was the last-stage copepodid (Fig. 1), some 0·86–0·99 mm long, which was obtained by shaking the gills in water. It has the full complement of segments and limbs and resembles the adult in all respects except for the absence of wings and egg-sacs. Since the wings have not yet commenced development, the 6th thoracic segment abuts directly on the limb-bearing portion of the 5th. The last-stage copepodid is capable of swift, darting movements. After the last-stage copepodid is seen a whole series of stages of juveniles, showing the development of the wings, through individuals with small, bud-like growths, to those with large wings and the 6th thoracic segment well separated from the limb-bearing portion of the 5th (Fig. 1). The only increase in length after the last copepodid stage is due to the increase in size of the middle part of the wings. As growth

proceeds, the gonads develop, and, usually when the wings have attained a length of some 2·0–2·2 mm (but more or less in some individuals, see Table 2), egg-sacs are extruded and the parasite becomes adult. Growth continues (the largest adult recorded had wings 4·56 mm long), and the reproductive cycle is repeated.

There is thus a gap in our knowledge of the life history of *Nicothoë*. There would seem to be a free-living stage or a phase on an intermediate host, during which one or more moults occur. There is, however, little essential difference between the mouthparts in the cyclopid and last-stage copepodid, except that, in the latter, the sucker is slightly more complicated and the 1st maxilla, whilst retaining the same form, has an extra flagellum on the anterior branch (Gurney, 1929). In both, two thoracic segments are included in the cephalothorax. The only radical changes which occur in the gap are the increase in size and the acquisition of four more segments.

Cyclopid larvae were kept for more than nine days at 11° C in filtered sea water in flasks, some with *Skeletonema costatum*, *Chlorella ovalis* or *Dunaliella primolecta* added, and some without addition. No evidence of feeding was found, and no development of the cyclopids occurred. When first released, the cyclopids swim actively and are positively phototropic, tending to congregate on the side of the container nearest the source of light. After a time they settle on the bottom of the container and become attached to it by means of their suctorial mouths. They are easily stirred to activity again. The cyclopids are capable of crawling, drawing themselves along by means of their mouths.

Other attempts to rear cyclopids were made by keeping two or three lobsters in a tank and filtering samples of surface and bottom water every 2 days. The lobsters lived for periods of from 8 to 24 days, but the larvae obtained had not developed beyond the cyclopid stage.

Plankton hauls were made over lobster beds off the west coast of Scotland and in Orkney waters between July and September. Half-metre nets, 26 or 60 meshes to the inch, were used, and hauls varied in duration from 5 to 30 min. The beds were in depths of 10–20 fathoms (18·3–36·6 m); eleven surface hauls, five midway between surface and bottom and five just above the bottom were made. Only two cyclopids were caught, both in surface hauls, and both in 26-mesh nets; neither showed any development.

In an attempt to discover a possible intermediate host, the gills and soft parts of 239 individuals representing twenty-eight species of invertebrates, and also three fish, from the lobster beds or adjacent rocky shores, were examined, mainly during the summer months. The invertebrates from the lobster beds were caught by Agassiz trawl, scallop dredge or creel. The full list of animals examined is given in an appendix. No larval *Nicothoë* were found.

Attempts were made to obtain direct infestation with cyclopid larvae of

three hard and five soft (recently cast and therefore free from *Nicothoë*) lobsters in tanks of aerated sea water. The sides, but not the top, of each tank were covered with brown paper, so as to allow illumination only from above as in the sea. Active cyclopid larvae were introduced, and the lobsters were examined after times varying from 1 to 32 days. The only lobster newly infested was a soft one, left for 20 days before examination, which then carried one juvenile *Nicothoë* with wings 0·90 mm long. One isolated individual cannot be taken as indicating the successful direct settlement of a cyclopid and its subsequent moulting to a last-stage copepodid, since the lobster in question was under general circulation in the aquarium for 3 days before the commencement of the experiment, during which time it might have become infested with an intermediate larva which had been either free-living or on another host, and which had reached a stage of development at which it could moult into a last-stage copepodid. It does, however, suggest that repetition of this experiment would be valuable.

THE MALE OF *NICOTHOË*

The only individuals definitely recognized, and described and figured by previous workers, have all been females. Van Beneden (1850) described a specimen which he called a male, but Claus (1860) said that this did not even belong to the species *Nicothoë astaci*. From the description given by Van Beneden, it was almost certainly the harpacticoid copepod *Tisbe elongata*, which is frequently found on the gills of lobsters.

Claus (1860) found an individual without wings, which, from his description, was a last-stage copepodid. He concluded, however, that since the body had a full complement of segments, it was an adult, sexually mature form, and so must be a male. He supported his conclusion by quoting Rathke (1843), who described two types of larvae as being differentiated early in the egg-sac, the wings of the female appearing at a very early stage. The present investigation has shown, however, that all cyclopid larvae are of the same type (Figs. 1, 3), all with suctorial mouths, and show no sign of wings, which first appear after the last copepodid stage. The complete series of stages, from last-stage copepodids without wings, through juveniles with small wings to adults with large wings (Fig. 1), makes it certain that the copepodids develop into females.

Quidor (1906) examined five last-stage copepodids, and said that four of them had testes in various stages of development in the thorax and genital segment. The remaining one, which had no testes, he described as an immature female. In the present study 100 last-stage copepodids, taken at various times of the year, were stained with Ehrlich's acid haematoxylin and eosin and examined microscopically, but no testes were found. On the other hand, each had a pair of curved spermathecae, full of spermatozoa, in the

1st abdominal segment. These were also seen, still containing sperm, in juveniles and adults, opening into the genital duct near its opening. It would thus appear that females are impregnated at a very early stage, before settling on the lobster, and retain the spermatozoa for fertilizing each successive generation of eggs.

The males presumably develop from cyclopids during the gap in the life history between the cyclopid and last copepodid stages, but, unlike the females, they do not settle on the lobster. In addition to the last-stage copepodids, stained preparations of cyclopid larvae from six *Nicothoë* and stained sections of thirty-five juveniles and adults were examined, but no trace of a testis was found.

THE RELATIONSHIP BETWEEN *NICOTHOË* AND THE MOULTING OF THE LOBSTER

The most important moulting period of the lobster in Scottish waters is May–August, mature males casting every year and mature females every second year. Thomas (1958) has recently found some evidence of a subsidiary moulting season in younger lobsters in November. Observation of ten lobsters in the laboratory has shown that, at the moult, the outer covering of the gills is shed, and the parasites with it, leaving the gills clean. *Nicothoë* makes no attempt to leave the gills, but simply dies.

The preserved lobsters in each of the Orkney and Bernera samples were divided into three groups according to the state of the shell: soft (very recently moulted, free from epizoons), fairly soft (beginning to harden again, usually carries small epizoons, e.g. *Spirorbis*, *Pomatoceros*, *Balanus*), and hard (quite firm again, usually carries large epizoons). Their gills, whose outer layers are cast with the shell, are correspondingly soft, fairly soft and hard. The three groups are not represented in the samples in the same proportions as in nature; the samples contain a higher proportion of soft and fairly soft lobsters owing to the greater mortality among them than among hard ones during transit and storage.

Table 2 shows the numbers of last-stage copepodids, juveniles and adults of *Nicothoë* on the three types of lobsters in all the Orkney and Bernera samples, together with the mean lengths of their wings. The wings were measured from the tip to the junction of the anterior edge with the cephalothorax. The two wings of an individual are usually approximately equal in size, but, where this was not so, the longer one was measured. The length of the wing is the best index of growth owing to the small increase in body length after the last copepodid stage (p. 8).

Last-stage copepodids were found in most months of the year (none were found in September and no samples were obtained in March and May), and they occurred on soft, fairly soft and hard lobsters alike. Juvenile *Nicothoë*

TABLE 2. NUMBERS AND WING-LENGTHS OF LAST-STAGE COPEPODIDS, JUVENILES AND ADULTS ON LOBSTERS OF THE THREE SHELL-TYPES

(For convenience, the samples are considered as though taken in one year.)

Month	State of shell	No. of lobsters	Mean nos. per lobster: L.-s. copeps.	Mean nos. per lobster: Juvs.	Mean nos. per lobster: Adults	Length of wings: Juveniles: Mean length	Length of wings: Juveniles: Size range	Length of wings: Adults: Mean length	Length of wings: Adults: Size range
A. Orkney, 1954–55									
April	Soft	—	—	—	—	—	—	—	—
(26. iv. 55)	Fairly soft	1	—	10·0	4·0	1·94	1·20–1·49	2·12	1·94–2·41
	Hard	10	1·7	0·5	167·6	1·70	1·38–2·11	2·82	1·51–4·04
June	Soft	1	—	—	—	—	—	—	—
(7. vi. 55)	Fairly soft	—	—	—	—	—	—	—	—
	Hard	14	3·1	2·9	49·6	1·64	0·09–2·15	2·74	1·72–4·30
August	Soft	—	—	—	—	—	—	—	—
(2. viii. 55)	Fairly soft	6	0·7	60·8	0·5	1·72	0·04–2·71	3·11	2·80–3·40
	Hard	16	—	0·2	31·1	2·05	1·94–2·15	2·80	1·81–4·13
September	Soft	7	—	29·0	0·9	2·00	1·03–2·67	2·16	1·81–2·37
(21. ix. 54)	Fairly soft	12	—	1·8	3·4	1·97	0·99–2·58	2·55	1·72–3·40
	Hard	6	—	—	23·7	—	—	2·66	1·63–3·70
November	Soft	—	—	—	—	—	—	—	—
(8. xi. 55)	Fairly soft	14	—	1·0	9·9	2·12	1·72–2·37	2·96	1·81–4·09
	Hard	5	—	1·3	80·8	1·58	1·51–1·98	3·29	2·11–4·47
December	Soft	—	—	—	—	—	—	—	—
(14. xii. 54)	Fairly soft	3	—	0·3	25·7	1·42	1·42	2·79	2·37–3·48
	Hard	9	—	—	20·0	—	—	2·66	1·76–3·66
B. Bernera, 1955–56									
January	Soft	—	—	—	—	—	—	—	—
(26. i. 56)	Fairly soft	5	0·2	1·8	9·2	1·85	0·95–2·32	2·59	1·85–3·48
	Hard	3	—	—	103·7	—	—	2·81	1·85–3·87
February	Soft	—	—	—	—	—	—	—	—
(8. ii. 56)	Fairly soft	3	0·3	23·7	24·3	1·97	1·28–2·58	2·53	1·59–3·83
	Hard*	8	0·5	2·0	81·2	1·44	0·43–2·36	2·74	1·55–4·13
April	Soft	3	—	10·7	4·0	1·88	0·90–2·32	2·31	1·89–2·32
(12. iv. 56)	Fairly soft	3	—	26·0	171·3	2·06	1·46–2·75	2·78	1·72–3·87
	Hard	2	—	1·0	4·0	1·26	0·77–1·76	2·71	2·15–3·48
June	Soft	1	6·0	4·0	—	1·06	0·73–1·33	—	—
(19. vi. 56)	Fairly soft	4	0·2	41·0	15·5	2·12	0·82–2·92	2·45	1·98–3·05
	Hard	5	1·6	0·4	112·2	1·66	1·63–1·68	2·99	2·28–4·56
July	Soft	1	9·0	180·0	—	1·05	0·09–1·89	—	—
(24. vii. 56)	Fairly soft	6	4·8	47·2	46·0	1·63	0·04–2·80	2·52	1·72–3·66
	Hard	2	—	1·5	266·5	1·99	1·59–2·58	2·94	2·02–4·30
August	Soft	—	—	—	—	—	—	—	—
(24. viii. 56)	Fairly soft	6	0·2	3·2	122·7	2·03	1·16–2·49	2·57	1·29–4·00
	Hard*	5	0·8	0·6	83·2	1·91	1·51–2·15	2·65	1·63–3·70
October	Soft	—	—	—	—	—	—	—	—
(4. x. 55)	Fairly soft	8	2·2	22·5	38·4	1·15	0·09–2·32	2·49	1·38–3·66
	Hard*	3	—	0·3	90·7	0·22	0·22	2·88	1·94–4·21
November	Soft	—	—	—	—	—	—	—	—
(2. xi. 56)	Fairly soft	10	0·4	9·9	55·6	2·06	1·16–2·75	2·77	1·36–4·47
	Hard	3	—	5·0	174·7	1·76	1·20–2·75	2·68	1·59–4·26
December	Soft	—	—	—	—	—	—	—	—
(7. xii. 55)	Fairly soft	15	17·9	9·3	19·0	1·67	0·09–1·76	2·85	1·89–4·26
	Hard*	4	3·8	1·5	122·2	0·77	1·29–2·24	3·07	2·32–4·21

Each sample marked * excludes one hard lobster with badly damaged gills, which carried more than the usual numbers of juvenile *Nicothoë*, as below (see text):

February	Hard	1	—	10	390	1·87	1·68–2·06	2·69	1·72–3·74
August	Hard	1	2	14	508	0·88	0·22–1·89	2·70	1·85–3·78
October	Hard	1	1	40	288	1·69	0·69–2·11	2·93	1·72–3·87
December	Hard	1	16	44	756	1·95	1·29–2·24	3·07	2·32–4·31

were found in all samples, but, with only four exceptions, were present in numbers only on lobsters which had recently moulted (soft and fairly soft). Hard lobsters had the most, and also the largest (adult) *Nicothoë*. It appears probable that the last-stage copepodid cannot pierce a gill filament if the latter is hard. If, on the other hand, the gills are soft, the parasite attaches itself by its suctorial mouth to a filament, which it pierces by means of its mandibles. Feeding on the host's blood then results in the growth of the wings and development, through the juvenile, to the adult state.

TABLE 3. PERCENTAGE OF INDIVIDUALS OF *NICOTHOË* IN EACH STAGE OF DEVELOPMENT—HARD LOBSTERS

(For convenience, the samples are considered as though all taken in one year.)

Month	Gonad stage: Empty	De-veloping	Half-full	Full	Ripe	Spawning	No. examined
	A. Orkney, 1954–55						
April (26. iv. 55)	46·1	13·9	3·1	11·0	23·5	2·4	1185
June (7. vi. 55)	18·5	25·6	15·8	15·7	23·1	1·3	671
August (2. viii. 55)	15·1	33·0	23·0	13·0	15·9	—	339
September (21. ix. 54)	26·1	22·5	21·8	25·4	4·2	—	142
November (8. xi. 55)	12·4	27·2	14·8	15·1	28·0	2·5	404
December (14. xii. 54)	15·0	8·4	16·1	52·2	7·2	1·1	180
	B. Bernera, 1955–56						
January (26. i. 56)	3·9	31·5	28·0	21·2	13·2	2·2	311
February (8. ii. 56)	11·7	25·5	21·0	22·5	19·3	0·1	1040
April (12. iv. 56)	4·8	16·1	28·2	27·4	23·0	0·6	522*
June (19. vi. 56)	20·9	24·4	11·2	13·5	30·0	—	561
July (24. vii. 56)	32·3	15·2	13·7	17·1	21·7	—	533
August (24. viii. 56)	27·7	20·4	5·4	21·6	22·2	2·7	924
October (4. x. 55)	47·5	18·0	5·9	16·3	12·1	0·2	560
November (2. xi. 56)	23·7	18·1	12·0	14·1	31·1	1·0	524
December (7. xii. 55)	27·0	20·6	15·4	15·4	21 4	0·2	1245

* Includes two lobsters not quite hard.

The four exceptions referred to above, lobsters with hard shells which carried respectively 10, 14, 40 and 44 juvenile *Nicothoë*, all had badly damaged gills. It is probable that the last-stage copepodids became attached, and the damage to the gills permitted them to suck the host's blood without the necessity of penetrating the filaments.

One lobster, caught in December 1955, was noteworthy in that, while the shell was hard, and the gills on the left-hand side were hard and greeny brown, those on the right-hand side were soft, clean and white. The left-hand gills carried 100 adult *Nicothoë* and no juveniles, while the right-hand gills carried no adults and 23 juveniles.

There is a seasonal rhythm in the release of cyclopid larvae of *Nicothoë*. Table 3 shows the percentages of adult *Nicothoë* in each of the six stages of gonad development (p. 7). Since lobsters of the three shell groups are not present in the same proportion as in nature, only hard ones, which are in the

majority in nature even in the moulting season, were considered. Adults in the ripe and spawning stages indicate the release, or impending release, of cyclopid larvae. Since these stages were present in all samples taken, release of larvae occurs throughout the year. Two peaks were shown in the release of cyclopid larvae in both Orkney and Bernera lobsters (Fig. 4). The first peak, in May or June, occurred at the beginning of the main moulting period, and the percentage remained relatively high throughout this period, while the second peak, in November, coincided with the subsidiary moulting period.

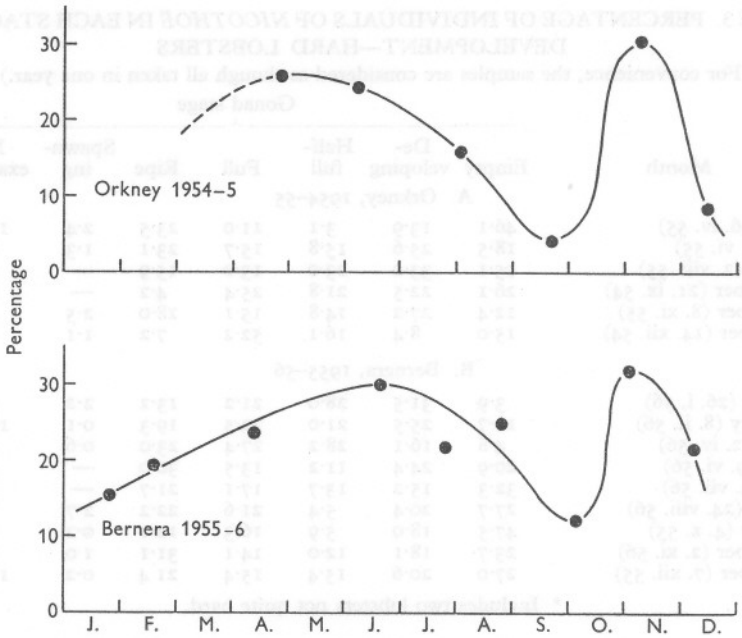

Fig. 4. Percentages of adult *Nicothoë* in ripe and spawning stages: Orkney, 1954–5; Bernera, 1955–6. See Table 3.

It appears, then, that *Nicothoë* can infest only recently cast lobsters, but it can do so at any time of the year. Most infestation will, however, presumably occur during the main moulting periods, when the highest proportion of soft lobsters is present, and when most cyclopid larvae are released.

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SUMMARY

The only individuals of *Nicothoë astaci* so far definitely recognized have been female.

Concurrent series of changes take place in the ovaries and egg-sacs, so that when the gonads are full of ripe eggs, and are ready to spawn, the egg-sacs either contain active cyclopid larvae or have just released them. After the release of the cyclopid into the sea there is a gap in our knowledge of the life cycle, the next stage known being the much larger last-stage copepodid on the gills of the lobster. From this a series of changes can be traced, with the appearance of wings and the development of gonads, through juveniles (which have never spawned) to adults with egg-sacs. All attempts to bridge the gap have failed; cyclopid larvae kept alive for up to 9 days showed no sign of development, and no intermediate stages have been found, either free-living in the plankton or parasitic on the lobster or other animals. Attempts to parasitize lobsters by means of cyclopid larvae have failed with one exception whose significance is doubtful.

Individuals described as males by previous workers either belonged to another genus or were almost certainly last-stage copepodids. All last-stage copepodids examined had spermathecae containing sperm, and must have been impregnated at a very early stage, the male presumably developing in the gap between cyclopid and last-stage copepodid, though all the cyclopids were of one type. The sperm are retained and fertilize successive generations of eggs.

When the lobster moults the *Nicothoë* are shed with the old shell and die, and re-infestation by settlement of last-stage copepodids can only occur in significant numbers shortly after the moult, before the gills become hard again. There is a seasonal rhythm in the release of cyclopid larvae by the adult females, there being two peaks, of which one coincides with the lobster's main moulting season (May–August) and the other with a subsidiary moulting period of younger lobsters (November).

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APPENDIX

Animals examined for intermediate stages of Nicothoë

		No. examined
Porifera	*Halichondria panicea*	4
Coelenterata	*Aurelia aurita*	1
	Actinia equina	9
Annelida	*Nereis pelagica*	6
Crustacea	*Balanus* sp. (from lobsters' shells)	30
	Gammarus sp.	7
	Pandalus montagui	8
	Palaemon serratus	2
	Crangon vulgaris	1
	Nephrops norvegicus (trawled nearby)	10
	Munida bamffica	1
	Eupagurus bernhardus	4
	Portunus puber	39
	Carcinus maenas	17
	Cancer pagurus	22
	Hyas araneus	1
	Inachus dorsettensis	2
Mollusca	*Patella vulgata*	7
	Gibbula cineraria	2
	Littorina littorea	10
	Nucella lapillus	12
	Mytilus edulis	8
	Chlamys opercularis	10
Echinodermata	*Astropecten irregularis*	1
	Porania pulvillus	4
	Asterias rubens	11
	Ophiura texturata	2
	Psammechinus miliaris	8
Pisces	*Zoarces viviparus*	1
	Cottus bubalis	2

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THE LARVAL AND POST-LARVAL STAGES OF *GYMNAMMODYTES SEMISQUAMATUS* (JOURDAIN)

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In the course of investigations (1955–8) into the Ammodytidae of the south of the Isle of Man, five species of sand eel were identified: *Gymnammodytes semisquamatus* (Jourdain, 1879), the Smooth Sand Eel; *Ammodytes lanceolatus* Lesauvage, 1825, the Greater Sand Eel; *A. immaculatus* Corbin, 1950; *A. tobianus* Linnaeus, 1758 (=*A. lancea* Cuvier), the Lesser Sand Eel; *A. marinus* Raitt, 1934.

Five different types of post-larvae were obtained and investigated. Four of these were the post-larvae of the above four *Ammodytes* species and the fifth type proved to be *Gymnammodytes semisquamatus*.

A. lanceolatus and *A. marinus* post-larvae were identified according to Einarsson (1951) and Corbin & Vati (1949), and *A. tobianus* was identified according to Einarsson (1955). The results agreed with Einarsson's conclusions on the identification of these post-larvae. Very few post-larvae of *A. immaculatus* (Corbin & Vati, 1949—*Ammodytes* Species IV) were obtained and these were identified by vertebral counts as they are externally very similar to *A. lanceolatus* post-larvae.

Previous confusion in the identification of *Ammodytes* post-larvae has now been cleared up by the investigations of Einarsson (1951, 1955). In 1949 Corbin & Vati published a description of four Ammodytidae post-larval types. These were ascribed to the species *A. lanceolatus*, *A. marinus*, *A. tobianus* and *Ammodytes* Species IV (=*A. immaculatus* Corbin, 1950*a*). Corbin noted a marked discrepancy between vertebral counts made on the post-larvae ascribed to *A. tobianus* and counts made on a sample of adult *A. tobianus*. Subsequent investigations into *Ammodytes* post-larvae by Einarsson (1951) proved that the *A. marinus* post-larvae of Corbin & Vati (and of Kändler, 1941) were correctly identified, but that the post-larval type which Corbin & Vati called *A. tobianus* was in fact *A. lanceolatus*.

The post-larval type ascribed by Corbin & Vati (also by Ford, 1920; Kändler, 1941) to *A. lanceolatus* therefore belonged to some other species.

Einarsson (1951) had no opportunity to examine intact specimens of this post-larval type, but he discussed some of its peculiar features, distinct from other Ammodytidae post-larvae, and suggested the possibility of its being the young of *G. semisquamatus*: 'The data on post-larvae of *A. lanceolatus*

must be referred to another species of Ammodytidae, not definitely known as yet, but most probably *G. semisquamatus*.' After the present work was completed it was brought to my notice that the Council of the Marine Biological Association of the United Kingdom reported (*J. mar. biol. Ass. U.K.*, 1954, Vol. 33, p. 771) that Mr P. G. Corbin obtained several artificial fertilizations of the eggs of *G. semisquamatus* in 1953, and that the larvae from the artificial fertilizations provided independent confirmation of Einarsson's identification.

Post-larvae of this type are abundant in the plankton off the south of the Isle of Man from May to September, and it has been possible to obtain large numbers for investigation.

A series of larvae and post-larvae from 3 mm through the late post-larval to juvenile stages of 40–50 mm have been examined and there is no doubt that these post-larvae are *G. semisquamatus*.

Post-larval stages of *G. semisquamatus* can be identified by external characters alone. Several identifying characters were found to be important. These come under the following headings and are discussed below: (1) the pattern of pigmentation, (2) 'teeth' on the upper jaw, (3) protrusibility of the upper jaw, (4) vomerine teeth, (5) juvenile and adult characteristics.

During the course of post-larval development the above characters overlap successively so as to give a complete sequence of specific characters from the smallest larva obtained (3 mm) to juvenile fish of 30–50 mm in which adult characteristics are already developing.

CHARACTERS OF POST-LARVAL *GYMNAMMODYTES SEMISQUAMATUS*

The pattern of pigmentation

The nomenclature of the post-larval pigmentation is shown in Text-fig. 1 (after Corbin & Vati, 1949).

The presence of a ventral fin-membrane pigment row is specific to the early post-larvae of *G. semisquamatus*. It occurs in the smallest specimens obtained and persists through all stages until about 19 mm. In the post-larvae of the *Ammodytes* species there is no ventral fin-membrane pigment at any stage.

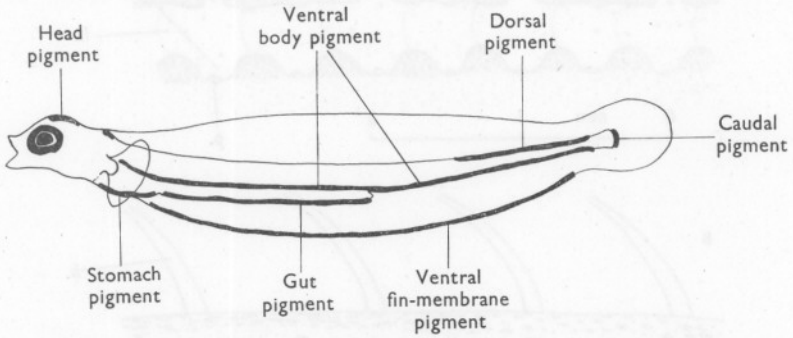
'Teeth' on the upper jaw

At about 7 mm the post-larva develops a row of tooth-like structures along the outer edge of the rim of the upper jaw (pre-maxilla). These are pointed, shaped like thorns and can be seen without staining with alizarin. They are found only in the post-larvae of *G. semisquamatus* and not in the post-larvae of the *Ammodytes* species. They persist until the post-larva is 20–25 mm long, by which length the growing tissues around the lips have obliterated the larval 'teeth'.

Protrusibility of the upper jaw

This becomes detectable at 8–10 mm and from then on it is a very important feature. Protrusibility becomes increasingly more marked in increasingly larger post-larvae and this therefore rules out the possibility of the post-larvae belonging to the species *A. lanceolatus* or *A. immaculatus*, both of which species have a non-protrusible jaw.

In juvenile and adult *G. semisquamatus* the upper jaw is very protrusible. When the upper jaw is shot forward during feeding the whole mouth forms a long tube. The mouth can be protruded farther than that of either *A. tobianus* or *A. marinus* and the mechanism of protrusion and the shape of the head and jaws are quite characteristic in juvenile and adult *G. semisquamatus*. These adult features of the head and jaws can be recognized to be developing in the post-larva of 18 mm or earlier. From there they can be traced through different stages to the juvenile.



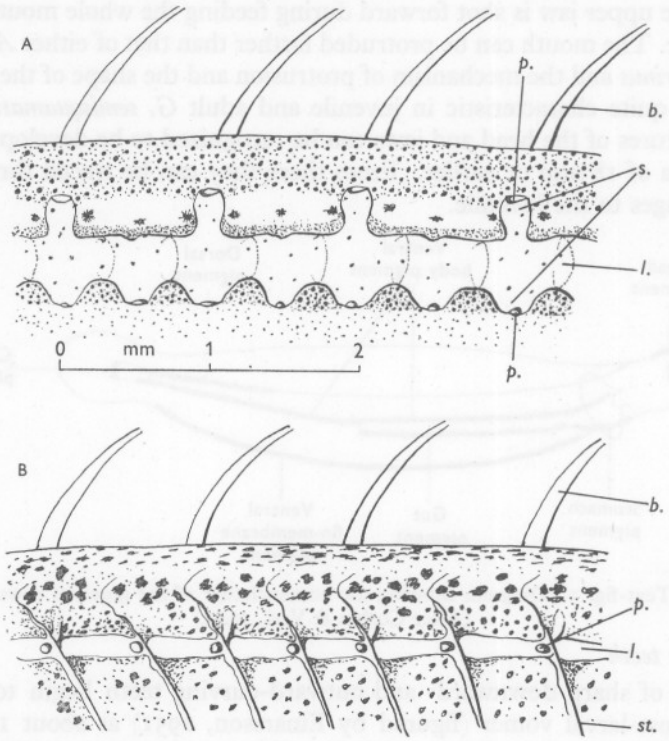
Text-fig. 1. Diagram showing the nomenclature of the pigment rows. (After Corbin & Vati, 1949.)

Vomerine teeth

A pair of sharp downward- and outward-curving teeth begin to develop on the post-larval vomer (figured by Einarsson, 1951) at about 12–15 mm length. These were previously taken to be diagnostic characters of *A. lanceolatus*, but their structure and the shape of the vomer is different from that in the *A. lanceolatus* post-larva (see Einarsson, 1951, pp. 24–5, figs. 6, 7). Moreover, the vomerine teeth of *A. lanceolatus* are not visible until the post-larva has reached 20–25 mm in length; they persist throughout development and are present in the adult. The vomerine teeth of post-larval *G. semisquamatus* do not persist in the adult but they remain until after the ventral fin-membrane pigment row and the 'teeth' on the upper jaw have gone. They disappear when the fish is between 40 mm and 50 mm long, but by then it is a late post-larva-to-juvenile, some of the adult characteristics being already present and the fish recognizable as *G. semisquamatus* by the criteria applied to adults.

The important identifying characters of juvenile and adult *G. semisquamatus* are as follows.

(1) The structure of the lateral line is characteristic (see Text-fig. 2). Transverse side-channels of the lateral-line canal lead to the pores, in contrast to the lateral line of the *Ammodytes* species which is linear (Duncker & Mohr, 1939, p. 11, fig. 1; Jourdain, 1879, figs. 13, 14). The scales along the lateral line are not pierced by pores as they are in the *Ammodytes* species.



Text-fig. 2. The structure of the lateral line (lateral view). A, *Gymnammodytes semisquamatus*. B, *Ammodytes marinus*. *b*, base of dorsal fin-ray; *l*, lateral line canal; *p*, pore; *s*, side-channels; *st*, skin-folds or striae.

(2) The upper jaw is markedly protrusible.

(3) There are no vomerine teeth.

(4) The body is smooth and unstriated.

(5) The ventro-lateral skin-fold extends from the base of the pectoral fin to a point level with, or just beyond, the tip of the pectoral fin when this is pointing towards the tail.

(6) The colour of the head and back is golden-brown or dark purplish brown, while the sides and belly are silvery and iridescent.

A diagnosis of the species *G. semisquamatus* from the newly hatched larva, up to the stage at which it can be recognized by criteria applied to the adult, is given below.

DIAGNOSIS

Larvae, 3–4 *mm* (Pl. I, figs. 1, 2)

Ventral fin-membrane pigment row present. No 'teeth' on upper jaw. Upper jaw cannot be protruded. No vomerine teeth.

Yolk-sac present, partially absorbed. The yolk-sac may be completely absorbed at 4 mm. No dorsal or head pigment present. Stomach pigment consists of four, five or six brown, large and many-branched melanophores along the ventral mid-line of the yolk-sac, with two or more melanophores on the sides of the yolk sac. Ventral body pigment shows clearly pre- and post-anally. The ventral fin-membrane pigment row extends from the stomach region nearly to the tail.

Post-larvae, 5–7 *mm* (Pl. I, figs. 3, 4)

Ventral fin-membrane pigment row present. 'Teeth' become visible at 7 mm (Pl. I, fig. 4). Upper jaw cannot be protruded. No vomerine teeth.

Yolk-sac absent. There may be a single median melanophore over the occipital region of the head. One or two dorsal melanophores are present directly in front of the tail. There are two caudal melanophores ventral to the tip of the notochord. The first rudiments of caudal fin-rays are visible at 6–7 mm.

The notochord is straight.

Post-larvae, 8–10 *mm*

Ventral fin-membrane pigment row present. 'Teeth' present on upper jaw. Upper jaw can be protruded at 9–10 mm. Vomerine teeth not visible.

The notochord begins to turn up posteriorly at 9 mm, and at this length caudal fin-rays are beginning to develop. There may now be three to five dorsal melanophores at the posterior end, but usually only two or three. Pigment is otherwise as before.

Post-larvae, 11–19 *mm* (Pl. I, fig. 5; Pl. II, figs. 1–3)

Ventral fin-membrane pigment row present. 'Teeth' present on upper jaw. Upper jaw protrusible and increasingly so with increasing size of fish. Vomerine teeth visible from 12 to 15 mm.

The notochord is turned up and the tail is in the adult position at 11 mm (Pl. I, fig. 5). Also at 11 mm five or six dorsal fin-rays can be seen to be developing midway between anus and tail. Below these, five or six anal fin rays are developing. By 19 mm all anal fin-rays are present, and dorsal fin-rays extend from the tail farther forward than the level of the anus.

Head pigment begins to show at 11–12 mm—two stellate melanophores at first, later up to five. Dorsal pigment is now at maximum for post-larvae. It consists of never more than five melanophores all close to the tail. The dorsal pigment in the post-larva rarely extends as far as half-way between the tail and the level of the anus. The ventral body pigment is becoming obscured pre-anally by the downward growth of the abdomen walls but can still be seen in side view as about seventeen dark spots. Stomach pigment is now made up of four to five small compact melanophores. Gut pigment consists of about seventeen very small black dots extending from stomach to anus. Both stomach and gut pigment are usually lost at a post-larval length of

16–17 mm. Ventral fin-membrane pigment becomes more reduced as anal fin-rays develop. By 19 mm there are only a few ventral fin-membrane melanophores remaining—all anterior to the anus. In fresh or freshly preserved specimens of 16–19 mm there are very small well-defined orange chromatophores along the ventral surface of the gut and stomach, and lines of these chromatophores extend forwards between the gills (not shown in illustration).

Post-larvae, 20–24 *mm* (Pl. II, fig. 4)

Ventral fin-membrane pigment row absent. 'Teeth' present on upper jaw. Upper jaw protrusible. Vomerine teeth present.

Dorsal fin-rays extend to half-way between head and anus. There is more pigment on the head, consisting of four or more stellate melanophores. The occipital melanophore remains and there is usually one melanophore or a small cluster on the operculum behind the eye. There is now no trace of stomach or gut pigment. The dorsal pigment is the same as before. Ventral body pigment is still visible but obscure in the pre-anal region. There is a single, central caudal melanophore. Ventral orange chromatophores are as above.

Post-larvae, 25–29 *mm*

'Teeth' no longer visible on upper jaw. Upper jaw protrusible. Vomerine teeth present.

The full number of dorsal fin-rays are present. The dorsal fin extends forward to a point level with the tip of the pectoral fin when this is turned to the posterior.

Ventral body pigment is now very obscured behind the abdomen wall but is still well-marked post-anally. There is now more head pigment.

Post-larvae, 30–37 *mm*

No specimens examined.

Post-larva-to-juvenile, 38–47 mm (Pl. II, fig. 5)

Upper jaw markedly protrusible. Vomerine teeth present. Vomerine teeth are reduced but still visible at 47 mm.

Brown juvenile pigment is developing especially on the top of the head, around the jaws, and along the dorsal mid-line at the base of the dorsal fin on each side. Brown chromatophores are also present along the lateral lines, at the base of the caudal fin and along the caudal fin-rays.

The lateral lines are close to the base of the dorsal fin, and extend on either side of the dorsal fin from a point level with the posterior edge of the operculum and the base of the pectoral fin to a small distance in front of the tail. The lateral lines already show adult characteristics.

Juveniles, 48–50 *mm* (Pl. II, fig. 6)

Upper jaw markedly protrusible. Vomerine teeth lost.

The fish are otherwise as above (38–47 mm) with increasing juvenile-adult pigment forming along the lateral lines (large brown chromatophores), on the head, the sides of the body and on the caudal fin.

Juveniles, 50–60 *mm*

The juveniles resemble adults in colour and proportions.

NUMBER OF VERTEBRAE

Vertebral counts were made on 150 adult *G. semisquamatus* and also on 33 post-larvae. The post-larvae were stained with alizarin and afterwards cleared. The urostyle was included in all counts.

The results are given in Tables 1 and 2, together with the results of Corbin & Vati (1949) and Corbin (1950*b*) which are the only vertebral counts of *G. semisquamatus* I have been able to obtain. The Celtic Sea post-larvae of Corbin & Vati (1949) were ascribed to *A. lanceolatus* but are now known to have been *G. semisquamatus* (see p. 17 above).

TABLE 1. RESULTS OF VERTEBRAL COUNTS ON *GYMNAMMODYTES SEMISQUAMATUS*

Adults, all age-groups		Post-larvae	
No. of vertebrae	No. of specimens	No. of vertebrae	No. of specimens
65	1	65	1
66	15	66	4
67	53	67	13
68	67	68	11
69	13	69	4
70	1	70	·
Total	150		33
Mean no. of vertebrae	67·53 ±0·069		67·39 ±0·169

TABLE 2. THE NUMBER OF VERTEBRAE IN *GYMNAMMODYTES SEMISQUAMATUS*

Area and age of specimens	Author	No. of specimens	Range of no. of vertebrae	Mean no. of vertebrae	Standard error of mean
West Scotland and northern North Sea adults	Corbin & Vati (1949)	51	65–70	68·16	±0·144
Celtic Sea post-larvae	Corbin & Vati (1949)	52	64–70	68·08	±0·082
Plymouth adults	Corbin (1950*b*)	108	66–72	68·44	±0·098
Irish Sea adults	Present records	150	65–70	67·53	±0·069
Irish Sea post-larvae	Present records	33	65–69	67·39	±0·169

The range of number of vertebrae of the Irish Sea specimens is within the ranges for previous records, but the mean number of vertebrae for the Irish Sea is slightly lower than previous records.

SUMMARY

Larval and post-larval stages of *Gymnammodytes semisquamatus* are described from recently hatched larvae up to juvenile stages.

Late post-larvae and juveniles are identified as *G. semisquamatus* by the criteria applied to adults.

The Ammodytidae post-larvae ascribed by Ford (1920), Kändler (1941) and Corbin & Vati (1949) to *Ammodytes lanceolatus*, are shown to be identical with post-larval stages of *G. semisquamatus*.

G. semisquamatus post-larvae can be isolated from all other Ammodytidae by the following external characters which, occurring in combination, are diagnostic: (1) presence of ventral fin-membrane pigment row, (2) tooth-like structures on the edge of the upper jaw, (3) protrusible upper jaw, (4) larval vomerine teeth lost in development when the fish is between 40 and 50 mm long, and (5) adult characters of *G. semisquamatus* which are present in the late post-larval and juvenile stages.

During the course of post-larval development the above characters overlap successively giving a complete series of specific characters from the smallest larva obtained (3 mm) to juvenile fish of 30–50 mm in which adult characteristics are developing.

Vertebral counts of post-larvae of *G. semisquamatus* taken near the Isle of Man are consistent with those of adults of the same area.

The mean number of vertebrae of adult *G. semisquamatus* from this area was $67{\cdot}53 \pm 0{\cdot}07$. This is lower than previous records for other areas which range from $68{\cdot}08 \pm 0{\cdot}08$ to $68{\cdot}44 \pm 0{\cdot}1$.

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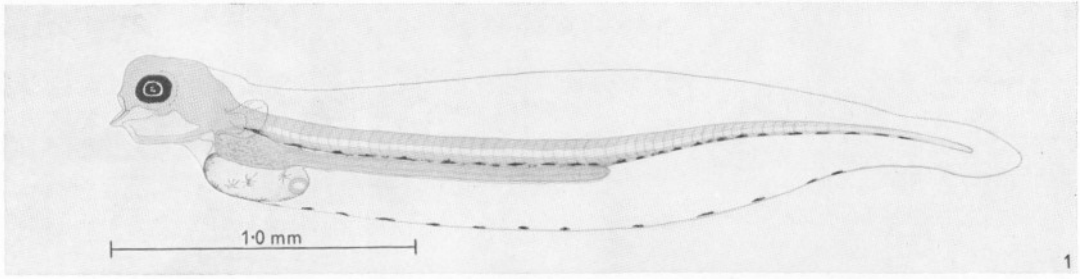

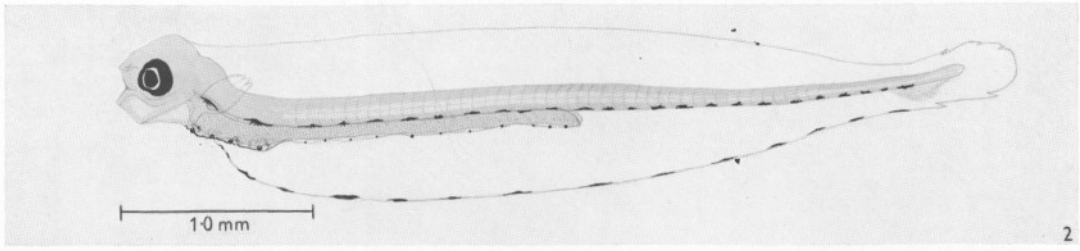

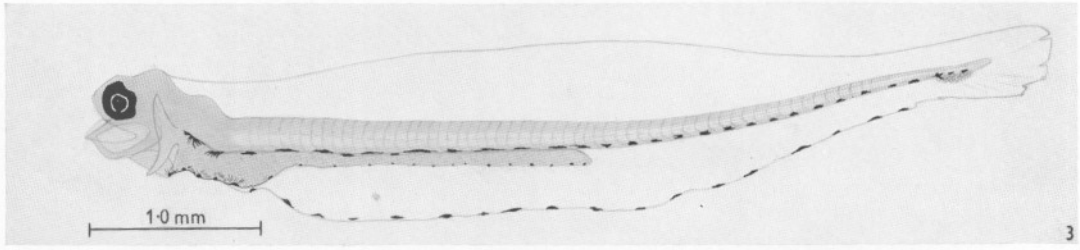

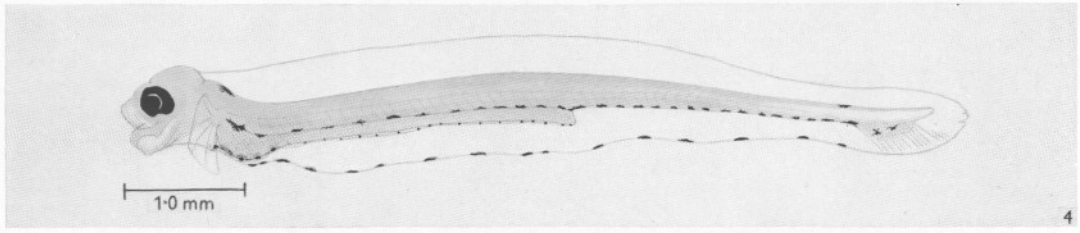

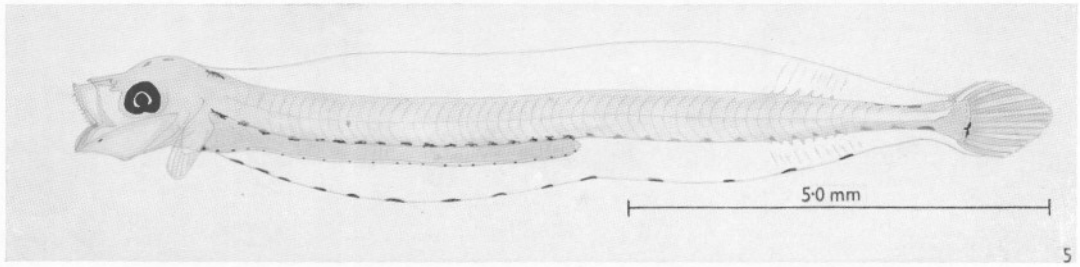

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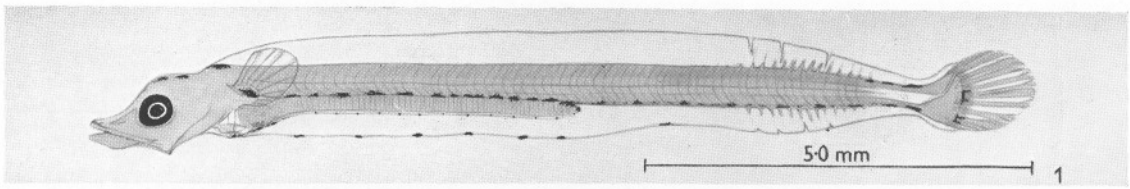
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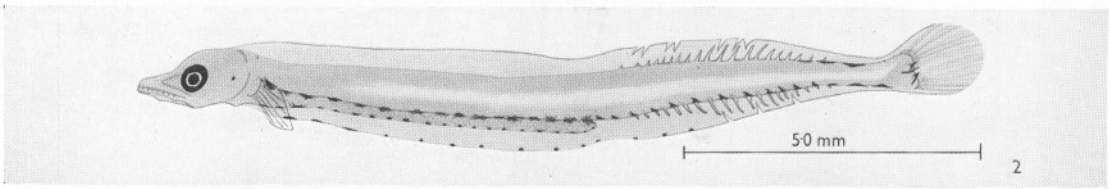
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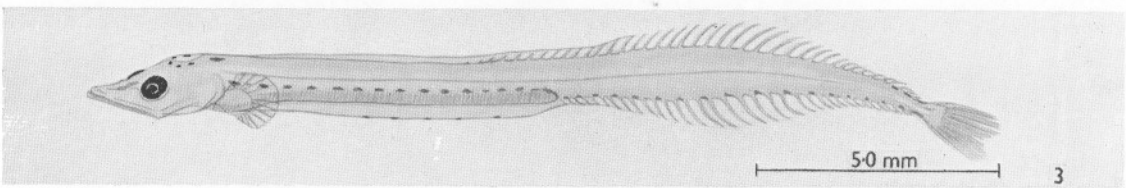
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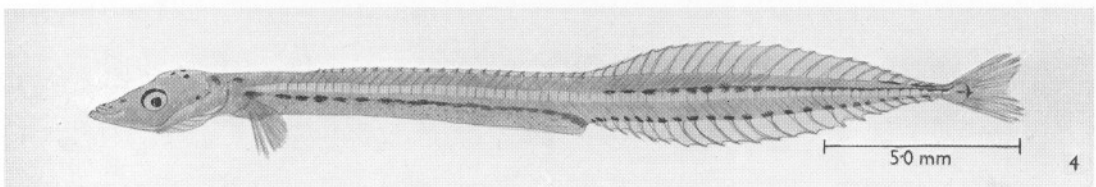
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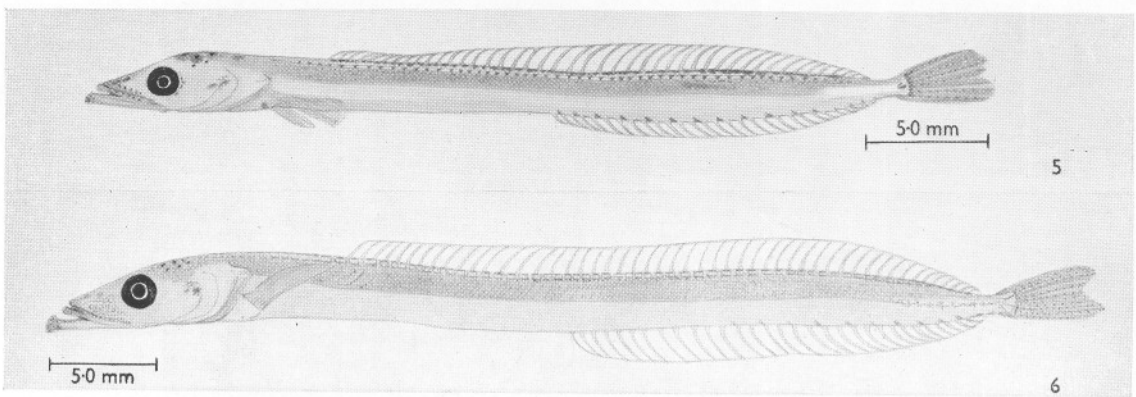
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5
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6

EXPLANATION OF PLATES I AND II

Development stages of *Gymnammodytes semisquamatus* larvae and post-larvae. The drawings were made from specimens preserved in formalin. Measurements represent total length.

PLATE I

Fig. 1. Larva, 3 mm.
Fig. 2. Post-larva, 4·75 mm.
Fig. 3. Post-larva, 5·75 mm.
Fig. 4. Post-larva, 7·0 mm.
Fig. 5. Post-larva, 11·75 mm.

PLATE II

Fig. 1. Post-larva, 12·5 mm.
Fig. 2. Post-larva, 14·0 mm.
Fig. 3. Post-larva, 19·5 mm.
Fig. 4. Post-larva, 24·0 mm.
Fig. 5. Post-larva, 38·0 mm.
Fig. 6. Juvenile, 48·0 mm.

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A PORPHYRIN PIGMENT IN THE INTEGUMENT OF *ARION ATER* (L.)

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MacMunn (1886) extracted a porphyrin from the integument of the starfish *Asterias rubens*—then known as *Uraster rubens*—and he considered that this and similar pigments which he had obtained from the slug *Arion empiricorum* and the coelenterates *Flabellum variabile* and *Fungia symmetrica* were identical with the haematoporphyrin of Hoppe-Seyler (1871), which was then the only porphyrin known. Dhéré & Baumeler (1928*a*) confirmed the presence of a porphyrin in *Arion empiricorum*, but did not specify which porphyrin they had found. Kennedy & Vevers (1953), working at the Plymouth Laboratory of the Marine Biological Association, found that the pigment of the integument of *Asterias rubens* L. was protoporphyrin, and in a further survey of the porphyrins of marine invertebrates (Kennedy & Vevers, 1954), they examined the integuments of two molluscs, *Aplysia punctata* Cuvier and *Duvaucelia plebeia* (Johnston), and showed that each contained uroporphyrin I. This pigment was also found by Kennedy & Vevers (1956) to be present in the integument of the tectibranch mollusc *Akera bullata* (O. F. Müller). The present paper describes the isolation and identification of the porphyrin from the integument of the black garden slug *Arion ater* (L.). *Arion empiricorum* was a synonym introduced by Férussac, Férussac & Deshayes (1819–51) to cover the numerous colour and pattern varieties of the slug more generally known as *Arion ater*. The work appears here since it is a continuation of investigations of mollusc pigments initiated in the Plymouth Laboratory, the results of which have already been published in this *Journal*.

The writer is very grateful to Mr O. Thornburn of the Cancer Research Unit, University of Sheffield, for collecting the specimens of *Arion ater* for this work.

METHOD

Twenty-seven large specimens of the black *Arion* were collected from Lodge Moor, near Sheffield, and killed by chloroform vapour. The very viscous yellow slime was removed with a cloth and the integuments dissected off. The internal surfaces of the integuments were scraped clean and the tissue chopped with scissors into 500 ml. of a mixture of absolute methanol 19 parts and concentrated sulphuric acid 1 part. The extraction was allowed to proceed overnight at room temperature, and the residue then filtered off and

re-extracted for 4 h with a further 500 ml. of the methanol-sulphuric acid mixture. The extracts were pooled, diluted with an equal volume of water, cooled to 5° C, and extracted with chloroform until the hypophases were no longer fluorescent. The chloroform extract was washed with 2% sodium chloride twice, followed by six washes with distilled water, dried roughly by filtration through chloroform-soaked paper, and concentrated *in vacuo* at 60° C.

The extract was dark brown and red-fluorescent, and obviously contained a great deal of porphyrin. A sample diluted with chloroform gave the following spectrum (Hartridge):

626·7 572·0 537·3 500·7 mμ.

This spectrum very closely resembles that given by uroporphyrin.

CHROMATOGRAPHY

Column chromatography

The chloroform extract of the pigment was evaporated to dryness and the residue redissolved in fresh dry chloroform. The solution was passed down a column of magnesium oxide grade III (Nicholas, 1951), packed in chloroform, and the chromatogram developed with chloroform containing 0·5, 1·0 and 2·0% methanol successively. A brownish very red-fluorescent band formed rapidly and moved down the column on adding the 2·0% methanol in chloroform mixture. The dark brown non-fluorescent band at the top of the column did not move, and was discarded. The red-fluorescent band was collected, filtered, and the methanol washed out with water. This band gave a spectrum (Hartridge)

626·1 570·5 536·4 501·4 mμ (in $CHCl_3$).

No shift of the bands was observed on substituting authentic uroporphyrin I for the *Arion* pigment in the spectroscope. The spectrophotometer (Unicam) readings were:

626 570 536 501 mμ (in $CHCl_3$).

Fischer (1926) obtained a spectrum for uroporphyrin:

626·2 570·5 537·3 500·8 mμ (in $CHCl_3$).

No other bands were formed on the column.

Paper chromatography

Long paper. A sample of the *Arion* pigment ester was hydrolysed by allowing it to stand in contact with concentrated hydrochloric acid at room temperature overnight, and the acid was removed by standing solution over solid potassium hydroxide in a vacuum desiccator. The free porphyrin was dissolved in a

little 2:6-lutidine and spotted on strips of Whatman No. 4 filter-paper 50 cm long and 4 cm wide in the apparatus devised by the writer (1953). Authentic uroporphyrin I, coproporphyrin I and mesoporphyrin IX were used as markers in both adjacent and mixed spots, and the chromatograms were run at 23° C with 2:6-lutidine:water (5:3) in an atmosphere of ammonia for 12 h. The *Arion* pigment formed one spot only corresponding with the one given by the uroporphyrin marker at R_F 0·15. The spot of 'pseudo-uroporphyrin' described by Falk, Dresel, Benson & Knight (1956) was not observed.

Separation of isomers. The esterified pigment was examined by the technique of Falk & Benson (1953) for the separation of uroporphyrins I and III. Uroporphyrin I was the only isomer detected, without trace of uroporphyrin III.

Decarboxylation

The *Arion* pigment was heated in solution in 1% (w/v) hydrochloric acid in a sealed tube for 3 h at 180° C, and the contents chromatographed by the technique of Chu, Green & Chu (1951) using coproporphyrins I and III and uroporphyrin I as markers. The *Arion* pigment gave one spot only corresponding with coproporphyrin I.

Melting-point

The *Arion* pigment ester was crystallized from chloroform-methanol, and recrystallized. The melting-point, determined in a Gallenkamp brass-bobbin apparatus was 292·2° C (uncorrected). The following melting-points for uroporphyrin I have been recorded:

293° C	Fischer & Orth, 1937, pp. 501–2
284° C	Granick & Gilder, 1947
290° C	Fischer, quoted by Carrié, 1936
293° C	Rimington & Miles, 1951

The evidence presented leads to the conclusion that the porphyrin of the integument of *Arion ater* is uroporphyrin I.

EXAMINATION OF OTHER COLOURED FORMS OF *ARION*

Specimens of the other coloured forms of *Arion* were collected, and the integuments examined in the same way for uroporphyrin. The amount of porphyrin in each individual was roughly estimated by direct visual comparison with the same volume of an extract from a black slug in a fluorimeter. The results were rather striking, in that the amount of porphyrin present was directly proportional to the amount of dark pigment in the integument; thus, in the brown animals, there was less porphyrin than in the black; in the red, less than in the brown, and so on, until in the pale grey integuments there was no porphyrin at all.

DISCUSSION

The identification of uroporphyrin I in the integument of *Arion ater* provides yet another example of the occurrence of this pigment in molluscs (Kennedy & Vevers, 1954, 1956). The associated black pigment, which appears to be melanin, is clearly present as a protection against the effects of light upon the animal, since uroporphyrin is known to cause photosensitivity (Fischer & Zerweck, 1924; Schreus & Carrié, 1931; Macgregor, Nicholas & Rimington, 1952), and in those individuals which have little or no associated pigment, there is no uroporphyrin in the integument. It seems also that the red, brown and orange pigments occurring in the integuments of the various coloured forms of *A. ater* are protective in this way, since, as the colour becomes paler, the amount of porphyrin decreases. Perhaps these red, brown and orange pigments are stages in the formation of melanin, each of which is sufficient to protect the animal according to the amount of uroporphyrin present. (The writer has not been able to examine the integument of *A. rufus*, in which the red pigment called 'rufine' by Dhéré & Baumeler (1928*b*) appears.)

Specimens of the land snail *Cepaea nemoralis*, which had brown and yellow or brown and pink striped shells with grey integuments, had no uroporphyrin at all in either the shell or the soft parts.

Kennedy & Vevers (1954) and Kennedy & Dales (1958) have discussed the occurrence of porphyrins in invertebrates, and the significance of associated pigments in protecting the animals against photosensitivity.

A further interesting point is provided by the sea-cucumber, *Holothuria forskali* Delle Chiaje, which has two pigments in the integument, a melanin and a yellow pigment with a very intense green fluorescence, visible even in daylight. The animal is black all over, except for the ventral surface, which is yellow, and if it is turned with the yellow ventrum towards the light, the animal immediately begins to turn back so that the yellow part is concealed. This suggests that the yellow pigment photosensitizes the animal, and that the black melanin protects that portion of the integument which is normally exposed to light. The yellow pigment may act as an orientating mechanism, as suggested by Crozier (1914). Grassé (1948, p. 91) wrote: 'La surface dorsale tout entière est photoréceptive; quand on fait tomber en un point quelconque une lumière ponctiforme, la peau se déprime à l'endroit touché; presque toutes les espèces ont un phototropisme négatif et fuient la lumière d'une fenêtre; le passage d'une ombre devant un animal épanoui le fait se contracter; il y a sans doute un rapport entre cette sensibilité à la lumière et la présence dans les téguments d'un pigment jaunâtre à belle fluorescence verte.' In some experiments carried out by the writer (unpublished) the pigment behaved in many ways like a flavin. The integument of *Cucumaria normani* Pace when exposed to light darkens and becomes black.

Kennedy & Dales (1958) have suggested that there is some parallel between the occurrence of free porphyrins in invertebrates and of these pigments in human porphyrias. In molluscs, if free uroporphyrin I is present, it occurs in the shell if there is one, or in the integument if there is not. The shell and the integument are both mantle products, and this is another example of the great affinity of uroporphyrin for tissues with a high calcium content.

SUMMARY

The porphyrin of the integument of *Arion ater* (L.) has been identified as uroporphyrin I. Chromatographic behaviour, reactions and melting-point are described. In the coloured forms of *A. ater*, the amount of porphyrin is shown to be directly proportional to that of the associated melanoid pigment. Reasons for this are suggested.

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SOME OBSERVATIONS ON THE SCYPHOMEDUSA *ATOLLA*

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(Text-figs. 1–3)

During the last four years collections of plankton from deep water have been made regularly on the cruises of R.V. 'Sarsia'. The opportunity has been taken to study the biology of the scyphomedusa *Atolla wyvillei*. It was hoped that with material collected from the same area at different times of the year it might be possible to gain some information on the growth and length of life of this medusa. The collections have been supplemented by a number of specimens taken on recent cruises of R.R.S. 'Discovery II', and a total of nearly 300 medusae have been examined. The collections were made with the 2 m stramin ring trawl and the Isaacs–Kidd pelagic trawl mostly from the Bay of Biscay.

On all specimens sufficiently well preserved the following observations were made: diameter of the umbrella in millimetres, including marginal lappets; number of marginal tentacles; and degree of development of the gonads. In assessing the development of the gonad the specimens were grouped into three categories: (1) those in which there were no gonads, or in which the gonads were just appearing as crescent-shaped growths in which the sex could not be distinguished; (2) those in which the gonads were obviously not mature, but in which the two sexes could be determined; and (3) males and females which appeared to be mature or, at any rate, in which the gonads were completely full. In mature females the gonads are always distinctly separated one from the other, but in mature males the gonads become folded and touch one another so as to form an almost continuous ring.

The results of relating size to maturity of 281 specimens are given in Fig. 1. It will be seen that there are two separate peaks of mature specimens, one between 10 and 20 mm and the other between 60 and 70 mm. I first thought that this bimodality might indicate two breeding periods, perhaps at yearly intervals. Further examination of the data showed, however, that the small and the large mature specimens corresponding to the two peaks occurred in all months of the year in which samples were collected, namely February, March, April, May, June, July and November. It was impossible, therefore, to gain any information on rate of growth from these observations. This in

itself was disappointing, but it left the occurrence of the two peaks of maturity to be explained.

There was the possibility either that some specimens mature at an early size and die, or that after spawning they continue growth and, after recovery of the spent gonads, spawn a second time. In the latter event it might have been expected that the two peaks of maturity would not be so completely separated.

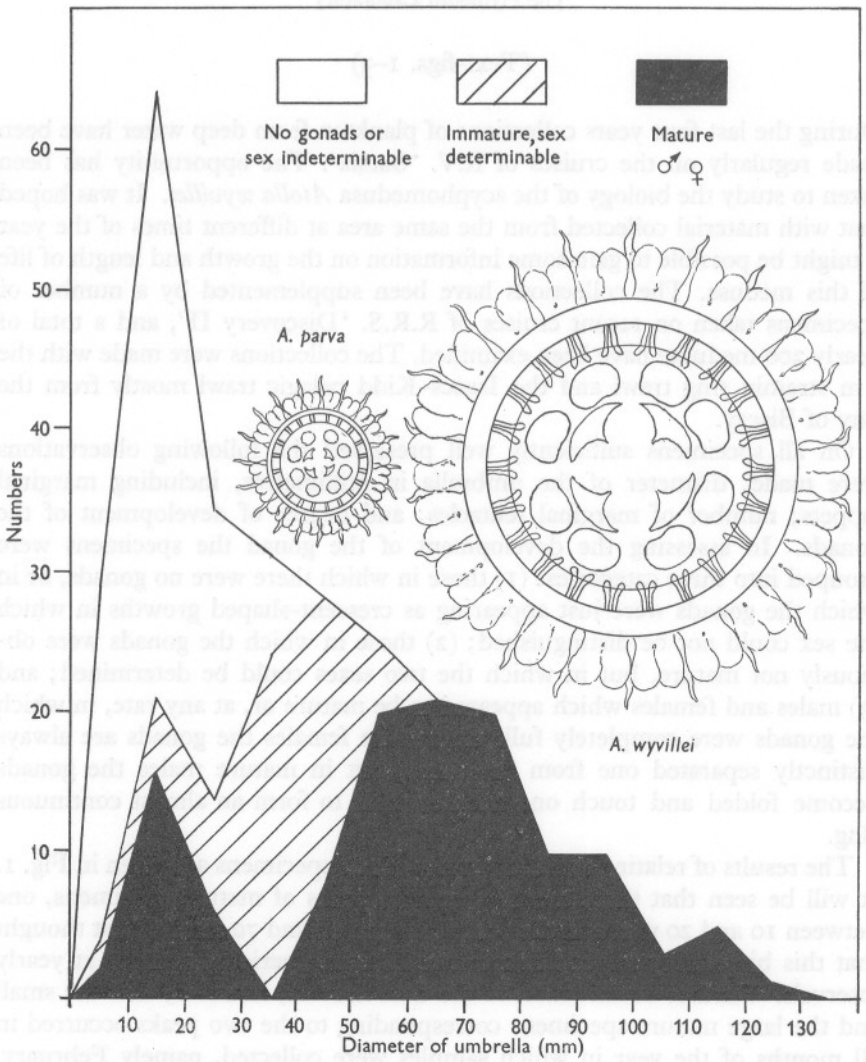

Fig. 1. Graph showing numbers of *Atolla* at different stages of maturity plotted against the diameter of the umbrella in millimetres. Diagrammatic outline drawings are given to show roughly the average natural size of mature female specimens of *A. parva* and *A. wyvillei*.

But when a comparison of the number of marginal tentacles in relation to the diameter of the umbrella was made a curious anomaly was noticed. Table 1 shows that the normal number of tentacles in full-grown medusae is 22, the number characteristic of *A. wyvillei*. Furthermore, this number was never exceeded in large specimens. There are, however, a few specimens less than 35 mm in diameter with as many as 24 tentacles. A special examination was therefore made of these specimens, and it was found that they were mature or already had gonads which were sexually distinguishable. Now, if these specimens were to continue growing it is most improbable that their marginal tentacles would be reduced in number, which alone would account for the complete absence of any larger specimens with more than 22 tentacles. If, on the other hand, these small medusae died after spawning, why should they grow more tentacles than the normal large adult?

The only reasonable explanation seemed that these medusae which mature at a small size are a different species from *A. wyvillei* which form the bulk of the collection.

Examination was made of the numbers of tentacles in all those specimens less than 35 mm in diameter with mature or sexually determinable gonads, or with more than 22 marginal tentacles. The results are given in Table 2, from which it can be seen that the number of tentacles ranges from 18 to 24; and that seventeen out of thirty-seven specimens have 20 tentacles, twelve have 24, and only one has 22.

All these specimens, and a number of others with 20 marginal tentacles, were then examined to see whether any morphological character could be found to distinguish them from *A. wyvillei*, other than size at maturity or number of tentacles.

A distinctive character which appears to be constant was found in the septa which separate the tentacular and rhopalar canals (Fig. 2). In *A. wyvillei* these septa tend to diverge widely towards the gastric sinus with their ends turning slightly inwards again. The thin part of the coronal muscle does not reach the ends of the septa so that there are always appreciable portions of the septa projecting centripetally beyond the muscle margin. In the medusae which mature at a small size the septa are nearly straight; some of them tend to have pointed ends and they only diverge slightly if at all near the gastric sinus. The thin portion of the coronal muscle covers the septa almost completely to their ends and some septa do not project at all centripetally beyond the muscle margin.[1] This continuation of the muscle ring to the ends of the septa emphasizes the points of entry of the tentacular and rhopalar canals into the gastric sinus and tends to increase the geometrical regularity of the colour pattern round the umbrella in this region (Fig. 3). The thin portion of the muscle itself also appears to be more strongly developed than in *A. wyvillei*. In some specimens, probably due to contraction, the ends of the

[1] I have examined specimens of *A. vanhöffeni* and find that they also have this character.

septa extend farther than usual beyond the margins of the coronal muscle. These, however, can still be distinguished by the straightness of the septa themselves; usually also they have the typical number of 20 or 24 marginal tentacles.

TABLE 1. RELATION OF NUMBER OF MARGINAL TENTACLES TO DIAMETER OF UMBRELLA IN *ATOLLA*

Diameter (mm)	Number of marginal tentacles							
	17	18	19	20	21	22	23	24
1–9	.	.	.	5	.	6	.	1
10–19	.	2	3	19	5	28	1	5
20–29	.	.	1	7	.	27	.	5
30–39	.	.	.	3	2	23	.	1
40–49	1	.	2	3	4	18	.	.
50–59	.	.	1	1	1	23	.	.
60–69	1	.	.	3	2	17	.	.
70–79	.	.	.	4	2	10	.	.
80–89	.	1	1	.	1	15	.	.
90–99	.	.	.	1	.	8	.	.
100–109	.	.	.	.	.	4	.	.
110–119	.	.	.	.	.	3	.	.
> 120	.	.	.	.	1	4	.	.
Totals	2	3	8	46	18	186	1	12

TABLE 2. SPECIMENS OF *ATOLLA* LESS THAN 35 mm, INCLUDED IN TABLE 1, WITH MATURE OR SEXUALLY DETERMINABLE GONADS, OR 23 OR 24 TENTACLES

Diameter (mm)	Number of marginal tentacles							
	17	18	19	20	21	22	23	24
1–9	.	.	.	2	.	.	.	1
10–19	.	2	3	11	.	.	.	5
20–29	.	.	.	4	1	1	1	5
30–35	.	.	.	.	.	.	.	1
Totals	.	2	3	17	1	1	1	12

On the above characters I concluded that the small mature specimens were a distinct species and published a brief description under the name *Atolla parva* (Russell, 1958).

In the north-eastern Atlantic we thus have three species of *Atolla*: *A. wyvillei*, *A. vanhöffeni* and *A. parva*. There can, I think, be no doubt that the large medusae with 22 tentacles are *A. wyvillei* as they agree well with Haeckel's original description of the species based on five specimens 38–68 mm in diameter, all of which had 22 marginal tentacles except the smallest in which there were 19 (Haeckel, 1880, p. 488; 1881, p. 113). It is most unlikely that any of the existing specific names could be used for *A. parva*, although it must be present in other collections as it is generally stated that mature specimens are found at all sizes. Indeed, among the eight specimens on which Fewkes (1886, p. 939) based his description of *A. verrilli* there were

two specimens 14 and 25 mm in diameter, each of which had 24 marginal tentacles.

As far as I have found at present *A. parva* differs from *A. wyvillei* only in its smaller size, the characteristic number of 20 or 24 marginal tentacles, and the form of the septa and their almost complete covering by the coronal muscle. The coloration of *A. parva* seems to be similar to that of *A. wyvillei*, and in some specimens the stomach alone is deeply pigmented.

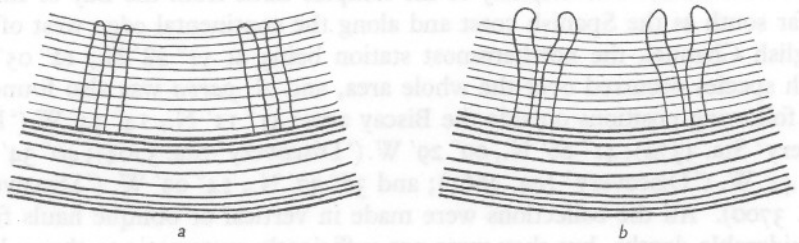

Fig. 2. Diagrammatic drawings to show the shapes of the septa separating the tentacular and rhopalar canals and their positions in relation to the thin portion of the coronal muscle: *a*, *Atolla parva*; *b*, *A. wyvillei*. Note that in *A. parva* the sides of the tentacular canals are approximately straight, and in *A. wyvillei* they are converging and constricted at the entrance to the gastric sinus.

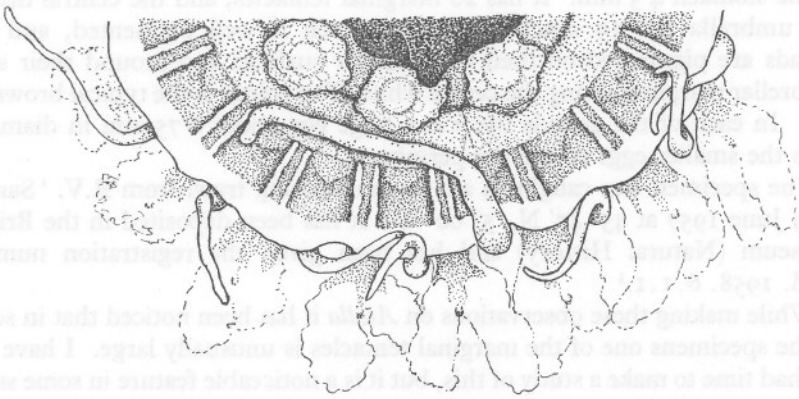

Fig. 3. Drawing of portion of the type specimen of *Atolla parva* to show the large marginal tentacle.

Since number of marginal tentacles is evidently a specific character the question naturally arises whether those specimens with 24 tentacles are specifically distinct from those with 20. I have examined the specimens carefully and can find no other character in which they differ, except that there is a tendency for those with 24 tentacles to be larger. I have now seen nearly fifty specimens: while the majority are between 9 and 21 mm in diameter there are four specimens which measure 25, 26, 29, and 30 mm in

diameter respectively; each of these has 24 tentacles. Of these the largest, 30 mm in diameter (paratype B.M. 1958, 6.1.8), has only the stomach pigmented. As it cannot be said for certain that the medusae with 24 tentacles may not be a separate species I have selected as the holotype specimen of *A. parva* one with 20 tentacles.

From the data available there does not appear to be any difference in distribution between *A. wyvillei* and *A. parva* in the area from which the collections were made. The majority of the samples came from the Bay of Biscay as far south as the Spanish coast and along the continental edge west of the English Channel, the northernmost station being at 51° 28′ N., 12° 05′ W. Both species occurred over the whole area, and *A. parva* was also found at the following positions outside the Biscay area: 41° 11′ N., 14° 34′ W ('Discovery' Sta. 3374); 41° 26′ N., 09° 29′ W. ('Discovery' Sta. 3704); 40° 34′ N., 19° 42′ W. ('Discovery' Sta. 3661); and 36° 37′ N., 14° 09′ W. ('Discovery' Sta. 3700). All the collections were made in vertical or oblique hauls from considerable depths, but they were not sufficiently systematic to throw light on the vertical distribution of the medusae.

I have selected as the holotype a mature female specimen 18 mm in diameter. In this specimen the diameter to the periphery of the coronal muscle is about 13 mm; the diameter of the central umbrella disc is 7 mm and that of the base of the stomach 4·3 mm. It has 20 marginal tentacles, and the central disc of the umbrella has 19 notches. The specimen is well pigmented, and the gonads are pigmented on their exumbrellar surfaces and around their subumbrellar margins leaving the centre white. The colour is the typical brownish red. In each of the gonads there is a large egg about 0·75 mm in diameter with the smaller eggs round the periphery.

The specimen was caught in a 2 m stramin ring trawl from R.V. 'Sarsia' on 3 June 1957 at 45° 47′ N., 5° 00′ W. It has been deposited in the British Museum (Natural History) and has been given the registration number B.M. 1958. 6.1.1.[1]

While making these observations on *Atolla* it has been noticed that in some of the specimens one of the marginal tentacles is unusually large. I have not yet had time to make a study of this, but it is a noticeable feature in some small

[1] I have also deposited the following specimens as paratypes, B.M. 1958. 6.1.2–8:

	13.vi.56. 48° 29′ N., 9° 5′ W.		R.V. 'Sarsia'
2.	16 mm diameter	19 tentacles	Female
3.	26 mm diameter	24 tentacles	Immature
4.	7 mm diameter	20 tentacles	Immature
	4.vii.56. 47° 02′ N., 5° 53′ W.		R.V. 'Sarsia'
5.	20 mm diameter	20 tentacles	Male
6.	20 mm diameter	20 tentacles	Immature
7.	7 mm diameter	24 tentacles	Immature
	29.ii.57. 41° 11′ N., 14° 34′ W. ('Discovery' Sta. 3374)		
8.	30 mm diameter	24 tentacles	Female (stomach only pigmented)

specimens and is a further indication of the bilateral symmetry indicated by the number of notches or grooves in the central disc of the umbrella, which is usually one less than the number of marginal tentacles (Stiasny, 1934, p. 370). It will be necessary to get very young specimens to see whether this bilateral symmetry is a significant indication of the sequence of early development in the number of marginal tentacles.

The type specimen of *A. parva* has one such tentacle very much larger and more heavily built than the others (Fig. 3); and this is situated opposite the widest of the sectors of the central disc of the umbrella, that is at its point of asymmetry.

Luminescence has been observed in *A. parva* by Nicol (1958, p. 719).

My thanks are due to Captain C. A. Hoodless and the crew of R.V. 'Sarsia', the captain and crew of R.R.S. 'Discovery II', and a number of members of the staff of the Plymouth laboratory and the National Institute of Oceanography for their care in picking out some of the specimens from the catches.

SUMMARY

In a study of the biology of *Atolla* it has been found that at any time of year the population from the Bay of Biscay shows two peaks at maturity, one between 10 and 20 mm diameter and the other between 60 and 70 mm.

It is shown that the smaller of the two peaks is composed of specimens of *A. parva*, while the larger specimens are *A. wyvillei*.

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Note added in proof

Through the kindness of Dr P. L. Kramp I have been able to see additional specimens which were picked out by Dr Kay Petersen from the collections of *Atolla* from the Atlantic in the Universitetets Zoologiske Museum in Copenhagen. Many of these were in rather poor condition with gonads missing; but the fact that none of these specimens had 22 tentacles confirms their identification. Of these eight had 20 tentacles,

eight had 24, and four had 26, the highest number so far seen. It is interesting to note that the four specimens with 26 tentacles came from the farthest north stations in the Norwegian Sea, and that one of these was 33 mm in diameter.

			Metres wire	Diameter (mm)	Sex	No. of tentacles
Ingolf						
20. vii. 1896	St. 112	67° 56′ N., 6° 44′ W.	—	15	♀	26
				22	—	26
				23	—	24
				25	—	26
Tjalfe						
3. v. 1909	St. 322	60° 07′ N., 48° 26′ W.	2000	22	—	24
8. v. 1909	St. 336	64° 06′ N., 55° 18′ W.	1040	*c.* 13		
			−1100	(damaged)		
				14	—	24
Thor						
28. ii. 1909	St. 68	36° 13′ N., 9° 44′ W.	3000	13	—	20
				13	—	20
				16	—	24
				20	—	20
4. iii. 1909	St. 71	39° 35′ N., 9° 45′ W.	1600	11	—	24
				13	♀	24
9. ix. 1910	St. 232	36° 28′ N., 9° 06′ W.	2000	7	—	? 20
				10	♀	24
				(shrunk)		
				15	—	24
Dana						
24. v. 1934	St. 5143	65° 14′ N., 6° 06′ W.	2400	33	♂	26
Atlantide						
29. i. 1946	St. 82	5° 27′ N., 0° 07′ E.	1700	8	—	20
2. iv. 1946	St. 139	1° 30′ N., 10° 10′ W.	1750	10	—	20
				10	—	20
				12	—	20
				25		
				(damaged)		

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CHEMICAL CHANGES IN SEA WATER OFF PLYMOUTH DURING 1957

By F. A. J. ARMSTRONG and E. I. BUTLER
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(Text-figs. 1–3)

Analyses of sea water collected during 1957 at the International Hydrographic Station E 1 (lat. 50° 02′ N., long 4° 22′ W.) are given here in the same form as in earlier reports (Armstrong, 1954, 1955, 1957, 1958). The methods of collection and of analysis for phosphorus and silicon are substantially unchanged. Some analyses were made for ammonia by a vacuum distillation method (Riley, 1953), and for inorganic nitrogen (nitrate + nitrite + ammonia) by reduction of nitrate and nitrite with nickel (Riley & Sinhaseni, 1957) to ammonia, which was vacuum distilled. Salinities were determined by the Government Chemist's Department.

We wish to express our thanks to Lt.-Cdr. C. A. Hoodless and the crew of R.V. 'Sarsia' and to Capt. W. J. Creese and the crew of R.V. 'Sula', for assistance at sea.

RESULTS

Temperature and salinity

The vertical distribution of temperature during the year is shown in Fig. 1. The lowest surface temperature recorded was 9·7° C. on 15 February, and the highest was 16·11° C. on 16 July. Some vertical irregularities of temperature and salinity occurred in March and April, being most marked on 24 April, when water of salinity higher than on 11 April, higher than in the layers above, and marked by its lower silicate content, was present at 50 and 70 cm. (Table 2). As is seen there was a temperature minimum at 20 m, but the densities show the vertical stability.

A sharp thermocline between 15 and 20 m was established by 11 June, and persisted with some change of level until September. From October until the end of the year the water column was isothermal.

Phosphate

Vertical distribution is shown in Fig. 2, and integral mean concentrations in Table 1. The winter maximum found was 0·47 μg atom P/l. on 15 February, and the lowest concentrations were 0·08–0·09 μg atom P/l. at the 5 and 10 m levels in May and June. Phosphate remained low in the upper 20 m until September; the vertical distribution had become uniform by 15 October, and so remained until the end of the year.

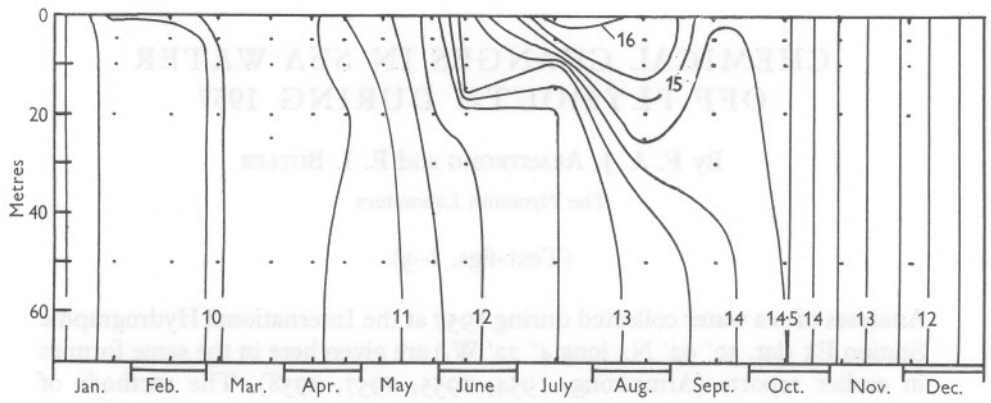

Fig. 1. Vertical temperature distribution at International Hydrographic Station E1, 1957. Contour lines at 0·5° C intervals.

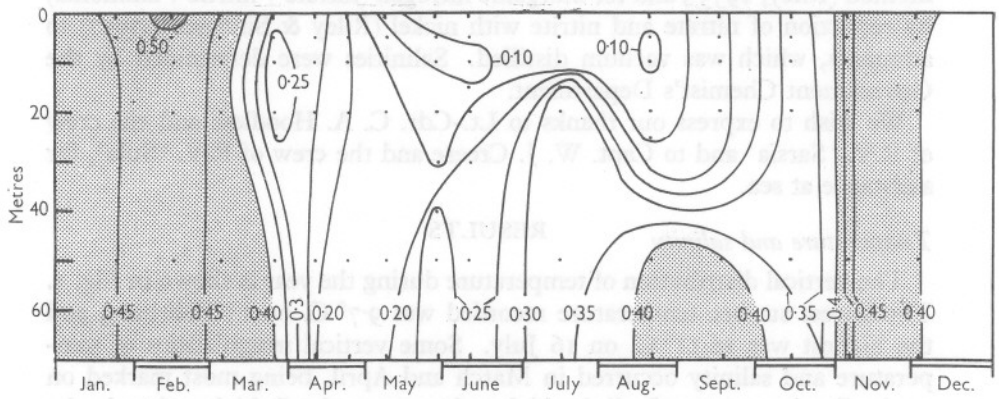

Fig. 2. Vertical distribution of phosphate at International Hydrographic Station E1, 1957. Contour lines at 0·05 μg atom P/l. intervals.

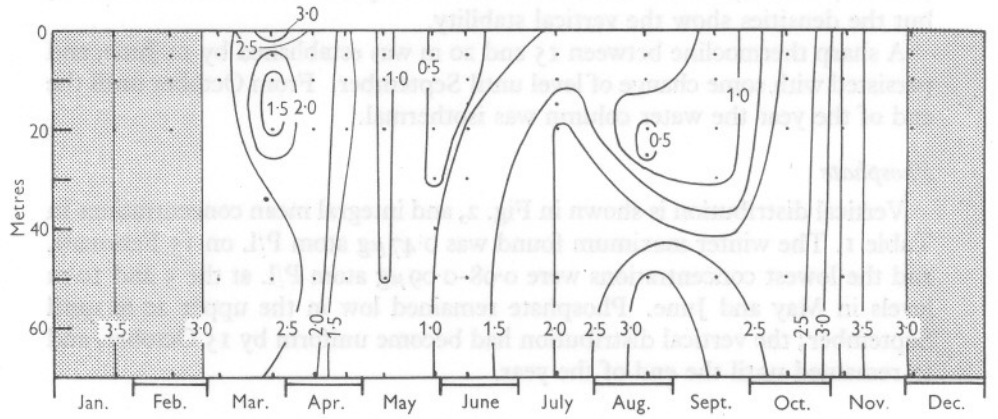

Fig. 3. Vertical distribution of silicate at International Hydrographic Station E1, 1957. Contour lines at 0·5 μg atom Si/l. intervals.

'Total phosphorus'

Determinations were made in January, February and March only, to find the winter maximum value. This was 0·63 μg atom P/l. on 15 February.

Silicate

Vertical distribution is shown in Fig. 3, and integral mean concentrations in Table 1. The maximum found at the beginning of the year was 3·5 μg atom Si/l. on 24 January. On the whole, higher silicon concentrations than usual were maintained during the year, as Table 1 shows. Values of less than 0·5 μg atom Si/l. were found only on 29 May and 11 June, above the thermocline, and, surprisingly, at 20 and 25 m on 21 August. These low values came between considerably higher ones in the water above and below, as shown in Table 3.

TABLE 1. INTEGRAL MEAN CONCENTRATIONS IN WATER COLUMN AT STATION E1, 1957

Date	Phosphate (μg atom P/l.)	'Total-P' (μg atom P/l.)	Silicate (μg atom Si/l.)	Ammonia (μg atom N/l.)	Inorganic N (μg atom N/l.)
24 Jan.	0·45	0·52	3·47	0·7	9·8
15 Feb.	0·47	0·63	3·35	—	9·6
5 Mar.	0·43	0·54	2·71	—	—
26 Mar.	0·31	—	2·30	0·7	1·7
11 Apr.	0·24	—	2·25	—	—
24 Apr.	0·21	—	1·22	—	—
9 May	0·16	—	1·07	—	—
29 May	0·20	—	0·72	1·1	2·6
11 June	0·18	—	1·03	0·7	1·6
16 July	0·30	—	1·83	—	—
21 Aug.	0·26	—	1·87	—	—
17 Sept.	0·31	—	1·62	1·2	6·9
15 Oct.	0·31	—	2·28	1·2	—
6 Nov.	0·44	—	3·58	—	—
3 Dec.	0·42	—	3·07	0·4	3·7

There was a significant fall in salinity in the upper 10 m between July and August. This may show that water at this level has been replaced by other of different chemical properties, for although phosphate fell, silicate rose slightly, at the same time. There were also slight changes in the composition of the bottom water, but the change of salinity here may not be a significant one, and the changes in phosphate and silicate could be put down to a normal regeneration of these nutrients. The data are insufficient to explain the curious vertical distribution of silicate.

Layering of water masses at this station (apart from the annually developed thermocline) has been found from time to time in the past 8 years, having been revealed by irregularities in the silicate figures. Occasionally, laminar as well as bodily displacements of water must occur at E1.

TABLE 2. OBSERVATIONS AT STATION E1, 24 APRIL 1957

Depth (m)	Temperature (° C)	Salinity (‰)	Density *in situ*	Phosphate (μg atom P/l.)	Silicate (μg atom Si/l.)
0	11·0	35·19	26·94	0·20	1·5
5	10·88	35·13	26·91	0·19	1·5
10	10·83	35·14	26·93	0·20	1·4
20	10·45	35·16	27·01	0·21	1·8
50	10·73	35·29	27·06	0·17	0·8
70	10·65	35·30	27·09	0·25	0·8

TABLE 3. OBSERVATIONS AT STATION E1, 16 JULY AND 21 AUGUST 1957

Depth (m)	Salinity (‰)		Phosphate (μg atom P/l.)		Silicate (μg atom Si/l.)	
	July	Aug.	July	Aug.	July	Aug.
0·5	35·13	35·12	0·11	0·11	1·2	1·6
5	35·16	35·10	0·15	0·09	1·3	1·4
10	35·17	35·08	0·14	0·10	1·3	1·4
15	35·18	—	0·36	—	1·7	—
20	35·20	35·16	0·34	0·12	2·0	0·2
25	—	35·16	—	0·14	—	0·3
50	35·20	35·17	0·33	0·43	2·0	3·2
70	35·21	35·18	0·34	0·42	2·0	3·3

Nitrogen

Enough analyses to draw an isopleth could not be done, and integral mean values only are given here. The vertical distribution did, however, resemble that for phosphate. The values (Table 1) in winter and summer resemble those obtained at E1 by other methods in earlier years (Cooper, 1933). The winter (maximum) ratio, N/P = 20/1 by atoms or 9·2/1 by weight, was a little higher than the 16 or 17/1 atomic ratio found in 1931 by Cooper.

Integral mean concentrations

The spring decreases representing consumption of nutrients were: phosphate 0·29 μg atom P/l., silicate 2·75 μg atom Si/l., inorganic nitrogen 8·0 μg atom N/l. The ratio N/P consumed was 27·6/1 μg atoms or 12·4/1 by weight and is rather higher than the mean ratio, 16·3/1, for a number of analyses of plankton from this area (Cooper, 1937).

SUMMARY

The results of analysis of sea-water samples from the International Hydrographic Station E1 during 1957 are given in graphical form and as integral mean values for the water column of 70 m. The seasonal variation shows the consumption of nutrients during the spring growth of plants to have been: phosphate 0·29 μg atom P/l., silicate 2·75 μg atom Si/l., inorganic nitrogen 8·0 μg atom N/l. At the time of winter maximum the N/P ratio was 20/1 by

atoms or 9·2/1 by weight. The ratio of these elements consumed was 27·6/1 by atoms or 12·4/1 by weight.

Unusual vertical distributions of silicate were found in April and August, and are attributed to laminar water movements.

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THE GROWTH AND FRUITING OF *GRACILARIA VERRUCOSA* (HUDSON) PAPENFUSS

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(Text figs. 1–3)

Several workers have observed, in Europe and elsewhere, that *Gracilaria verrucosa* is a more conspicuous component of the flora in the summer months (Cotton, 1912, p. 134; Rosenvinge, 1931, pp. 602–6; Gibb, 1939, p. 378; Causey, Prytherch, McCaskill, Humm & Wolf, 1946; May, 1948), with the natural inference that its growth rate is greater in that season. However, the quantity present on the shore at any time depends also on the rate of defoliation by the waves. This will be higher in winter. Observation under more controlled conditions was therefore considered desirable.

Fragmentary records of the fruiting of *G. verrucosa* extend over many years. Hudson (1762, pp. 588, 591) gave the fruiting period (for female gametophytes) as being from June to September. Greville (1830, p. 123) agreed but added that occasional fruiting plants could be found at all seasons. Feldmann (1954, p. 86) recorded, in Brittany, cystocarps in January, April, July, August, September, October and December and tetraspores in August and September. Rosenvinge (1931, pp. 602–6) recorded, in Denmark, ripe cystocarps in July and August; empty ones in October and April; ripe tetrasporangia in June, July and August and empty ones in October; spermatangia in July and August. The present attempt to obtain a more complete picture has involved the examination of collections of plants from various shores at all times of the year; and estimation of the relative numbers of cystocarpic and non-cystocarpic plants on a shore. These field observations have been supplemented by testing plants in the laboratory for their readiness to shed spores and the capacity of the latter to germinate.

THE VEGETATIVE GROWTH CYCLE

Criterion of growth

The increasing length of a frond of *Gracilaria* probably furnishes a satisfactory measure of its growth since, in a uniformly cylindrical thallus, the bulk is proportional to the length. However, the simple measurement of the maximum length of the thallus did not appear to be satisfactory, since the

growth of the more or less numerous branches would not necessarily be represented by this. Instead, in the present investigation, the fresh weight of the plants concerned was periodically measured.

Methods

In their experiments on factors affecting growth in *Gracilaria verrucosa* in N. Carolina, Causey *et al.* (1946) measured the 'green weight' of the plants after shaking off the surface water. As the plants used in the present investigation were not large, incomplete removal of surface water was thought likely to cause inaccuracies, as was the inevitable loss of weight by desiccation during weighing; in addition the careful blotting of plants is very time-consuming. To avoid this, weighing was carried out with the plants completely immersed in sea water, as described elsewhere (Jones, 1959, p. 155).

The material used consisted of plants or parts of plants divided at the holdfast and attached by nylon fishing 'gut' to 'Tufnol' plastic bars. The bars were mounted in a box with sides, top and bottom of half-inch mesh wire-netting which allowed a free flow of water round the plants while preventing the entry of floating debris. The box was suspended in one compartment of an open-bottomed barge anchored in the Menai Straits. The bars, with the attached plants, were brought into the laboratory periodically for inspection.

Numerous algal spores settled on the plants while on the barge and a heavy growth of epiphytes resulted in which silt was often bound. This reduced the amount of light reaching the plant. In addition some shade was given by the sides of the barge and, occasionally, by masses of floating weed (*Ascophyllum nodosum* and *Fucus vesiculosus*) which entered the barge and had to be removed. These conditions did not appear to be ideal for the growth of the plants which, during the first season, did not survive indefinitely in an actively growing state. In the subsequent season a more continuous record was obtained. Epiphytes, which had to be removed laboriously by hand, were a major difficulty in the later stages of growth, particularly in the second season.

Results

In the first season batches of six plants were used which were replaced by freshly collected batches when signs of mortification appeared or when the growth of epiphytes became particularly heavy. Results were not obtained for all months: the general pattern was that a comparatively low growth rate of 1% increase in fresh weight per day was observed in November, December, January and April and that in May a sudden increase in the growth rate to 2·6% per day occurred. This rate was maintained through June and gradually declined through the summer, falling more rapidly with the approach of autumn.

These experiments also suggested that the growth rates of cystocarpic and tetrasporic plants were not always the same. In the second season, therefore,

the growth rates of three cystocarpic and three tetrasporic plants were recorded separately. In this series the changes in weight of the same individuals were followed from September until the following July. Deterioration of the plants, resulting mainly from their having grown so large as to be damaged by abrasion against the sides of the box, then made it necessary to conclude the experiment. Fig. 1 shows the changes in the total weight of the three tetrasporic and three cystocarpic plants. In general these results confirm those of the previous season, showing a tendency for the weight of the plants to decline through the winter with a slight rise in early spring followed by a rapid increase in May. Examined separately, however, the results for tetrasporic and cystocarpic plants show some differences.

(i) The spring burst of growth began about a fortnight later in cystocarpic than in tetrasporic plants. A parallel increase in weight was shown by two additional batches, of three tetrasporic and three cystocarpic plants respectively, collected in late April and grown in the box together with the original plants during the period of the May increase. These results are included in Fig. 1 and offer some confirmation of the observations, the parallel being particularly close in the cystocarpic plants.

(ii) From September onwards, while the weight of the tetrasporic plants rose steadily, that of the cystocarpic decreased at almost the same rate. Occasional increases in the weight of the cystocarpic plants (as between 13 and 25 Oct. in Fig. 1) suggest that their potential growth rate at that time of the year is as high as that of tetrasporic plants. Their loss of weight seems to result from more rapid decay of the thallus. It has been observed that decay in the autumn is more pronounced in cystocarpic plants, apparently because pathogens find easy entry into their thalli through the ostioles of cystocarps after spore shedding has ceased. Very frequently decay may be seen to be beginning in a cystocarp while the thallus remains healthy above and below it. Decay soon spreads to the thallus itself and that part above the diseased area breaks off and is lost. In tetrasporic plants decay is largely limited to damaged tips, spreading slowly down the branches and causing comparatively slow loss of material. Probably pathogenic organisms do not enter as easily into the comparatively small opening left after the discharge of the tetraspores, while the copious mucilage left in the cystocarp, and often exuded through the ostiole as fruiting finishes, offers a good substrate for the settlement and development of the spores of pathogens.

In the sheltered conditions of the raft a steady state was reached by the end of November in tetrasporic plants and by January in cystocarpic, during which loss and growth were roughly balanced and little change in weight occurred until the rapid spring growth commenced.

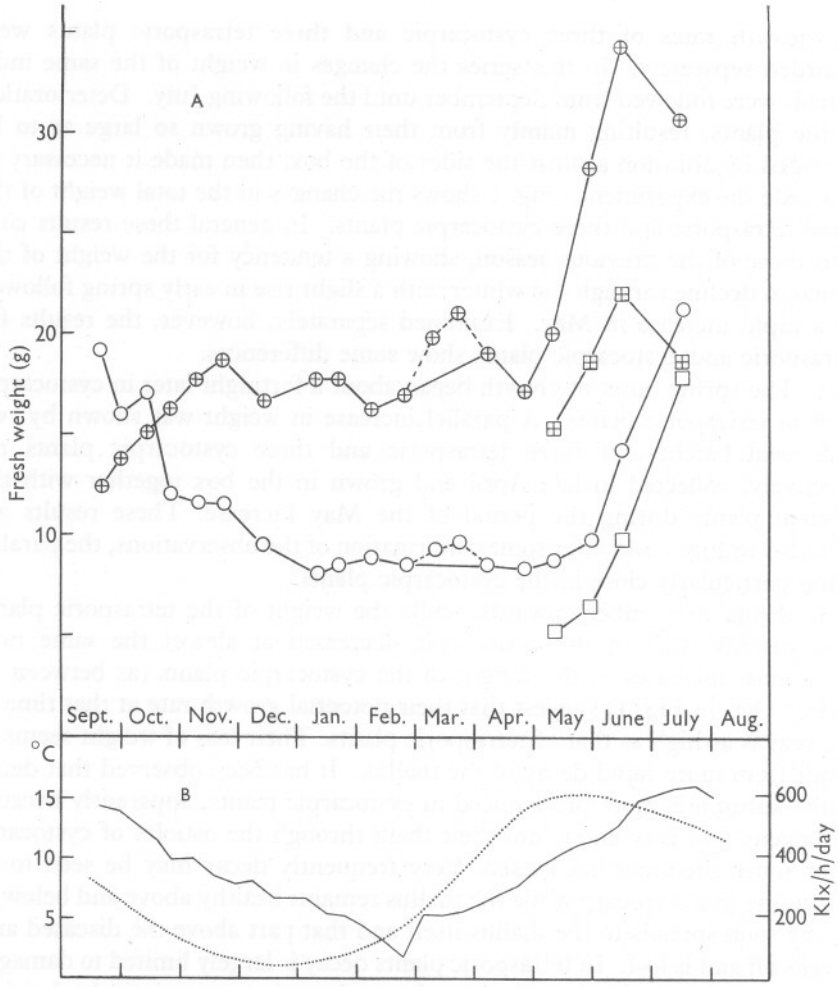

Fig. 1. A. Changes in the total weight of four groups of three plants of *Gracilaria verrucosa* grown on a barge in the Menai Straits. ⊕, tetrasporic, ○, cystocarpic, grown from September 1955; ⊞, tetrasporic, □, cystocarpic, grown from May 1956. The broken line in the period February–March shows the growth recorded without removing epiphytes which were removed at the beginning of April. The solid line gives the more correct picture of the growth of *Gracilaria*. B. Continuous line, sea surface temperatures (10-day averages) over the same period, measured at Menai Bridge Pier. Dotted line, average illumination for Plymouth, 1930–37 (from Atkins, 1938, and Harvey, 1955).

Discussion

In these experiments the plants, though growing in the open, were not under exactly the same conditions as in a normal littoral habitat. In particular:

(i) There was no tidal effect, i.e. no emersion, no pressure fluctuation and no alteration of light intensity by absorption by varying depths of water.

(ii) Although movement of the barge caused plants to sweep against the sides of the box, there was no effect comparable to wave action as on a beach.

(iii) Owing to shading by the sides of the barge the light intensity in the box was never as high as the maximum obtainable on the shore at the same season.

(iv) Temperature changes in the Straits are more pronounced than in the open sea. There may, for instance, be rather sudden falls of temperature in February to as little as 2° C.

The effect of these differences, with the exception of the last, should be to even out the seasonal changes in weight so that, while the experiments indicate the general trend, more pronounced changes might be expected on the shore. This is particularly true of shelter from wave action; the loss resulting from wave damage is severe in winter on the shore and certainly greater than that shown in the experimental results. The equilibrium between the growth rate and the rate of loss by decay and damage, mentioned above, is not so readily established on the shore where plants decrease in size throughout the winter and early spring.

The results show an increase in the weight of both tetrasporic and cystocarpic plants in March. This may be attributed, in the main, to the growth of epiphytes which became noticeable at the end of February. Some real increase in weight did, in fact, occur during this period but was small, as shown by the values for 25 April when careful cleaning of the plants, with the removal of all epiphytes, was commenced. The spring burst of growth began about 3 weeks after this (in the tetrasporic plants) so that it seems that *Gracilaria* begins active growth later than some other species.

In considering the relationship of the seasonal environmental changes to the growth cycle the two factors with obvious summer maxima are the sea temperature and the daily quantity of light. Conversely, the acceleration of growth occurs when the supply of dissolved nitrogen and phosphorus in the sea water is approaching its lowest annual value (Harvey, 1955, pp. 44–59). In Fig. 1 the annual cycles of temperature and light are shown on the same time scale as the growth cycles of tetrasporic and cystocarpic plants over the period September 1955–July 1956. It will be seen that, whilst growth broadly follows the trend of both factors, there is no exact coincidence. For instance, the burst of growth in May does not coincide with a sudden increase in either temperature or light, which have both been increasing for several months before this. Certain correlations do, however, appear reasonable, though hypothetical at the moment.

Accepting the loss of weight of cystocarpic plants in autumn as being due to decay, the potential growth rate may best be seen in the tetrasporic plants. In these growth continued until late November, when, as has been noted above, it decreases below that required to maintain the weight of the plant. At this time the falling temperature of the sea reached about 8° C. Until the end of April, when the growth rate again overtook the rate of loss, the tem-

perature remained below 8° C, suggesting that, under the conditions on the barge, this represents a critical temperature below which the level of metabolism of the plants is too low to replace all the material lost by accidental damage. The amounts of light available at these times are, on the other hand, very different. At the end of November the daily quantity of light is approaching its minimum value, while in late April it has reached about 85% of its maximum. This critical temperature hypothesis receives some support from the fact that a slight rise in the growth rate may be seen coincident with the rise in temperature after the February minimum; this is small and not necessarily significant but appears to occur in both tetrasporic and cystocarpic plants. Again, the results of Causey *et al.* (1946) are in general agreement with this hypothesis; from their observations on *Gracilaria* in N. Carolina they state that growth begins in spring when the water temperature rises above 10° C and ceases when it drops below 10° C in the autumn. It should be remembered, however, that although some growth occurred in the cystocarpic plants at the same time as the tetrasporic, the main burst of growth began a fortnight later, by which time the temperature had risen to nearly 10° C.

This time lag may perhaps be explained by analogy with the behaviour of unicellular algae in culture. Spencer (1954) showed that when, after a period of growth in suboptimal conditions, the plants are subcultured to media containing ample nutrients, there is a time lag before rapid growth recommences. The duration of this lag is related to the length of the period of suboptimal nutrition. Something similar may be taking place in the present instance. Cystocarpic plants suffer greater loss by winter decay and damage than tetrasporic plants and may have larger deficiencies to make good in spring before rapid growth can begin.

When the necessary experimental facilities become available it is hoped that these questions will be more completely investigated.

Ecological significance of the results

The results described above are in agreement with the cycle of events observed on the shore, where plants reach their maximum size in late summer, suffer considerable defoliation in autumn and continue to be reduced by damage through the winter. The fact that growth continues to some extent through the winter, although it is usually outweighed by damage, is of significance in determining some of the variations in form of plants in exposed and sheltered habitats, which will be described in another paper.

THE REPRODUCTIVE CYCLES

Tetraspores

Tetraspore production begins early in the year. Plants may be found in February from the older parts of which almost all tetraspores have been shed

but whose younger branches contain immature sporangia. Such plants have been found mainly in the more sheltered localities (such as Porth Penrhyn Mawr, within the Holyhead breakwater). Elsewhere there is little survival of the parts which bore tetraspores in the previous season and the tetrasporic plants found in February contain only immature sporangia. These are generally located in the distal parts of the branches, which are swollen to about twice the diameter of the sterile parts. This is a point of some taxonomic interest (Jones, 1957). No spores are shed naturally from plants brought into the laboratory at this stage. In March mature tetraspores can be found which, in the latter part of the month, are shed (though not as readily as later in the year) and begin division normally. Mature, viable tetraspores are produced continuously in the succeeding spring and summer months, the quantity increasing with the enlargement of the thalli. The maximum production appears to occur in July.

As autumn approaches an increasing number of plants is to be found which have shed most of their tetraspores. Such plants are common in August and, by October, the majority of the spores have been shed. As the loss by wave damage increases, less and less of the summer's tetrasporangial branches are to be found. However, as has been shown, vegetative growth continues into the autumn and early winter and, in the young branches resulting from this growth, some tetraspore production continues. Thus in November and December mature tetraspores may be found in the younger branches where their development causes a local swelling of the distal part of the branches similar to that seen in the early part of the year. Natural shedding and subsequent development of tetraspores has been observed in November from the young branches but the older parts of the thalli which produced spores in the summer do not readily shed any remaining spores after September. The tetraspores produced in the autumn branches form only a small proportion of the total crop. Fig. 2 summarizes the cycle of tetraspore production.

Carpospores

Female gametophytes bearing cystocarps may be found at all times of the year but the proportion of the total population which they constitute varies seasonally. Fig. 3 shows the percentage of plants bearing obvious cystocarps on the boulder beach at Dinas Dinlle. In recording these results the plants were not, as a rule, collected since the removal of samples of 100–150 plants on each visit would quickly destroy the population. Thus no differentiation of tetrasporic and male material was possible and, also, some underestimation of the total number of female plants might be expected in winter, when some plants bore only a few cystocarps which might be overlooked. This also occurred during the occasional rises in the sand level, particularly in the winter when, in general, the female gametophytes have suffered greater decay and damage and, being therefore smaller than the tetrasporophytes, are more

likely to be obscured by the sand, as in the case of the first December value shown in Fig. 3. Nevertheless, the general trend is quite clear: plants bearing cystocarps are scarcest in April; their number increases in May and rises rapidly through the summer, reaching a maximum in autumn. The number

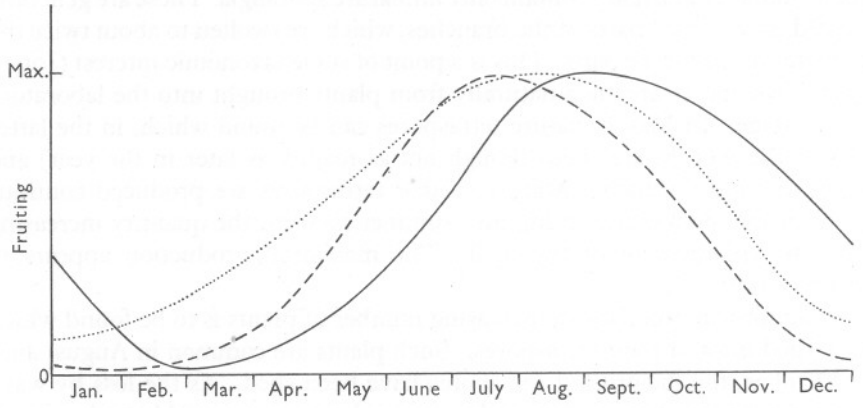

Fig. 2. Diagram of fruiting cycle in *Gracilaria verrucosa* indicating seasonal production of spores and spermatia. —, carpospores; - - -, tetraspores; ....., spermatia.

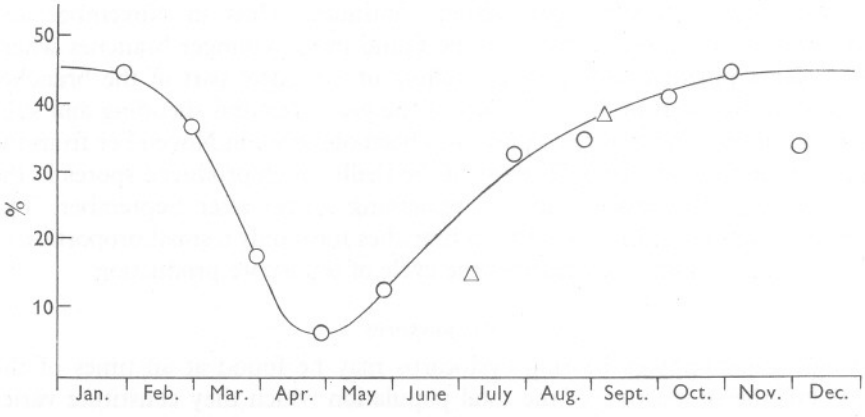

Fig. 3. Percentage of female gametophytes bearing cystocarps in a population of *Gracilaria verrucosa* at Dinas Dinlle. △, 1955; ○, 1956.

remains high until January when a rapid fall begins and continues until the minimum is again reached. Except for a period in spring viable carpospores can be obtained at all times.

It should be pointed out that, although the maximum number of plants bearing cystocarps is found towards the end of November, this is not necessarily the time either of the largest total number of cystocarps or the maximum carpospore production. In fact the plants, in all but the most sheltered places,

are considerably reduced in size by this time and the amount of frondage capable of bearing cystocarps is very much smaller than in July and August. Since the loss by decay and damage generally begins to be noticeable in late August and September, the maximum production of carpospores apparently occurs just before this (Fig. 2).

Comparison of the curves in Figs. 1 and 3 shows that there is a close correlation between the number of plants bearing cystocarps on the shore and the vegetative growth cycle. This is to be expected, for the severe loss of frondage that occurs in late winter and early spring often leaves only the basal parts of the plants and these are not usually fertile. Thus the appearance of cystocarps must await the growth of the new season's branches.

Spermatia

Male plants are very much less common than tetrasporic or female plants, and have not been found in most of the collections made. For this reason the cycle of spermatium production is not as clear.

Male plants have been observed in January, February, March, May and November, while in June and September, when the largest numbers were seen, the active emission of spermatia has been witnessed. The observations suggest a summer maximum of spermatium production, occurring before the carpospore maximum (presumably coinciding with the most active production of mature carpogonia) and a winter minimum, probably in December (Fig. 2).

Discussion

As may be seen from the foregoing, the vegetative growth and fruiting cycles are closely related. The most active production of tetraspores and spermatia takes place during the period of fastest growth, when the bulk of plant material is reaching its maximum. The maximum of carpospore production appears to be later than the others, probably because the production of mature carpospores from a carpogonium, which involves fertilization and the production of a massive gonimoblast 'tissue', requires more time than the development of mature tetraspores or spermatangial sori from a modified cortical cell.

Thus numerous large plants producing immense numbers of tetraspores and carpospores are present on the shore in June, July and August. During this period the calmest weather may be expected in most years in the N. Atlantic (Bigelow & Edmondson, 1947) and conditions for spore settlement should be most favourable.

This work formed part of an autecological study of *G. verrucosa*, carried out at the suggestion of Prof. L. Newton, whose advice and encouragement I am pleased to acknowledge.

SUMMARY

The annual cycles of vegetative growth and reproduction of *Gracilaria verrucosa* are described. The former has been investigated by growing plants on a barge in the Menai Straits. Growth occurs throughout the year, being slow in winter and suddenly increasing in May–June to a higher level. It is suggested that the temperature of the sea water is the most important factor in controlling the growth rate.

The study of the reproductive cycles shows that spore production continues throughout the year, except for a short period in early spring (February–March). The maximum production is in summer, tetraspores in July and carpospores in August–September. Spore production can be closely related to the vegetative growth cycle.

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THE OCCURRENCE OF *MICROCHARON* IN THE PLYMOUTH OFFSHORE BOTTOM FAUNA, WITH DESCRIPTION OF A NEW SPECIES

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(With Text-figures 1–2)

In September 1958, Prof. J. E. Harris, F.R.S., treated freshly collected Eddystone shell gravel with a magnesium sulphate solution and so produced a rich sample of the microfauna. This has never been adequately investigated, though the macrofauna is well known. The animals collected were mostly small Malacostraca, in which Amphipoda predominated, and Prof. Harris kindly passed on to me the whole sample to examine. I have found in it thirty-four species of amphipods, isopods, tanaids and cumaceans of which no fewer than fifteen are additions to the Plymouth fauna list (see Marine Biological Association, 1957). Some indeed are new to British waters, three or four being evidently undescribed species. One of the most striking of these is described here. The collection as a whole will be reported on later.

While the animals were mainly still living, Prof. Harris mentioned having noticed a small narrow pale form of unfamiliar appearance. Occasionally one came into his view revealing possession of fairly long antennae balanced, at the posterior end, by a pair of backwardly directed processes, dilated and more or less parallel-sided. The possible identity remained a puzzle until the preserved sample had been sorted. About twenty-five specimens were eventually picked out. Their body length ranged between 1·0 and 2·8 mm., a size-range that included (above 1·8 mm) mature adults of both sexes. The structure of the pleon and its appendages showed them to be asellote isopods related to *Janira*. But they lacked eyes and pigment and (as shown by the few examples intact in this respect) possessed a most unusual development of the uropod, of which the peduncle was elongate and swollen. From these features they were readily identifiable as belonging to the blind subterranean genus *Microcharon*, as has been confirmed in detail.

THE GENUS *MICROCHARON*

In recent years various small aberrant crustaceans have been discovered living in subterranean ground water and interstitially in wet sand or gravel. Some of these (bathynellids, mystacocarids) belong to whole groups confined to this

phreatic[1] realm, others (*Stenasellus*) are representative of normal freshwater families, or even, like the anthurid *Microcerberus*, of otherwise marine families. *Microcharon* Karaman, 1934, is one of a small group of genera which have such clear affinity to one or other of the marine Janiridae that they may well be included in that family (see Bocquet & Lévi, 1955), though for a time a separate family Microparesellidae was erected for them. The species included in these genera are all small and blind and most of those known to date live in terrestrial underground freshwater habitats of one sort or another.

Microcharon itself was first discovered in the Skopolje district of Macedonia, where four species (*M. stygius*, *M. latus*, *M. profundalis*, *M. major*) are known to date (Karaman, 1933, 1934, 1940, 1954). They occur well up into the mountain areas and subspeciation is already recognizable even within this territory. *M. stygius* has a subspecies *hellenae* in Greece. Another species, *M. acherontis*, is known from ground-water west of the Carpathians (Chappuis, 1944), and another unnamed from Herzegovina (Karaman, 1953). Chappuis & Delamare Deboutteville (1953) have reviewed the genus, adding *M. sisyphus* from ground-water in Corsica, and, of even greater interest, introducing two further species from coastal sand, showing that the genus extends into marine habitats. *M. marinus* was found in three localities on the southern coast of France and on the Italian coast south of Naples. *M. teissieri* (Lévi, 1950, as *Duslenia*) occurred in coarse marine sand dredged just below low-water mark off Roscoff. However, as Bocquet & Lévi (1955) have pointed out, the occurrence in bottom deposits near the coast is not conclusive evidence that the species is truly marine, since its presence may depend on seepages of terrestrial ground water bringing with it its native fauna.

It is therefore of some interest to record a third species from the sea, living in a bottom deposit sufficiently far from the shore and occurring in such a geological setting that contamination with seeping ground-water from the land seems impossible.

Microcharon harrisi sp.nov.

This species is close to *M. teissieri* (Lévi) from coarse sand near Roscoff, as shown by the detailed structure of the mouthparts and other appendages. In particular, the form of male pleopod 1 is identical and pleopod 3 bears three plumed setae. The differences are seen in the larger size of *harrisi*, its relatively more elongate mesosome segments, its very distinctly longer antenna, and its somewhat more elongate pereiopods and uropod. *M. teissieri* has been well described and figured by Lévi (1950) and Chappuis & Delamere Deboutteville (1953). Various details shared in common between the two species are not necessarily repeated below.

[1] A convenient (French phréatique) name for underground waters of all types, ranging from cave pools to interstices between coarse soil particles.

The body length of adults (i.e. length excluding antennules, antennae and uropods) is 1·8–2·8 mm, hence longer than other species except possibly *M. major* Karaman, and between 1·5 and 2·0 times the length of *M. teissieri*. The corresponding mean body width is 0·18–0·28 mm, i.e. one-tenth of the length. (This assumes that no artificial pressure is applied, as by a coverslip on a mounted specimen. Also the loose intercalary connexions of the segments allow about a ±15% expansion or contraction from the mean length.) Middle body segment about 85% the width of the head and pleotelson. See Fig. 1A.

Head subrectangular, somewhat narrowed posteriorly, with mean dorsal length 1·1 to 1·2 times the central width; a short rounded prominence anteriorly between the antennae. No vestiges of eyes.

Pereion segments typically of proportions shown in Fig. 1. Segment 1 about half length of head; segments 4 and 5 may be a little shorter than wide, the rest at least as long as wide, longer in the larger animals. (In *M. teissieri* all segments are described as shorter than wide.) There is a graded narrowing of mean width from both ends towards the middle, but only to an extent of about 10%.

The separate first pleon segment is 0·4 to 0·6 the length of the last pereion segment. The pleotelson is usually about the same length as the head, but is distinctly longer in the larger individuals.

The antennula has five segments. This, with the mandible, maxilla and maxillipede of a 2·10 mm male are shown in Fig. 2. The antenna drawn is that of a 2·05 mm female; this limb is normally 3·2 to 3·4 times the length of the head, hence about twice as long (relatively) as described in *M. teissieri*, and furnishing the most obvious difference from that species (it is longer than the head + the first three mesosome segments). The squama on the third segment bears one or two long setae.

The pereiopods (Fig. 2E) are more elongate than in *M. teissieri*, though the difference is small in the younger adults.

The male pleopods (Fig. 1B, Fig. 2F, G, H) are as described for *M. teissieri* except that in pleopod 2 the distal region is shorter and less acute apically, conforming more nearly to the illustration of this limb in *M. marinus* Chappuis & D. Debouteville. Pleopod 3 (Figs. 1C, 2H) of both sexes bears three stout plumed setae, as does *M. teissieri*, but not any other known species.

The enlarged peduncle (sympode) of the uropod (Fig. 1A, D) seems typically to be close to 1·4 times as long as the pleotelson (1·5 times in one male). This is relatively a little larger than in *M. teissieri*, *M. marinus* and *M. major*, and so is larger than in any of the species yet described. The endopodite is 0·30 to 0·33 the length of the peduncle, and the laterally directed exopodite is about half the length of the endopodite.

Females bear two eggs or young in the mesosomic ventral brood-pouch, as described in other species, and carry them up to the length of at least 0·85 mm (i.e. about half the body length of the mother).

Type locality: North of Eddystone Rock, in shell gravel, below depth of 23–28 fm. The site is 9 miles from the nearest point to the mainland.

Type specimens will be deposited in the British Museum.

Over seventy examples have now been examined. Only eight, however, of these retain one or both uropods, and only twenty-one possess one or other of the antennae. (The most complete specimen, the adult female figured, carried both uropods and one antenna.) The antennae easily break off at the end of the 4th peduncle segment. Other limbs are not readily shed. This liability to lose the uropod and most of the antenna has been noted in other species, though *M. teissieri* is said to be much less liable to damage.

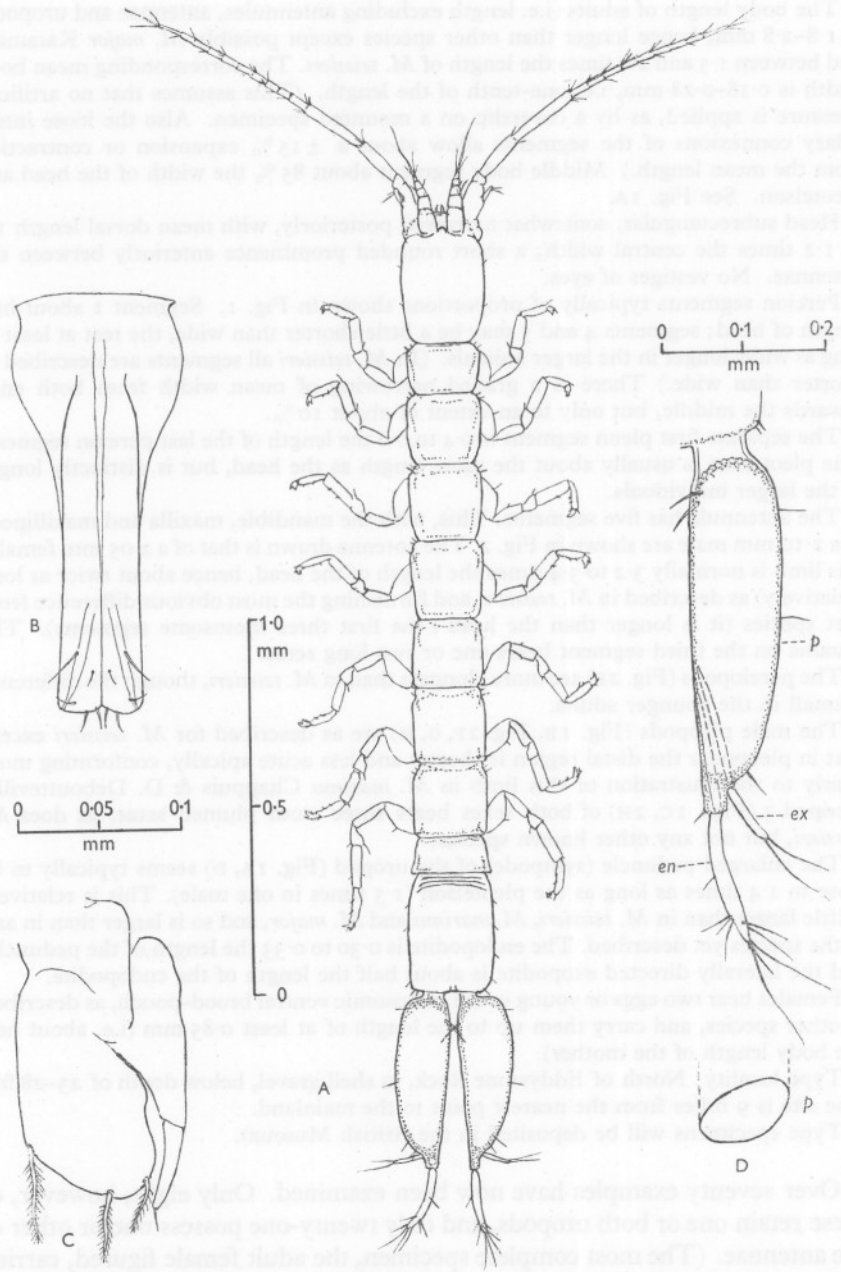

Fig. 1. *Microcharon harrisi* sp.nov. A, adult female of 2·05 mm body length. B, pleopod 1 of male of 2·10 mm. C, pleopod 3 of a female of *ca.* 2·3 mm. D, uropod of male of 2·04 mm, with section through middle given below, to show thickness: *p*, peduncle; *ex*, exopod; *en*, endopod.

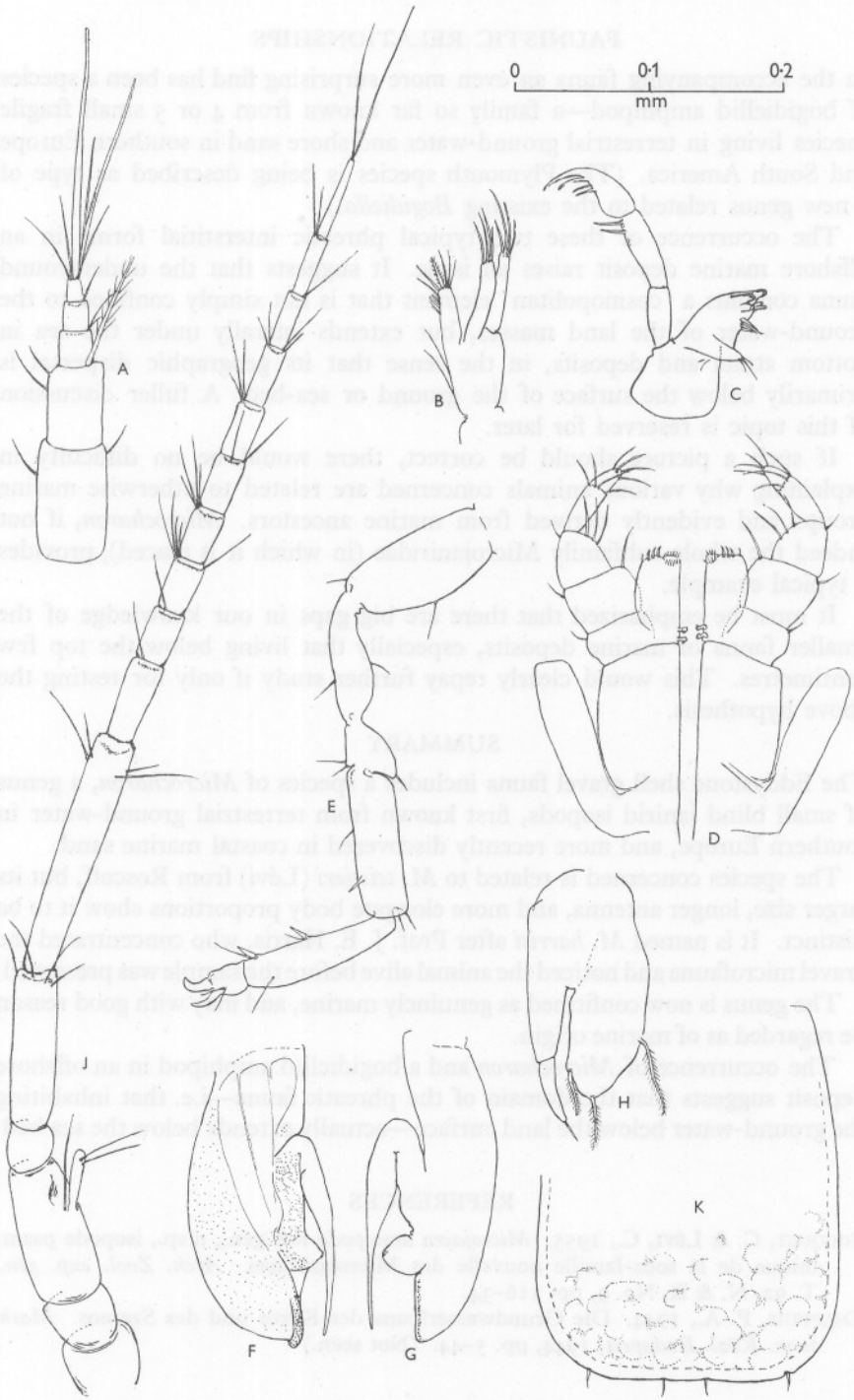

Fig. 2. *Microcharon harrisi* sp.nov. Limbs of male of 2·10 mm: (A) antennula; (B) maxilla; (C) mandible; (D) maxillipede; (E) pereiopod 7; (F, G) pleopod 2, right and left from somewhat different angles; (H) pleopod 3. J, antenna of female of 2·05 mm. K, female operculum (fused pleopod 1 pair).

FAUNISTIC RELATIONSHIPS

In the accompanying fauna an even more surprising find has been a species of bogidiellid amphipod—a family so far known from 4 or 5 small fragile species living in terrestrial ground-water and shore sand in southern Europe and South America. (The Plymouth species is being described as type of a new genus related to the existing *Bogidiella*.)

The occurrence of these two typical phreatic interstitial forms in an offshore marine deposit raises an issue. It suggests that the underground fauna contains a 'cosmopolitan' element that is not simply confined to the ground-water of the land masses, but extends laterally under the sea in bottom strata and deposits, in the sense that its geographic dispersal is primarily below the surface of the ground or sea-bed. A fuller discussion of this topic is reserved for later.

If such a picture should be correct, there would be no difficulty in explaining why various animals concerned are related to otherwise marine groups and evidently derived from marine ancestors. *Microcharon*, if not indeed the whole subfamily Microjaniridae (in which it is placed), provides a typical example.

It must be emphasized that there are big gaps in our knowledge of the smaller fauna of marine deposits, especially that living below the top few centimetres. This would clearly repay further study if only for testing the above hypothesis.

SUMMARY

The Eddystone shell gravel fauna includes a species of *Microcharon*, a genus of small blind janirid isopods, first known from terrestrial ground-water in southern Europe, and more recently discovered in coastal marine sand.

The species concerned is related to *M. teissieri* (Lévi) from Roscoff, but its larger size, longer antenna, and more elongate body proportions show it to be distinct. It is named *M. harrisi* after Prof. J. E. Harris, who concentrated the gravel microfauna and noticed the animal alive before the sample was preserved.

The genus is now confirmed as genuinely marine, and may with good reason be regarded as of marine origin.

The occurrence of *Microcharon* and a bogidiellid amphipod in an offshore deposit suggests that the domain of the phreatic fauna—i.e. that inhabiting the ground-water below the land surface—actually extends below the sea bed.

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THE REPRODUCTION AND LARVAL DEVELOPMENT OF *NEREIS FUCATA* (SAVIGNY)

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From the Plymouth Laboratory

(Text-figures 1–7)

The wide variety of reproductive patterns and behaviour in the many species of Nereidae already studied clearly justifies further research. But the life history of *Nereis fucata* (Savigny) is not only of interest from the comparative point of view. Its commensal habit (it occurs within shells occupied by hermit crabs) immediately gives it a special importance. This alone warrants a detailed study, particularly as no commensal polychaete has yet been reared through to metamorphosis and settlement on its host (Davenport, 1955; Davenport & Hickok, 1957). The numerous interesting problems which arise, and the experimental methods needed to study them, are, however, beyond the range of a paper on nereid development. It is therefore proposed to confine the present account to the reproduction and development up to the time when the larvae settle on the bottom. The complete life cycle, the mechanism of host-adoption, and related topics, will be reported in later papers.

MATERIAL AND METHODS

Many of the shells occupied by hermit crabs in the Plymouth area are also occupied by *Nereis fucata*. It is a large and easily recognized nereid, but a few specimens have been checked against the description given by Fauvel (1923) for this species. Ripe heteronereids were collected from Plymouth trawling grounds during 1955 and 1956. The area extended as far as the Looe Grounds, the Eddystone Inner Channel Grounds, and Bigbury Bay. All were from otter-trawl hauls except a few from the Rame Mud area where an Agassiz trawl was used.

Artificial fertilizations were made in the usual way. Clean oocytes were obtained by partially stripping a female. They were then thoroughly washed in three changes of water. Sperm was produced when a few oocytes were added to a dish containing a ripe male. The time when the oocytes and sperm were mixed has been taken as the time of fertilization. After fertilization the eggs were washed, either by allowing them to sink through a long column of water, or else by three changes of filtered 'outside' sea water. Each culture was divided amongst as many bowls as possible. A few of these were then

kept at laboratory temperature for close study, while the remainder were placed in cold rooms at 11° and 12–13° C. The after-care of the cultures was substantially that described by Just (1922). In the young stages food consisted of *Phaeodactylum* and *Isochrysis* cultures.

At frequent intervals 35 mm photographs were taken of each culture in order to obtain a continuous record of size and the grosser morphological changes (number of setigers, etc.). At less frequent intervals detailed drawings were made with a camera lucida. The very fine details were usually added by eye afterwards. Nicotine was the most useful narcotic for the young ciliated stages, but magnesium chloride was needed as soon as much muscular movement began. Details of the parapodia were obtained from larvae fixed in Bouin and then cut up under a dissecting microscope. Each parapodium was then mounted directly in polyvinyl pyrrolidine and drawn with a camera lucida.

REPRODUCTION

At maturity *Nereis fucata* undergoes a 'complete metamorphosis' (Herpin, 1926) to form a typical heteronereid with an anterior unmodified region and a posterior natatory region. It has been fully described and figured by Fage (1904), and Charrier (1921) has given a detailed account of the internal modifications which take place.

Mature worms from shells housing *Eupagurus bernhardus* were obtained in gradually increasing numbers from March to June in 1956. The numbers then rapidly declined, and in both 1955 and 1956 no mature worms were collected after the middle of June, while two females with degenerating oocytes were obtained on 30 June 1955. Breeding therefore occurs sometime during the period from April to the beginning of June. More detailed information has been difficult to find. There is some evidence to suggest that the main breeding season is between the middle of May and the middle of June, since the percentage of heteronereids dropped from 4 to 0·1% during this period. However there is no record of nereid eggs or larvae in the plankton at this time, although an examination was made of thirty standard hauls taken between 18 April and 28 June from the Looe, Looe-Eddystone and Rame-Eddystone grounds. This suggests that the eggs and larvae are not in the upper layers. On four occasions from 16 to 30 May the early part of the night was spent over the grounds with a submerged light, but no heteronereids were seen. Since this species occurs in 30 fathoms or more it is possible that the swarming and development of the eggs takes place near the bottom. It is presumed that *N. fucata* normally leaves the hermit crab and swarms, as do other nereids, since no spent worms have been collected and because ripe worms swarm readily in the laboratory. Their behaviour is exactly similar to the swarming nereids described by Herpin (1926).

These mature worms are conspicuously coloured as a result of the usual

morphological changes associated with epitoky. The body wall loses its pigment until the white sperm and coloured oocytes are clearly visible, and the vascularization of the parapodia becomes so increased that a red colour predominates. In *N. fucata* the creamy-white pre-natatory region of the male is divided down the middle by the bright red dorsal blood vessel. In the natatory region this order is reversed since the blood vessel disappears leaving a broad white band in the mid-line, bordered on either side by the rose-red parapodia. The female coloration, on the other hand, is much more variable because it is dependent on the colour of the oocytes. In *N. fucata* the females are either lilac, turquoise, or blue. As in the male the parapodia add a pink border down either side of the natatory region.

The sexes are therefore very easy to distinguish and 47% of the heteronereids collected during this period were males. This probably indicates a 1:1 sex ratio. This seems to be the normal ratio for epitokous species since Reish (1954) got a 1:1 ratio in his cultures of *N. grubei*, and Takahasi (1933) reported a 5:4 ratio in *Perinereis nuntia brevicirris*. In some atokous species (e.g. *Nereis diversicolor*) the ratio may be less (Dales, 1950; Bogucki, 1953).

Ripe males were readily stimulated by the presence of a few oocytes, shedding sperm within 30–40 sec. This could be repeated after rinsing the male in clean water, as described by Herpin for *N. irrorata* and *Perinereis marionii*. When both sexes were present ovulation usually occurred after the sperm was shed, but this was less consistent. *Nereis fucata* seems to resemble *N. succinea* closely in this respect (Lillie & Just, 1913, as *N. limbata*). In an aquarium sperm streams from the posterior end, apparently from the anus, but possibly from anal papillae (Defretin, 1949). The oocytes pour from the undersides of the last few segments. Many species shed their eggs through rents in the body wall (e.g. *Platynereis megalops*, Just, 1914; *Nereis grubei*, Reish, 1954).

EMBRYONIC DEVELOPMENT

The mature oocytes rapidly acquire a smooth regular outline when released from the female, and assume a diameter which varies between 200 and 250 μ, the range for any one female being about 20 μ. The average oocyte diameter for this Plymouth population was 225 μ. This is a little on the large side for most epitokous nereids, but compares favourably with the epitokous form of *Perinereis cultrifera*, a worm of approximately similar size (Herpin, 1926). The lilac, blue, or turquoise colour is obtained from numerous small oil droplets which are visible within the oocyte. The range of colour is presumably due to varying proportions of the turquoise and purple pigments distinguished by Green & Dales (1958).

The first indication of a successful fertilization is a separation and a piling up of the eggs on the bottom of the culture dish. This is due to the rapid formation of a gelatinous envelope round each egg. At 15° C it first appears

about 15–30 min after fertilization. The pile of eggs then begins to resemble diminutive frog-spawn, and this resemblance increases during the next $2\frac{1}{2}$ h until each egg is almost 1·5 mm in diameter. A thick non-adhesive envelope is a characteristic feature of those nereids with pelagic larvae. It is not adhesive in *Nereis fucata*. The elevation of the fertilization membrane is quite normal and first appears 1–2 h after fertilization at 15° C.

The embryology of the nereids has been described and figured by E. B. Wilson (1892). More recent workers have shown that all the species closely follow Wilson's description despite differing amounts of yolk in the different species: (compare, for instance, the pelagic eggs of *N. japonica* (150 μ, Izuka, 1908) and the incubated eggs of *N. caudata* (420–520 μ, Reish, 1957)).

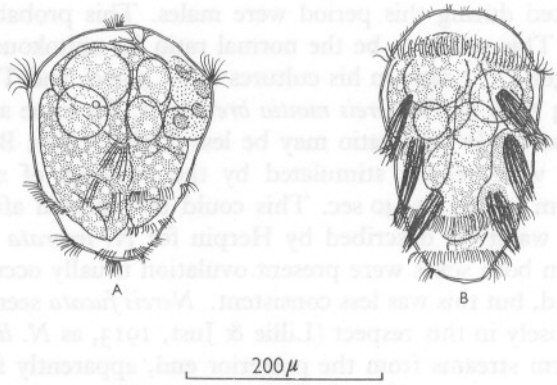

Fig. 1. A: trochophore; lateral view of the right side. Only the margins of the prototroch are shown. B: late trochophore; dorsal view.

In *N. fucata* the first cleavage occurs $4\frac{1}{2}$–5 h after fertilization at room temperature, and is closely followed by the second and third (6–7 h). Epibolic gastrulation proceeds in the normal way, and after about 12 h can be easily seen, since the small micromeres form a colourless cap of cells on top of the large coloured macromeres. By the end of the first day gastrulation is complete and sufficient cells have been formed to give a smooth regular outline to the embryo. With the further multiplication of cells the embryos continue to gain in compactness and regularity, but they remain more or less spherical with the fertilization membrane still standing out from the surface in places. Spasmodic rotation usually begins after about 33 h, although cilia cannot be seen. The prototroch first becomes visible some 3 h later, when the embryos are actively rotating. It is almost complete on the second day, and its cilia are large and conspicuous by the end of 3 days when the embryos have developed into monotrochophores. The typical shape has been achieved by an elongation of the body and some slight local swelling equatorially at the base of the prototroch.

During the next 24 h the larvae develop into complex and highly motile trochophores (Fig. 1A). The increase in motility is most marked and is derived from additional ciliary bands, especially the ventro-lateral paratrochs. In some larvae a band of pigment is formed at the base of the prototroch. Internally, continued differentiation has produced longitudinal muscles, shown by an occasional muscle twitch, and six pairs of setal bundles are clearly visible (Fig. 1B). It seems very probable that in nature hatching normally takes place at this stage, since it did so in all cultures kept between 11° and 13° C. In these cultures, hatching is only prevented by the presence of the gelatinous envelope. This disappears 4–6 days after fertilization irrespective of temperature so that larvae reared at 11° C hatch at an earlier stage (trochophores) than those reared at 15° C (3-setigers). As hatching is therefore not directly dependent on temperature or development, a comparison with other nereids is difficult. In general terms, however, *N. fucata* corresponds with other epitokous forms in having a shorter embryonic period than the atokous forms.

LARVAL DEVELOPMENT

Although swimming persists, the next stage (Fig. 2A) is characterized by the presence of long setae. These are highly mobile and each setiger is composed of noto- and neuropodial bundles. In *N. fucata* (at 15° C) their emergence occurs about 5 days after fertilization. This is rather later than in many species (e.g. 30 h in *N. irrorata*, see Herpin, 1926), but resembles *N. pelagica* ($4\frac{1}{2}$–5 days), which was also reared at Plymouth (D. P. Wilson, 1932). In *N. fucata* all three setigers are formed at about the same time, although the second may appear first, followed closely by the first and third. This order, however, is apparently determined only by the length of the setae in each setiger, which is in contrast to some species where there is a definite time lag before the formation of the third setiger (e.g. 20 h in *N. succinea* and *Platynereis megalops*, see E. B. Wilson, 1892).

At first these larvae are simply setigerous larvae (Fig. 2A), but during the next few days a gradual change takes place to form young 3-setiger worms (7 or 8 days at 15° C). Externally the features (Fig. 2B, C) which are most responsible for this change are: an increase in length, emphasized by the development of a pair of very small anal cirri; and, perhaps most characteristic, the formation of distinct parapodia, beginning as small lobes between the noto- and neuropodial bundles of setae. The rudiments of the cephalic appendages, each bearing sensory hairs (E. B. Wilson, 1892), then become prominent at about daily intervals. The anterior tentacular cirri are the first to appear, followed by the antennae, and, towards the end of this stage, a pair of small pimples on either side of the mouth which represent the future palps (they lie immediately beneath the prototroch in Fig. 2C). Two irregularly shaped patches of pigment are also often formed ventro-laterally on

either side of the head. These, however, are very variable and some larvae may not have them. Internally, blocks of tissue appear representing the proboscis, the large yolk-filled mid-gut, and the hind-gut.

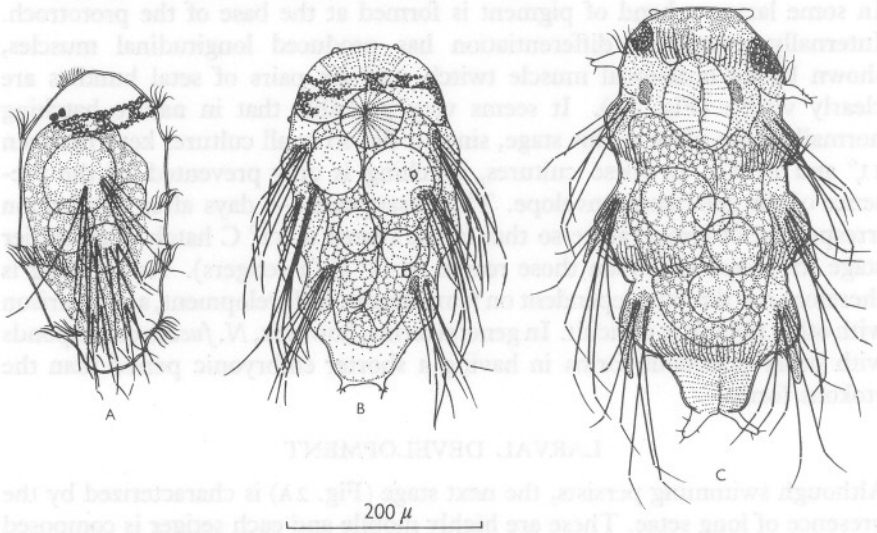

Fig. 2. A: setigerous larva; lateral view of right side. Only the margins of the prototroch are shown. B: early 3-setiger larva; ventral view. No cilia were seen in this specimen. C: 3-setiger larva; ventral view.

The growth rate now becomes a little more variable, and the cultures begin to contain larvae at different stages. At 15° C the fourth setiger is formed some time between 6 and 11 days after fertilization, while at 11° C it appears at 15–23 days. At first only a few setae project, but these rapidly increase in length and number (Fig. 3A). The cephalic appendages, the anal cirri, and all the parapodial lobes continue to grow in size. As in *Nereis pelagica* (see D. P. Wilson, 1932) and *N. costae* (see Durchon, 1956), the minute jaws become visible at this stage, and the gut, especially the proboscis and hind-gut, become more differentiated. In the 5-setiger stage (Fig. 3B), which occurs at about 2 weeks at 15° C and at about 3 weeks at 11° C, this process of elaboration continues. The setae are now very long and all the parapodia bear distinct noto- and neuropodial lobes with ventral cirri on the second to the fifth. In addition, the jaws and the proboscis can be everted and the gut is sufficiently formed for the larvae to swallow food, although yolk reserves are still present in the mid-gut. The cilia remain very active, but their disappearance has begun with the division of the prototroch into two lateral bands.

The appearance of the sixth setiger, which occurs at about 18 days, marks the beginning of the end of the larval period. By the time another setiger has been formed (at 26 days) the larvae have become juveniles and have commenced a crawling life upon the bottom (Fig. 4). Associated with this change

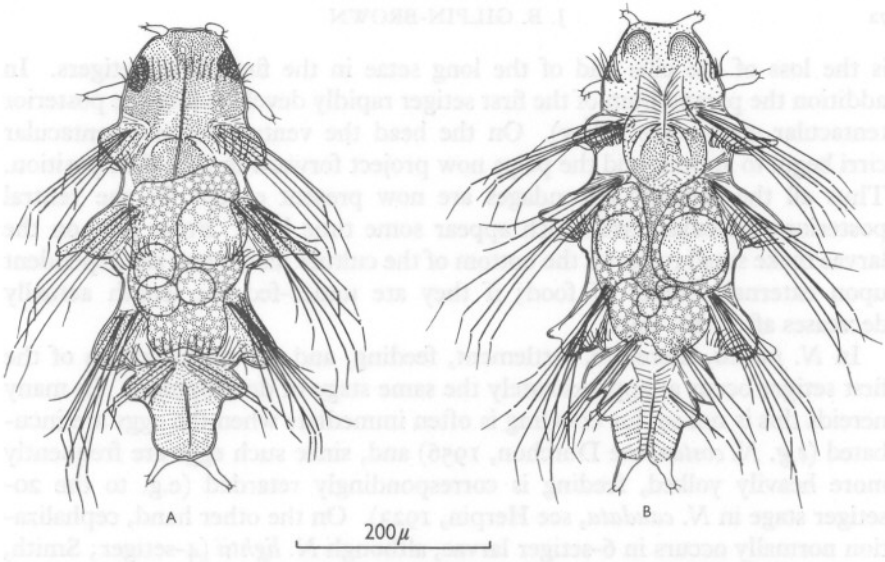

Fig. 3. A: 4-setiger larva; ventral view. B: 5-setiger larva; ventral view.

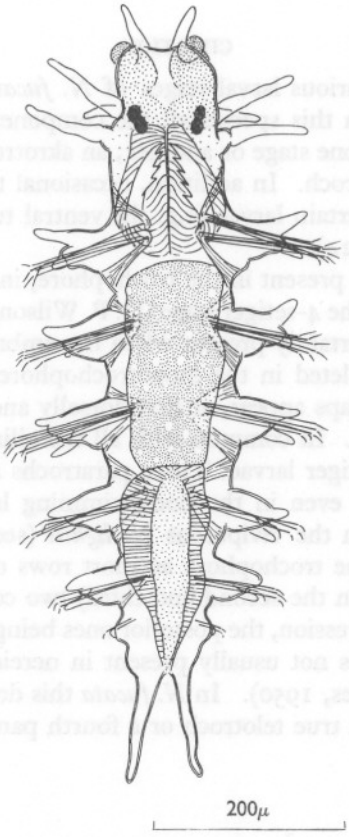

Fig. 4. 6-setiger (7-segmented) larva; dorsal view.

is the loss of the cilia and of the long setae in the first three setigers. In addition the parapodium of the first setiger rapidly develops into the posterior tentacular cirrus (see below). On the head the ventral anterior tentacular cirri begin to appear, and the palps now project forward in the adult position. Thus all the cephalic appendages are now present except for the ventral posterior tentacular cirri which appear some time later. From now on the larvae make small tubes on the bottom of the culture dishes and are dependent upon external sources of food; if they are under-fed the length actually decreases after this stage.

In *N. fucata*, therefore, settlement, feeding, and the cephalization of the first setiger occur at approximately the same stage of development. In many nereids this is not so, for crawling is often immediate when the eggs are incubated (*e.g. N. costae*, see Durchon, 1956) and, since such eggs are frequently more heavily yolked, feeding is correspondingly retarded (e.g. to the 20-setiger stage in *N. caudata*, see Herpin, 1923). On the other hand, cephalization normally occurs in 6-setiger larvae, although *N. lightii* (4-setiger; Smith, 1950) and *N. diversicolor* (9-setiger; Dales, 1950) are exceptions.

CILIATION

The ciliation of the various larval stages of *N. fucata* is set out diagrammatically in Fig. 5. In this species all the components of the basic nereid pattern are present at one stage or another; an akrotroch, a prototroch, three paratrochs, and a telotroch. In addition, occasional tufts of cilia may occur in other positions in certain larvae (e.g. the ventral tuft immediately behind the prototroch in Fig. 2A).

An akrotroch is only present in the trochophore, in contrast to *N. pelagica* where it remains until the 4-setiger stage (D. P. Wilson, 1932). An incomplete prototroch is almost certainly present when the embryos are rotating, but it is probably only completed in the monotrochophore. It then persists as a complete girdle until gaps appear, at first dorsally and then ventrally, in the 5-setiger stage (Fig. 5). In common with all the ciliary bands it disappears completely in the 6-setiger larvae. Three paratrochs are a regular feature in nereids, being present even in the non-swimming larvae of *N. costae* (see Durchon, 1956) and in the viviparous *N. lightii* (see Smith, 1950). In *N. fucata* they begin in the trochophore as short rows of cilia (Fig. 1A) which then join up to form (in the second and third) two complete rings. There is then a fairly steady regression, the posterior ones being a little more persistent (Fig. 5). A telotroch is not usually present in nereids, though it occurs in *N. diversicolor* (see Dales, 1950). In *N. fucata* this does not last long enough to show whether it is a true telotroch or a fourth paratroch.

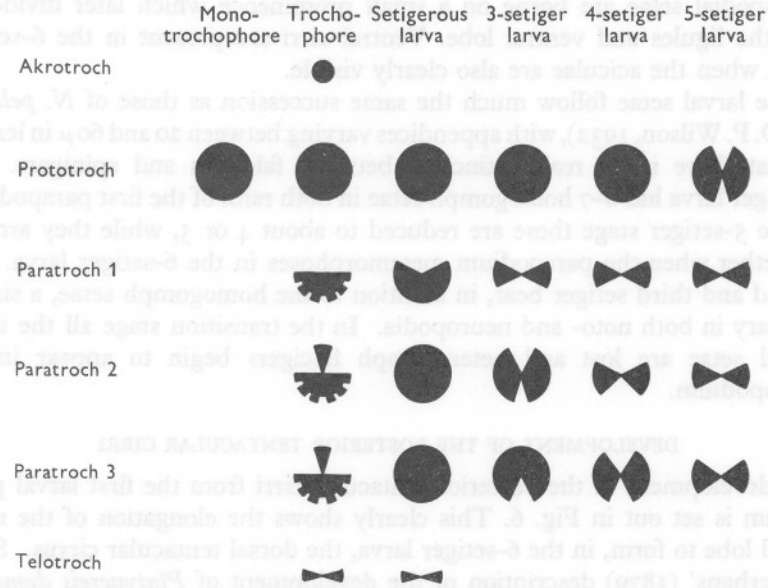

Fig. 5. Diagram of the larval ciliation. The black segments show the extent of each ciliary band at the various larval stages.

COLOUR

Pigment first appears in small patches around the prototroch (Fig. 2A, B). In the 3-setiger stage it has disappeared, but the majority of the larvae have two reddish patches ventro-laterally on either side of the head (Figs. 2C, 3A), which begin to diminish at the 5-setiger stage. The larvae are practically colourless at seven setigers. Irregularly shaped patches of pigment on the head are fairly common in this family. E. B. Wilson (1892) reported them first in the 3-setiger stage of *N. succinea*, where they were derived from the equatorial band of the trochophore. They are also present in the epitokous form of *Perinereis cultrifera* (see Herpin, 1926) and in some 3-setiger larvae of *Nereis pelagica* (see D. P. Wilson, 1932). They are not confined to the epitokous forms since they have also been reported in the 4-setiger larvae of both *N. costae* (see Durchon, 1956) and, occasionally, *N. diversicolor* (see Dales, 1950).

PARAPODIA AND SETAE

The early stages in the formation of the parapodia are very similar to those described and figured by Finke (1936) for *N. diversicolor*. A very small lobe between the noto- and neuropodial setae first appears in the setigerous trochophore. During the succeeding stages this increases in length and forms the notopodial lobe in the first two adult parapodia. In the 3-setiger stage the

neuropodial setae are borne on a small prominence which later divides to give the ligules and ventral lobe. Ventral cirri are present in the 6-setiger larva, when the aciculae are also clearly visible.

The larval setae follow much the same succession as those of *N. pelagica* (see D. P. Wilson, 1932), with appendices varying between 20 and 60 μ in length, so that there is no real distinction between falcigers and spinigers. The 3-setiger larva has 6–7 homogomph setae in both rami of the first parapodium. In the 5-setiger stage these are reduced to about 4 or 5, while they are lost altogether when the parapodium metamorphoses in the 6-setiger larva. The second and third setiger bear, in addition to the homogomph setae, a simple capillary in both noto- and neuropodia. In the transition stage all the notopodial setae are lost and heterogomph falcigers begin to appear in the neuropodium.

DEVELOPMENT OF THE POSTERIOR TENTACULAR CIRRI

The development of the posterior tentacular cirri from the first larval parapodium is set out in Fig. 6. This clearly shows the elongation of the notopodial lobe to form, in the 6-setiger larva, the dorsal tentacular cirrus. Since Langerhans' (1879) description of the development of *Platynereis dumerilii*, it is usually assumed that these cirri are derived from the dorsal and ventral cirri of the first parapodium. In *Nereis fucata*, however, this is not strictly true, for it can be seen that the dorsal tentacular cirrus develops from a lobe which is inferior to the notopodial setae at a time when the parapodium has no dorsal cirrus. *N. fucata* therefore agrees with *N. pelagica* in which the dorsal tentacular cirrus is derived from the middle lobe of the parapodium (D. P. Wilson, 1932). It probably also agrees with *N. diversicolor* (see Finke, 1936), and may further agree with *N. vexillosa* (see Johnson, 1943), *N. grubei* (see Reish, 1954), *N. succinea* (see Banse, 1954), and *N. lightii* (see Smith, 1950), since the derivation of this cirrus is not considered in detail. Many other species, however, resemble *Platynereis dumerilii* (see Hempelmann, 1911), where this cirrus is formed from the dorsal cirrus of the first parapodium (e.g. *Nereis caudata*, see Herpin, 1926; *N. costae*, see Durchon, 1956; *Perinereis marionii*, see Herpin, 1926; and *Micronereis variegata*, see Rullier, 1954). E. B. Wilson (1892), on the other hand, records that in *Platynereis megalops* and *Nereis succinea* the first parapodium never carries parapodial cirri.

GROWTH OF THE LARVAE

Although weight would be the best indication of growth and growth rates, its measurement is difficult and it has not been used for larval nereids. Length is more practical and provides a reasonable indication. It has been widely used, and the figures given by Bogucki (1953) for *N. diversicolor* give the usual sigmoid growth curve. In the same species Dales (1950) has shown that in the

early stages (0–9 weeks) length increases at a constant rate of 0·04277% per day. It will be seen from the graph (Fig. 7) that in the young stages of *N. fucata* the increase in length occurs at two speeds; an initial high rate during the first week, followed by a much slower one (Table 1). The length measured excludes appendages.

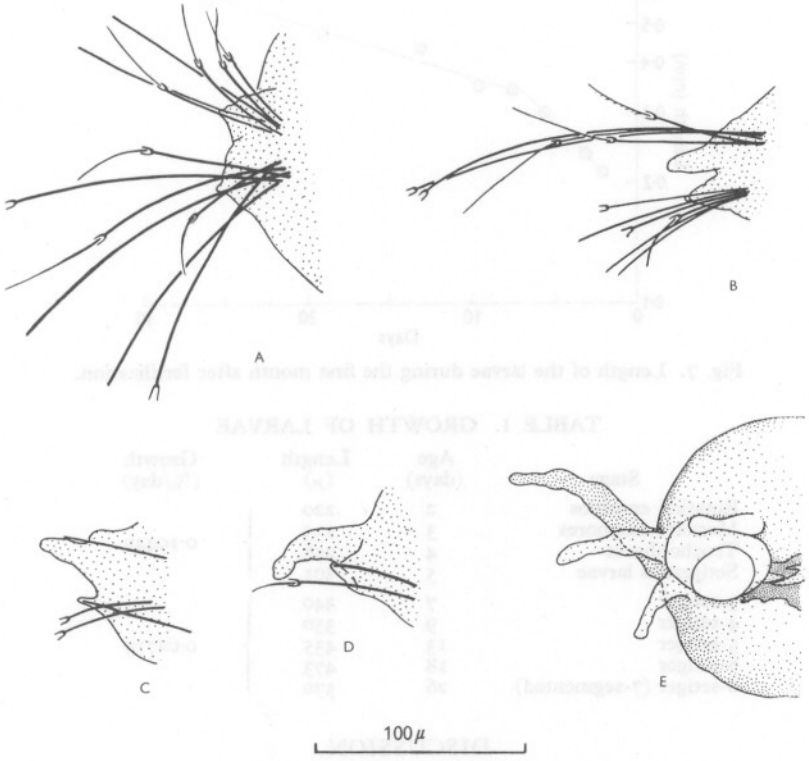

Fig. 6. Stages in the cephalization of the first parapodium. A: 3-setiger larva. B: 4½-setiger larva. C: 6-setiger larva, setae falling out. D: 6-setiger larva; elongation of the notopodial lobe. E: 6-setiger larva; frontal view after cephalization is complete.

The formation of segments is a natural and simple method of following development and has been recorded in most species. The figures for *N. fucata* are also given in the table and are in broad agreement with other species, though a close comparison is difficult. Segment-formation cannot be a strict measure of growth since it is always positive and may cease at a relatively early stage. Thus in *N. grubei* the production of segments stops when 8–85% of the final weight has been reached (Reish, 1954). In agreement with the high positive correlation between length and segments in the young larvae of *N. diversicolor* found by Dales (1950), their curves are a close fit, at least in the early stages. It seems likely that this similarity only holds good while the

embryonic yolk reserves last. The figures provided by Hempelmann (1911) for individual 'nereidogene' larvae of *Platynereis dumerilii* (since referred to *P. massiliensis* by Hauenschild, 1951) confirm this, for they show that after this stage the rate of segment formation varies considerably.

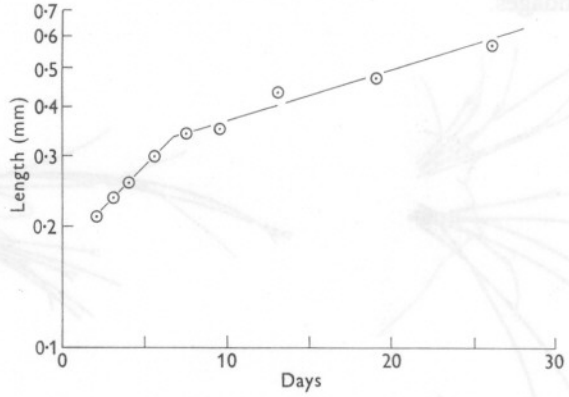

Fig. 7. Length of the larvae during the first month after fertilization.

TABLE 1. GROWTH OF LARVAE

Stage	Age (days)	Length (μ)	Growth (%/day)
Rotating embryos	2	220	
Monotrochophores	3	235	0·10449
Trochophores	4	256	
Setigerous larvae	5	301	
3-setiger	7	340	
4-setiger	9	350	
5-setiger	13	435	0·02719
6-setiger	18	473	
6-setiger (7-segmented)	26	570	

DISCUSSION

The development described in this paper refers to worms kept and reared in the laboratory. There must remain, therefore, some uncertainty about their behaviour and development under natural conditions. The rate of development is probably by far the most variable character and will presumably be mainly determined by temperature. The larvae are probably near the bottom, where the temperature will increase from about 9° C in May to about 12° C in July. It follows that the record of larvae reared at 11° C will give the best indication of their normal rate of development; but this remains a very rough approximation. This inaccuracy is further increased since, after settlement, growth will be closely linked with the availability of their natural food; and this, and its effects, are completely unknown. However, subject to these limitations the reproduction and early life history of *N. fucata* at Plymouth is probably as follows.

As no free-living population of this commensal is known (reports probably refer to the occasional single specimen, e.g. Hornell, 1891), the species may be presumed to come to maturity slowly, because only some 10% of the worms collected were mature. At maturity the development of the definitive heteronereid characters takes place while the worms are still within the shells of the host crabs. Then, probably in the month beginning in the middle of May, these brilliantly coloured worms come out of their shells to swarm in a normal nereid manner, perhaps just off the bottom. It is not known whether this is periodic or not, but some synchronization mechanism would seem necessary. The actual spawning and fertilization mechanism is again the same as in other epitokous species. Blue, lilac, or turquoise eggs are produced which, when fertilized, have the usual thick gelatinous envelope. The embryonic development is normal and highly motile larvae, with abundant cilia, are formed. These may swim around on or near the bottom, finally settling on to it when six setigers have been developed. The behaviour of the young worms in the laboratory strongly suggests that, some 4–6 weeks after fertilization, they will be living and feeding on the bottom within small tubes they have constructed. Their precise habitat, if they have one, is unknown. Young *N. fucata* have been recorded from Rame Mud, after sieving through stramin netting (Mare, 1942), but attempts to repeat this have been unsuccessful. However, McIntosh (1910) records them from *Filograna* and from stones and shells in deep water, so that they appear fairly widely distributed.

The reproduction and larval development is therefore very similar to the other members of the family. In particular, the feeding and tube-building habit is quite normal. Up to this stage, therefore, no special adaptation to commensalism can be seen. The young probably settle on the bottom first and enter hermit crab shells later. Davenport (1955) has discussed this problem of settlement in commensal polychaetes and has suggested that the young stages may first settle on the same substrate as their hosts. This would increase their chances of finding a host, and the development of a specific host reaction would then quickly lead to its adoption. *N. fucata* therefore fits the first part of this hypothesis very well, although it is not known if there is a preference for a particular substrate. This can only be determined by further experiments, but it seems possible that a high degree of selection may not be necessary for such motile and widespread hosts. The next problem is to determine the specific reaction which ensures the adoption of the host. Preliminary experiments suggest that in this respect *N. fucata* also fits Davenport's hypothesis.

It is a pleasure to record my gratitude not only to the Director and all his staff at the Plymouth Laboratory for their generous help during the course of this work, but also to the Council of the British Association for allowing me the use of their table. My thanks are due in particular to Mr P. G. Corbin

for first drawing my attention to the mature heteronereids, to Dr M. W. Parke for supplying the *Isochrysis* and *Phaeodactylum* cultures, to Mr A. C. G. Best for the use of his polyvinyl pyrrolidine mountant, and to Mr G. R. Forster for so willingly taking me over the grounds at night in his yacht 'Sunset'.

SUMMARY

The reproduction and larval development of *Nereis fucata* (Savigny) is described up to the time of settlement (6- to 7-setigers).

Mature heteronereids are found at Plymouth from March to June, in a 1:1 sex ratio. In an aquarium the spawning mechanism is similar to other species.

The embryonic development is typical of an epitokous species with pelagic development. The eggs, whose mean diameter was 225 μ, are lilac, blue, or turquoise in colour. Cleavage and gastrulation are normal. Rotation begins at 36 h and monotrochophores are formed after 3 days. Hatching probably occurs 4–6 days after fertilization when a highly motile trochophore has developed.

The setae of the first three segments appear after about 5 days. The differentiation of the parapodia, and the larval succession of setae, are essentially the same as in other species.

Settlement, the cephalization of the first parapodium, the loss of the cilia and the long larval setae, all take place between 6- and 7-setigers. After this stage the larvae construct small tubes and feed on the bottom.

The development of the dorsal posterior tentacular cirrus from the first larval parapodium is described and figured. This cirrus is formed by the elongation of the lobe lying between the noto- and neuropodial setal bundles. It is not, therefore, strictly derived from the dorsal cirrus of the first parapodium.

The reproduction and development is discussed and shown to be very similar to that of the other members of the family. No special commensal adaptation was observed during the larval period. It is therefore concluded that this occurs after settlement.

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CARBOHYDRATE LEVELS IN *PATELLA*

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(With Text-figs. 1–9)

The limited observations available on blood sugar levels of Mollusca suggest that they are very low. Values of 2–14 mg % glucose have been reported for *Aplysia* (see Kisch, 1929; Berthoumeyroux, 1935), and even the higher levels recorded for *Octopus* and *Sepia* species by Bierry & Giaja (1909), Berthoumeyroux (1935) and Derrien (1938) range only from 20 to 32 mg % glucose. The majority of these blood sugar analyses were based on the Hagedorn & Jensen (1923) technique. Landgrebe & Munday (1954) have shown that this technique may have an inherent blank error of 5 mg % glucose equivalent, and consequently it is not a suitable method for critical analyses of these low molluscan blood sugar levels.

Seasonal analyses of molluscan blood sugar levels have been restricted to the terrestrial *Helix pomatia* L. From monthly analyses, Schwarz (1935) could not detect any definite seasonal variation, beyond a possible increase before and at the end of hibernation. Wolf-Heidegger (1935) obtained higher mean blood sugar values (22 mg %) for summer as compared with hibernating *Helix* (11 mg %), but this seasonal difference was not confirmed by the investigations of Lustig, Ernst & Reuss (1937) and Holtz & von Brand (1940). It was desirable to extend these seasonal investigations to other Mollusca, using a method particularly suitable for small blood samples and low concentrations of glucose. The marine gastropod *Patella* was selected for these studies.

Rather more investigations have been carried out on polysaccharide reserves in Mollusca. Seasonal variation in the glycogen reserves of *Ostrea* species has been demonstrated by Mitchell (1915–16), Russell (1923) and Okazaki & Kobayashi (1929). From analyses of the individual tissues of *Gryphaea angulata* Lamk., Couteaux-Bargeton (1947) concluded that glycogen is used both during the overwintering period and in the formation of sexual products. The dual role of polysaccharides has been most clearly demonstrated in *Helix pomatia* (see von Brand, 1931; May, 1934), in which the two polysaccharides, glycogen and galactogen, have concentration maxima at different periods of the year. Glycogen is apparently used in the maintenance of metabolism

during hibernation, with a maximum concentration at the beginning of this period. Galactogen, which is restricted to the albumen gland, forms the main polysaccharide reserve of the eggs, and has a maximum concentration at the onset of egg-laying.

The work reported in this paper records the seasonal levels of blood glucose in *Patella* paralleled by tissue glycogen concentrations. In addition, starvation effects on these carbohydrate levels have been established under laboratory conditions, and the effects of glucose administration on blood glucose concentration studied.

We wish to thank the Department of Scientific and Industrial Research for financial assistance to R.J.C.B. and thanks are also due to Dr B. J. R. Taylor for assistance in some field collections.

MATERIALS AND METHODS

Patella, used in these studies, occurred as a sheltered population between two natural rock barriers, which project southwards into the sea at Pevril Point, Swanage. For laboratory investigation they were transported packed in sea-weed and then maintained under starvation conditions in sea-water aquaria. Under these conditions, *Patella* readily re-attached themselves to a rocky substrate and could be maintained in a healthy condition for several months; the maximum period of survival recorded being 11 months.

In blood sampling, the head was pushed gently to the back of the head cavity, which was dried out with cotton-wool. Uncontaminated blood was withdrawn into a hypodermic syringe from the large vessel, which runs from the pallial vessel dorsally into the heart (Fig. 1). In the field, sampling was completed within 2 min of prising the limpet from its substrate. The blood was immediately mixed with tungstic acid protein precipitant and the deproteinised supernatant analysed on return to the laboratory.

The blood total reducing value, taken as an estimate of the blood glucose concentration, was determined by Landgrebe & Munday's (1954) modification of the Folin & Malmros (1929) technique. Duplicate analyses of 0·5 ml. *Patella* blood in 5 ml. tungstic acid gave values agreeing within 0·4 mg % glucose equivalent, confirming the suitability of the technique at these low levels.

Tissue glycogen concentrations were estimated by the Good, Kramer & Somogyi (1933) technique, the glycogen hydrolysate having been chromatographically identified as glucose. Tissues dissected from the living animal were weighed and immersed in hot KOH solution within 10 min of removing the animal from its shell. A homogeneous solution was obtained within 45 min of heating in a boiling water-bath, using a maximum of 200 mg wet weight of tissue per ml. 30 % KOH. The alcohol-precipitated glycogen was redissolved

in 2 ml. 15% KOH and reprecipitated by adding 2 ml. absolute alcohol. After acid hydrolysis, the total reducing value was determined by the Landgrebe & Munday (1954) technique. Glycogen concentrations were expressed as % wet weight; that is, the weight of reducing substances, as g glucose, resulting from hydrolysis of the glycogen present in 100 g wet weight of tissue (glycogen as g glucose/100 g tissue).

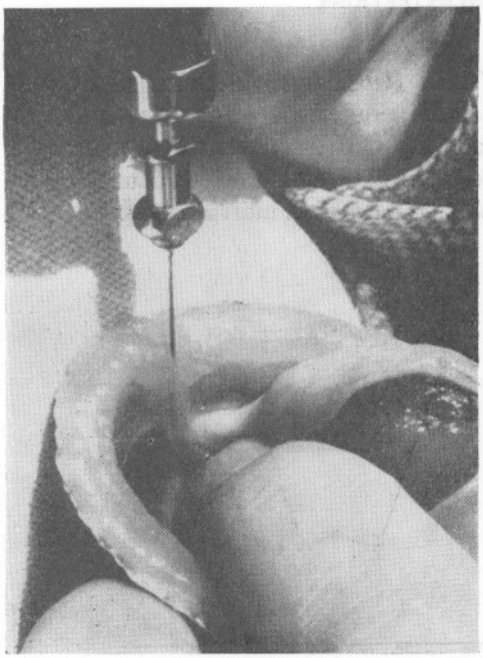

Fig. 1

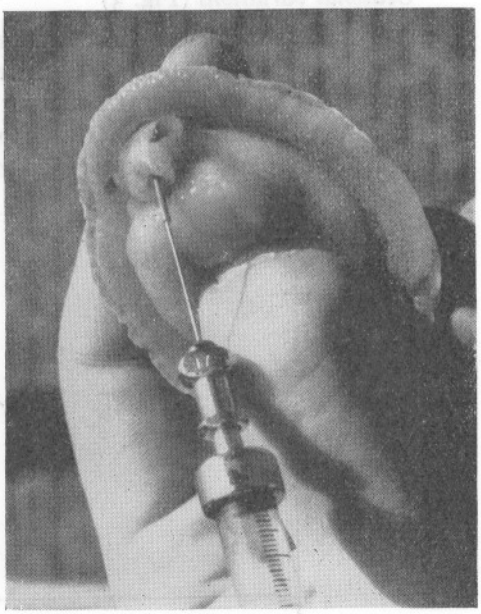

Fig. 2

Fig. 1. Methods of taking blood samples from *Patella*, showing the hypodermic needle in the vessel which runs dorsally from the pallial vessel into the heart.

Fig. 2. Method of oral administration of glucose solutions, after the tube has been passed down the gut into the stomach of *Patella*.

Glucose was administered intravascularly and orally. Glucose solutions were injected into the visceral sinus through the foot medianly from the ventral side. Oral glucose was administered by plastic tube (external diameter 1 mm and length 3 cm) passed over the buccal mass down the gut into the stomach (Fig. 2).

The three species of *Patella* present on the Swanage coast are not readily identified from their external characteristics, because of the considerable intergrading between species (Evans, 1953). Examination of the pleuricuspid teeth of a sample of *Patella* confirmed Evans's observation that *P. vulgata* L.

was the commonest species in sheltered habitats, such as exist at Pevril Point. All *Patella* used were of the same external appearance. Although most specimens were probably *P. vulgata*, this investigation has been assigned to the genus *Patella*, rather than to any one species.

RESULTS

BLOOD GLUCOSE CONCENTRATIONS

Seasonal variations (Fig. 3)

The blood glucose concentrations of field *Patella* were determined by analyses of blood samples taken in the field between February 1954 and July 1955. Limpets were taken from the full range of their vertical distribution and from different vertical faces of exposed rocks. No correlation was detected between the blood glucose level and the ecological position of individual *Patella*.

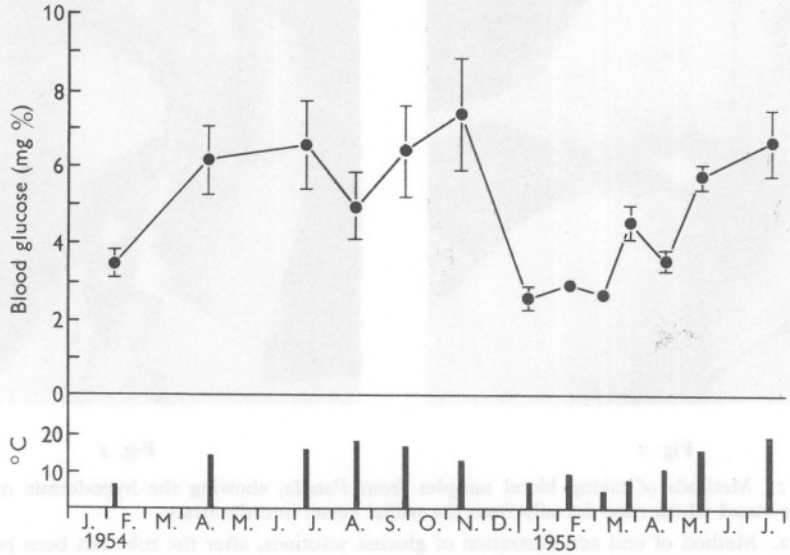

Fig. 3. Seasonal variation in blood glucose concentration of field *Patella*, showing the mean ± standard error of each series of analyses (10 individuals) and the sea temperature (shown below) at the time of blood sampling.

Between May and November, called the summer period, the mean glucose concentrations approximated to 6 mg % glucose. The means, with their standard errors, ranged from $4{\cdot}9 \pm 0{\cdot}85$ mg % to $7{\cdot}3 \pm 1{\cdot}45$ mg %, but this variation between means was not significant, because of the wide range of individual values in each series of analyses. A single very high value often accentuated the wide range in any particular series, the highest value recorded being 18·0 mg %. Between November and January, the mean blood glucose

concentration decreased to the relatively low level of $2{\cdot}5 \pm 0{\cdot}29$ mg %. This low level persisted from January to the early part of March, with means ranging from $2{\cdot}5 \pm 0{\cdot}29$ mg % to $2{\cdot}9 \pm 0{\cdot}12$ mg %. This winter period was also characterized by the narrow range of individual values in each series of samples. The late-March and April series in 1955 gave values intermediate between the low winter level and the higher summer level, the latter having been re-attained in the May limpets (mean $5{\cdot}7 \pm 0{\cdot}30$ mg %).

The results indicate a definite seasonal variation of the blood glucose concentrations of *Patella* in their natural environment, the very variable summer values contrasting with the low relatively constant winter values.

Effect of starvation (Fig. 4)

Patella were maintained under starvation conditions in laboratory sea-water aquaria at a temperature similar to that occurring in the natural environment. In July 1954 the individual *Patella* sampled in the field (sea temperature 17° C) were brought into the laboratory and starved in sea-water aquaria at 17° C. After 4 days starvation, a second series of blood samples from these individual *Patella* was analysed. The mean blood glucose level of eight field *Patella* was $6{\cdot}5 \pm 0{\cdot}84$ mg %, with a range of 3·1–13·8 mg %. After 4 days starvation the mean blood glucose level had decreased to $4{\cdot}9 \pm 0{\cdot}14$ mg % and the range narrowed to 4·2–5·6 mg %. This latter level approximated to the lower values recorded in the July field samples. After this initial starvation effect, the blood glucose concentration decreased more gradually up to 40 days starvation (Fig. 4). Similar results were obtained with *Patella* collected in November.

The lower and more constant blood glucose concentrations of starved *Patella* suggest that the relatively high concentrations of some individual field *Patella* result from an alimentary hyperglycemia. On this hypothesis, the wide range of individual field values results from differences in the degree of this hyperglycemia and the lower values of starved *Patella* represent a post-absorptive blood glucose level.

During the winter period, the low and relatively constant glucose concentrations of field *Patella* suggest that they do not feed during this period. This was supported by starvation experiments, in which January *Patella* were maintained in sea-water aquaria at the field sea temperature of 6° C. After 11 days starvation, the mean blood glucose concentration was $2{\cdot}9 \pm 0{\cdot}24$ mg %, as compared with $2{\cdot}5 \pm 0{\cdot}29$ mg % for the field analyses. In contrast to the summer *Patella*, the blood glucose had not decreased on starvation, indicating that it was already at a basal level in field *Patella* during the winter period. That the blood glucose concentration of January field *Patella* collected at 6° C could decrease was shown by raising the aquarium temperature to 17° C. From a mean field value of $2{\cdot}5 \pm 0{\cdot}29$ at 6° C, the mean blood glucose concentration after 5 days starvation at 17° C was $1{\cdot}9 \pm 0{\cdot}36$ mg %, and after

17 days starvation at 17° C 1·6 ± 0·13 mg %. The higher aquarium temperature at which these January field *Patella* were maintained may have caused an increased utilization of available carbohydrate. The results suggest that the disappearance of glucose from January starved *Patella* is temperature dependent.

Yeast fermentation experiments suggested that the true blood glucose concentrations of starved *Patella* were even lower than the total reducing values determined by the Landgrebe & Munday technique. In July *Patella* starved

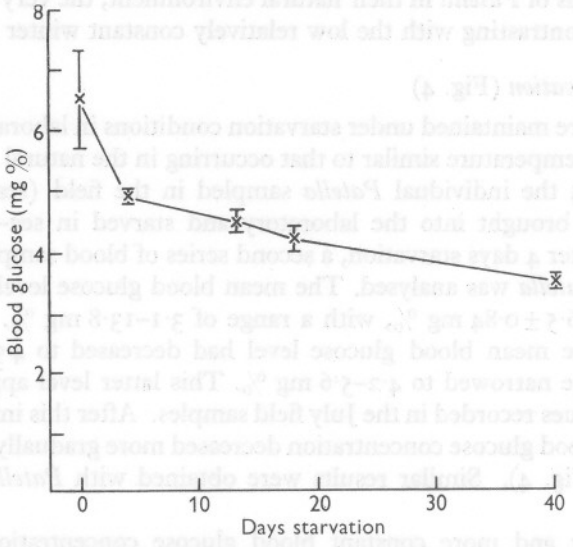

Fig. 4. Effect of starvation on the blood glucose concentration of *Patella*, showing the mean ± standard error of each series of analyses (8 individuals). July *Patella* collected at sea temperature of 17° C and maintained at that temperature in the aquaria.

for 4 days in the laboratory, the true blood glucose concentrations approximated to 40 % of the total reducing values. The decrease in the total reducing value of winter *Patella* starved at 17° C appeared to result from a decrease in the true blood glucose concentration. The marked individual variation of total reducing value of summer *Patella* also apparently represents a real variation in true blood sugar level. However, the yeast fermentation technique at these low glucose concentrations was liable to considerable error, and consequently this technique was not applied as a routine procedure to all blood samples.

Glucose administration experiments (Fig. 5)

The disappearance of glucose from the blood was investigated by injection experiments. 2 mg glucose in 0·2 ml. sea water was injected into the visceral sinus of starved summer *Patella* maintained at 17° C, and a hyperglycemia

of approximately 30 mg % was recorded 10 min after injection (Fig. 5). Within 4 h the blood glucose concentration had returned to the pre-injection level of 2·5 mg %. Injection of the same volume of sea water alone had no hyperglycemic effect. The sea water surrounding the limpet was analysed for glucose, in order to establish whether any glucose was being excreted during the experiment. Even after injection of up to 15 mg glucose, which induced a hyperglycemia of over 200 mg %, less than 2 % of the total glucose injected could be recovered from the sea water. Thus, there was no appreciable escape of glucose through the body surface of the limpet, nor was the injected glucose excreted by the kidney during the period of the experiment.

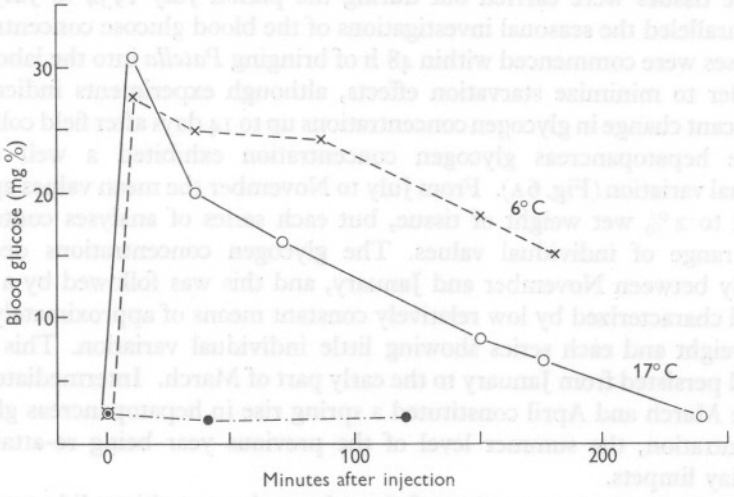

Fig. 5. Variation of blood glucose concentration of *Patella*: (○——○), after the intravascular injection of glucose solution at 17° C, mean 8 individuals; (× - - - - - ×), glucose solution at 6° C, mean 6 individuals; and (●–·–·–●), of sea water, mean 8 individuals, showing mean blood glucose values with increasing periods of time.

This rapid removal of glucose from the blood probably resulted from its metabolism to a non-reducing product. Using starved winter *Patella* maintained at 6° C, the rate of disappearance of injected glucose from the blood was considerably slower than in the summer *Patella* at 17° C. This also suggested that some active metabolic process was involved in the removal of glucose.

Similar results were obtained from April and May *Patella*, to which glucose was administered orally. Oral administration of small volumes of sea water had no effect on the blood glucose concentration, but oral administration of 0·3 ml. 1 % glucose/sea-water solution induced a hyperglycemia of approximately 30 mg % within 15 min. This suggested a rapid transfer of glucose from the alimentary canal to the blood stream. In animals at 17° C, the initial glucose levels were re-attained within 4 h, but animals maintained at 6° C still possessed elevated blood glucose levels 5 h after oral administration.

TISSUE GLYCOGEN CONCENTRATIONS

Seasonal variations (Fig. 6)

The hepatopancreas (including the intestine), the odontophore cushion and the foot were shown to be the main glycogen storage tissues of *Patella*, each normally having a glycogen concentration greater than 1 % wet weight during the summer months. In contrast, the glycogen concentrations of the gonad, the mantle skirt and the remainder of the head region never exceeded 1 % wet weight.

Seasonal determinations of the glycogen concentrations of the three main storage tissues were carried out during the period July 1954 to July 1955, and paralleled the seasonal investigations of the blood glucose concentrations. Analyses were commenced within 48 h of bringing *Patella* into the laboratory, in order to minimize starvation effects, although experiments indicated no significant change in glycogen concentrations up to 14 days after field collection.

The hepatopancreas glycogen concentration exhibited a well defined seasonal variation (Fig. 6A). From July to November the mean values approximated to 2 % wet weight of tissue, but each series of analyses contained a wide range of individual values. The glycogen concentrations decreased sharply between November and January, and this was followed by a winter period characterized by low relatively constant means of approximately 0·3 % wet weight and each series showing little individual variation. This winter period persisted from January to the early part of March. Intermediate values in late March and April constituted a spring rise in hepatopancreas glycogen concentration, the summer level of the previous year being re-attained in the May limpets.

The glycogen concentration of the odontophore cushion did not exhibit a marked seasonal pattern (Fig. 6B). Very variable values were obtained throughout the year. Following a sharp decrease in the mean value between November and January, low mean glycogen concentrations did not persist in the February and March series, although the majority of the individual values of < 1 % wet weight occurred during this period.

Foot glycogen concentrations were determined by analyses of pieces of tissue from the mid-foot region (Fig. 6C). The general pattern of the seasonal variation resembled that of the hepatopancreas. During July to November, the foot glycogen concentrations of individual *Patella* exhibited considerable variations, and the mean level tended to decrease in the October and November series. In January, the glycogen concentration had fallen to a low winter level of approximately 0·8 % wet weight, a somewhat higher level than that recorded in the hepatopancreas (0·3 % wet weight). The hepatopancreas also differed from the mid-foot, in that the spring rise in its glycogen concentration preceded that of the mid-foot. The low winter level of mid-foot glycogen persisted until April and the spring rise was not evident before the May

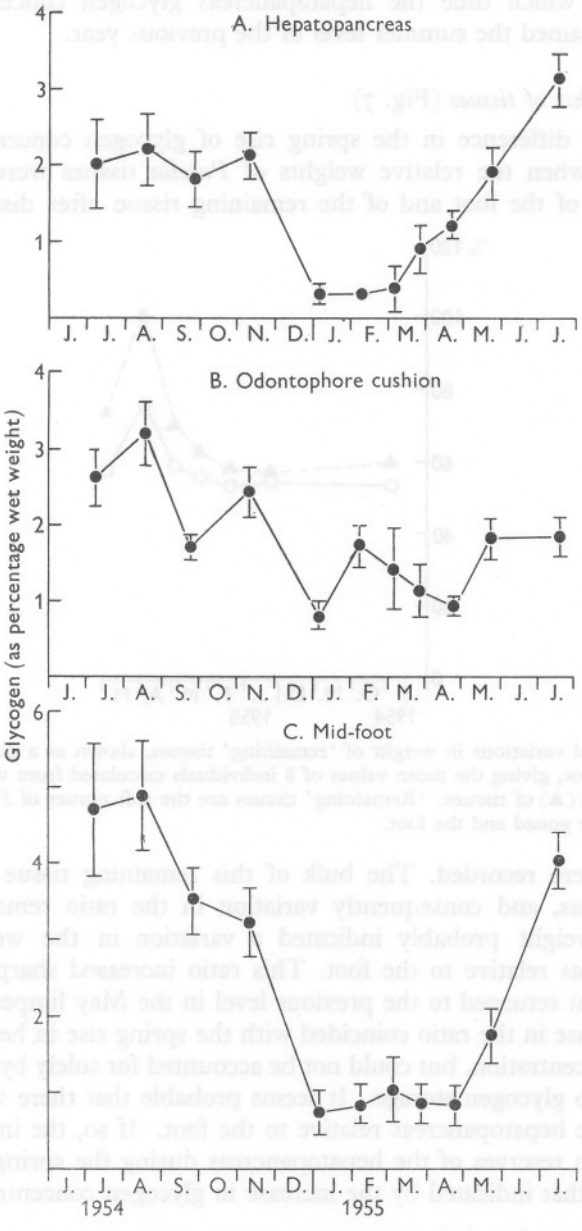

Fig. 6. Seasonal variations in tissue glycogen concentrations of (A) the hepatopancreas, (B) the odontophore cushion, and (C) the mid-foot of *Patella*, showing the mean ± standard error of each series of analyses (7 individuals).

analyses, by which time the hepatopancreas glycogen concentration had already re-attained the summer level of the previous year.

Relative weights of tissues (Fig. 7)

The tissue difference in the spring rise of glycogen concentrations was accentuated when the relative weights of *Patella* tissues were considered. The weights of the foot and of the remaining tissue after dissecting away

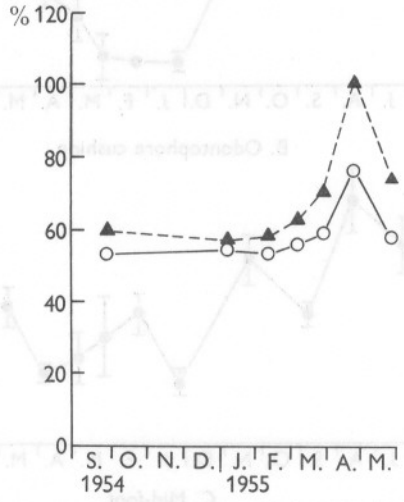

Fig. 7. Seasonal variations in weight of 'remaining' tissues, shown as a percentage of the weight of the foot, giving the mean values of 8 individuals calculated from wet weights (○) and dry weights (▲) of tissues. 'Remaining' tissues are the soft tissues of *Patella* after dissecting away the gonad and the foot.

the gonad were recorded. The bulk of this remaining tissue consisted of hepatopancreas, and consequently variation in the ratio remaining-tissue-weight/foot-weight probably indicated a variation in the weight of the hepatopancreas relative to the foot. This ratio increased sharply in March and April, but returned to the previous level in the May limpets (Fig. 7).

This increase in the ratio coincided with the spring rise in hepatopancreas glycogen concentration, but could not be accounted for solely by an increased weight due to glycogen storage. It seems probable that there was an actual growth of the hepatopancreas relative to the foot. If so, the increase in the total glycogen reserves of the hepatopancreas during the spring rise is even greater than that indicated by the increase in glycogen concentration.

Effect of starvation (Fig. 8)

Glycogen concentrations of the main storage tissues were determined with increasing periods of starvation. *Patella*, collected in July, were maintained

in sea-water aquaria at the July sea temperature of 17° C. During the first month's starvation there was no marked decrease in the tissue glycogen concentrations. After 60 days starvation, the concentration of the hepatopancreas (0·4 % wet weight) had decreased to the winter level. The concentrations of the odontophore cushion and mid-foot had also fallen, but they still contained

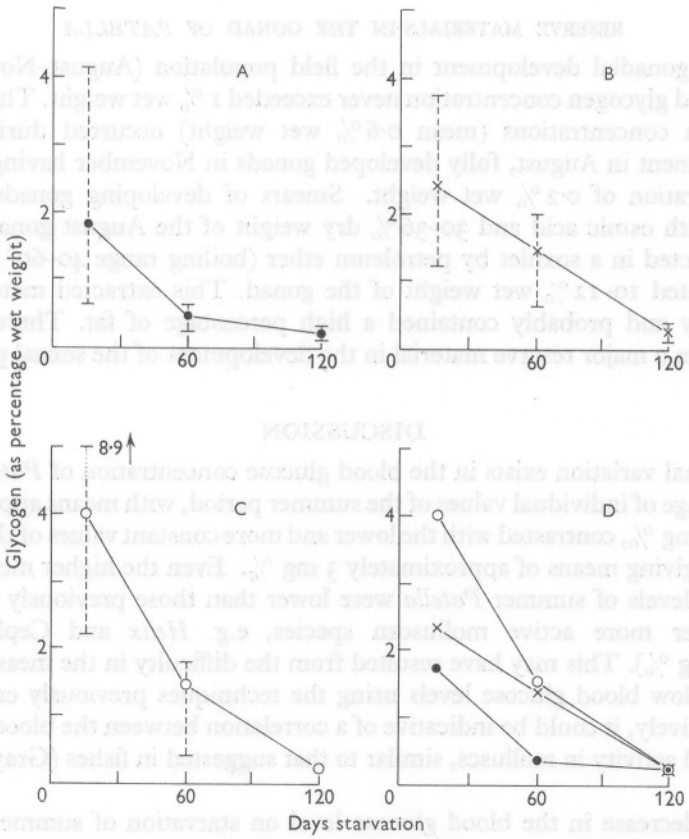

Fig. 8. Variations in tissue glycogen concentrations of *Patella* collected in July and maintained in sea-water aquaria at 17° C. Graphs A, B and C show the means and range of individual values (12 for 5 days, 4 for 60 and 4 for 120 days) with increasing periods of starvation for the hepatopancreas (●), odontophore cushion (×) and the mid-foot (○) respectively. Graph D shows the mean values for the three tissues superimposed.

appreciable glycogen concentrations with mean values 1·4 and 1·5 % wet weight respectively. On prolonged starvation of 120 days, the glycogen concentrations of all tissues were extremely low, no individual value exceeding 0·4 % wet weight.

Well-developed gonads were present in *Patella* starved for 60 and 120 days. This gonadial development paralleled that occurring in the natural population

over the same period (August–November). The decrease in the tissue glycogen reserves of starved *Patella* may have resulted from glycogen utilization both in maintaining metabolism and in the development of the gonads. However, in starved *Patella* the glycogen concentrations of the gonads themselves did not exceed 0·1 % wet weight.

RESERVE MATERIALS IN THE GONAD OF *PATELLA*

During gonadial development in the field population (August–November), the gonad glycogen concentration never exceeded 1 % wet weight. The highest glycogen concentrations (mean 0·6 % wet weight) occurred during early development in August, fully developed gonads in November having a mean concentration of 0·2 % wet weight. Smears of developing gonads stained black with osmic acid and 30–36 % dry weight of the August gonads could be extracted in a soxhlet by petroleum ether (boiling range 40–60° C). This represented 10–12 % wet weight of the gonad. This extracted material was very oily and probably contained a high percentage of fat. Therefore, fat may form a major reserve material in the development of the sexual products.

DISCUSSION

A seasonal variation exists in the blood glucose concentration of *Patella*. The wide range of individual values of the summer period, with means approximating to 6 mg %, contrasted with the lower and more constant values of the winter period, giving means of approximately 3 mg %. Even the higher mean blood glucose levels of summer *Patella* were lower than those previously reported for other more active molluscan species, e.g. *Helix* and Cephalopoda (8–33 mg %). This may have resulted from the difficulty in the measurement of very low blood glucose levels using the techniques previously employed. Alternatively, it could be indicative of a correlation between the blood glucose level and activity in molluscs, similar to that suggested in fishes (Gray & Hall, 1930).

The decrease in the blood glucose level on starvation of summer *Patella* suggests that the higher concentrations in individual field *Patella* result from an alimentary hyperglycemia. The similarity between the low concentrations of both field and starved *Patella* during the winter months suggests that *Patella* do not feed during this winter period, and that they may pass into an inactive state comparable to the hibernation of terrestrial molluscs.

A close correlation exists between the seasonal variations of the blood glucose and hepatopancreas glycogen concentrations (Fig. 9). Between November and January, these concentrations decreased to a relatively low and constant winter level, which persisted into the early part of March. The spring rise in the concentration of the hepatopancreas glycogen also paralleled that of the blood glucose, but preceded the increase in foot glycogen concentration.

The total increase in the glycogen reserves of the hepatopancreas was probably even greater than indicated by the glycogen concentration alone, because of an actual growth of the hepatopancreas relative to the foot (March–April). This close parallel between the spring rise in blood glucose and hepatopancreas glycogen concentration may be associated with the function of the hepatopancreas as a digestive and absorptive organ and the recommencement of feeding. It is not suggested, however, that there is any functional analogy with the vertebrate liver as the main glycogen storage organ.

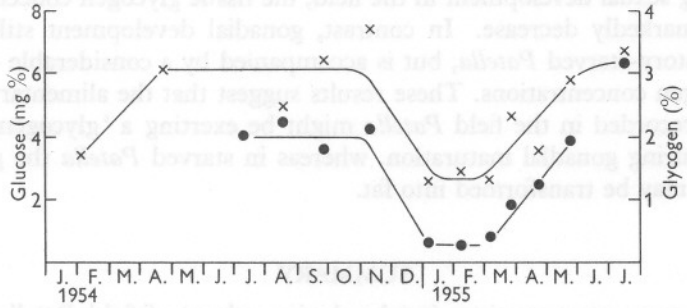

Fig. 9. Patterns of seasonal variations in blood glucose concentrations (upper line, ×) and hepatopancreas glycogen concentrations (lower line, ●) of field *Patella*.

The decrease in glycogen concentrations of all tissues of *Patella* between November and January coincided with the shedding of the genital products. The resultant low levels of hepatopancreas and foot glycogen remained constant throughout the winter period, no further decrease being detected before the spring rise commenced at the end of March. In the decrease of glycogen reserves with the shedding of the genital products, the seasonal pattern of tissue polysaccharide reserves in *Patella* resembled that reported for *Helix* (von Brand, 1931; May, 1934) and oysters (Couteaux-Bargeton, 1947). But in these latter species, this decrease was followed by a period of accumulation before the onset of the winter period, during which there was a second decrease in the polysaccharide reserves. It has been suggested that in *Helix* and oysters glycogen is utilized in maintaining the metabolism during the winter period. In *Patella* the absence of changes in the low levels of glycogen in the hepatopancreas and foot between January and March offer no evidence of a similar glycogen utilization.

In field *Patella* gonadial development occurred between August and November. At no period of the year did the gonad contain appreciable glycogen reserves, not even preceding sexual maturity. This contrasts with the large reserves of galactogen laid down in the albumen gland of *Helix* (May, 1934) and of glycogen in the gonad of oysters (Couteaux-Bargeton, 1947) prior to sexual activity. However, petroleum ether extracts of developing gonads of *Patella* suggest that fat rather than polysaccharide forms a

major reserve material in the sexual products, in a manner somewhat similar to the storage of fat rather than glycogen in the digestive gland of *Pila* (George & Desai, 1954). Nevertheless, the rapid decrease in glycogen reserves between November and January is unlikely to result solely from the maintenance of metabolism after the cessation of feeding, since short-term starvation (1 month) at a much higher temperature (+10° C) does not result in a rapid utilization of glycogen. Glycogen may be used up rapidly in the final stages of gonadial maturation.

During sexual development in the field, the tissue glycogen concentrations do not markedly decrease. In contrast, gonadial development still occurs in laboratory-starved *Patella*, but is accompanied by a considerable decrease in glycogen concentrations. These results suggest that the alimentary carbohydrate recorded in the field *Patella* might be exerting a 'glycogen-sparing effect' during gonadial maturation, whereas in starved *Patella* the glycogen reserves may be transformed into fat.

SUMMARY

Blood glucose concentrations (total reducing values) of field *Patella* showed a seasonal variation. The variable summer values, whose means approximated to 6 mg % glucose (May–November), contrasted with the relatively low and constant winter values, whose means approximated to 3 mg% glucose (January–March). On starvation of summer *Patella*, the higher field values rapidly decreased to a constant basal level, more comparable to the low winter field values. A hyperglycemia of 30 mg % induced by intravascular glucose injection was followed by a rapid adjustment of the blood glucose to the pre-injection level within 4 h.

Seasonal variations in the glycogen concentrations occurred in the hepatopancreas and foot, but were not evident in the odontophore cushion, the other main site of glycogen storage. The patterns of the seasonal glycogen variations were similar to those of blood glucose, the parallelism being closer in the hepatopancreas than in the foot glycogen changes. As with the blood glucose, the spring rise in hepatopancreas glycogen concentration occurred during March and April, and was accompanied by a growth of the hepatopancreas. The spring rise in the foot glycogen concentration did not commence until May.

The developing gonads of both field and starved *Patella* (August–November) contained no appreciable glycogen reserves, but petroleum ether extracts indicated considerable fat storage. The shedding of the genital products coincided with the sharp decrease in blood glucose and tissue glycogen concentrations (November–January). Unlike oysters, the glycogen levels remained low throughout the winter period.

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ON THE METAMORPHOSIS OF THE VISUAL PIGMENTS OF *ANGUILLA ANGUILLA* (L.)

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(Text-fig. 1)

The retinae of all the species of deep-sea fish which have been studied have been shown to contain golden coloured pigments, chrysopsins, which are especially suited to the light found in their natural environment (Denton & Warren, 1957; Munz, 1958). Amongst fish caught in shallow coastal waters this characteristic colour of retinal pigment is found only in the conger eel *Conger conger* (by Denton & Walker, 1958), and amongst freshwater fish only in the silver eel *Anguilla anguilla* (by Carlisle & Denton, 1957, referred to by Denton & Warren, 1957). Both these fish are species of Apodes, a group of which the vast majority of species are deep-water forms. Both species, moreover, begin their life in the deep sea and return to it again when mature to spawn and may therefore, in one sense, be regarded as deep-sea fish. Since immature conger eels in shallow coastal waters already have a retinal pigment characteristic of a deep-sea fish, it seems very unlikely that on returning to deep water they would change away from the deep-sea form which they already possess. It is probable therefore that the conger retains a deep-sea form of retinal pigment throughout the whole of its life.

There remained, on beginning these experiments, a curious difference between the silver form of the European eel, *A. anguilla*, with its golden coloured retina, and the North American eel, *A. rostrata*, which had been shown to have a reddish purple retina believed to contain a mixture of rhodopsin and porphyropsin (Wald, 1945). It appeared then that either there was a difference between these two species of the genus *Anguilla*, or that there was a change of pigments during the life of the freshwater eel similar to that known to take place when the tadpole of the bullfrog becomes adult (Wald, 1945).

The larva of *A. anguilla* is a leptocephalus, which metamorphoses to a juvenile elver as it approaches the coasts of Europe. The juvenile eel spends some years in the estuaries and rivers of Europe, where it is known as the yellow eel; a second metamorphosis then begins during which the eel assumes a silvery dress and the gonads begin to grow; this silver eel then migrates towards the deep Atlantic spawning grounds. This change of livery once begun can be hastened by injections of gonadotrophic hormones. Associated with the change in livery is an enlargement of the eye. D'Ancona (1927,

1929) and Ferriani (1954) have studied this increase in the size of the eye and have shown that the diameter is doubled and the retinal area increases four-fold. D'Ancona states that despite this increase in area the number of rods in the retina remains constant. From this Bertin (1951; English edition, 1956) argues that as the eye enlarges the retina '. . . must be less and less capable of light perception and that, on the whole, the enlargement of the eye constitutes degeneration rather than improvement' (English edition, 1956, p. 96).

We therefore posed ourselves two questions:

(1) Is there a change of retinal pigment at the change of livery in *A. anguilla*?

(2) Is the enlargement of the eye at this change of livery accompanied by any decrease in efficiency of the eye in absorbing light?

MATERIAL AND METHODS

The eels were all caught in fresh water; the deep-sea eel was caught in an Agassiz trawl and its retina was studied at sea aboard R.V. 'Sarsia'.

The retinae, from the eyes of eels which had previously been dark adapted for 2 days, were dissected out under a dim red light, mounted in a small chamber on a microscope slide in Ringer solution (Denton & Wyllie, 1955), and studied whilst fresh.

The spectral absorption of light by the retina was measured by methods described in detail by Denton & Walker (1958). Using one method (Method III of Denton & Walker) the total optical density[1] of the retina relative to an equal thickness of Ringer solution is determined as a function of wavelength; using another method (Method II of Denton & Walker) the difference in density between unbleached retina and the same retina after bleaching with strong white light is determined as a function of wavelength.

In addition to the normal yellow and silver eels eight of the latter which had been injected with gonadotrophins to advance the degree of sexual maturity were used. Each of these animals was injected weekly for 4 weeks with 500 international units of human chorionic gonadotrophin and the same amount of mare serum gonadotrophin. Of these animals one of the males reached sexual maturity, while the females all showed enlarged ovaries and ova up to 400 μ diameter. The eyes were further enlarged, but the retinae showed no significant differences from the normal silver eels and will not be considered further.

For histological purposes excised eyes were injected with Zenker's fixative and then fixed whole in this fluid, embedded in celloidin, sectioned and stained with Heidenhain's iron haematoxylin and van Gieson's stain.

[1] The densities referred to in this communication are all optical densities:

$$\log_{10}\left(\frac{\text{light incident}}{\text{light transmitted}}\right).$$

RESULTS

Several retinae of silver and yellow eels were dissected in quick succession and examined side by side in white light; the silver eel's retinae were golden in colour whilst those of the yellow eel were purple coloured. The density of pigment was seen to be at least as high if not higher in the silver eels than in the yellow eels. These simple observations confirmed observations made a year earlier on the silver eel and showed that there was a metamorphosis of the fresh water eel's visual pigments. Fig. 1A shows that on metamorphosis of the visual pigment there is a shift in the maximum of the retinal difference curve of about 33 mμ and Fig. 2B shows that the mature silver eel has a curve of total retinal density very close to that of the conger eel. The metamorphosis is accompanied by an increase in retinal density. The maximum retinal density changes on bleaching two specimens of yellow eel were 0·34 and 0·21, whilst the corresponding changes for the silver eel were 0·58 and 0·52.

A specimen of a deep-sea eel *Synaphobranchus* sp. caught in an Agassiz trawl at a depth of about 800 m off the north coast of Spain gave a total retinal density curve very close to those of the conger eel and the silver fresh-water eels.

The change in the eye as the eel changes from yellow to silver livery is well marked. In a specimen of yellow eel 61 cm long the longest diameter of the eyeball was 3·3 mm while in a silver eel of the same length which had been injected with gonadotrophins this diameter was 7·8 mm. The relative thickness of the various layers of the retina was slightly altered, but we have not sectioned enough specimens to be certain that this change is constant. Most layers are thinner in the silver eel. The number of rods in a median section of these two retinae is approximately the same. They are no wider spaced in the silver eel, however, for the external segments of the rods are about twice the diameter of the rods in the yellow eel (3 μ and 1·5 μ respectively). This enlargement in the rods seems adequate to account for the greater area of the retina. The rods are not increased significantly in length but we cannot find that they become shorter, as implied by D'Ancona (1927), who states that all the layers of the retina become distinctly thinner, though this is least marked in the layer of rods. ('I vari strati retinici sono distintamente assottigliati. Tale fatto è invece meno accentuato nello strato dei bastoncelli.') In comparable regions of the retina the thicknesses of the rod layer, measured from the external limiting membrane to the pigmented layer, were 92 μ in a silver eel and 86 μ in a yellow eel at the thickest part.

DISCUSSION

During the metamorphosis from the immature yellow to the mature silver form there are extensive changes equipping the eel for its deep-sea environment. These results show that these changes include one in which the retinal

pigment becomes similar to those of the deep-sea fish. This takes place even before the fish leaves fresh water. The change is analogous to that described 14 years ago in the bullfrog (Wald, 1945), and to the change in retinal pigments recently shown to take place in the lamprey (Wald, 1957). Wald, Brown & Brown (private communication) have now investigated the chemistry of the metamorphosis of the visual pigment in the freshwater eel and have not only confirmed these results but have elucidated in detail both the nature and

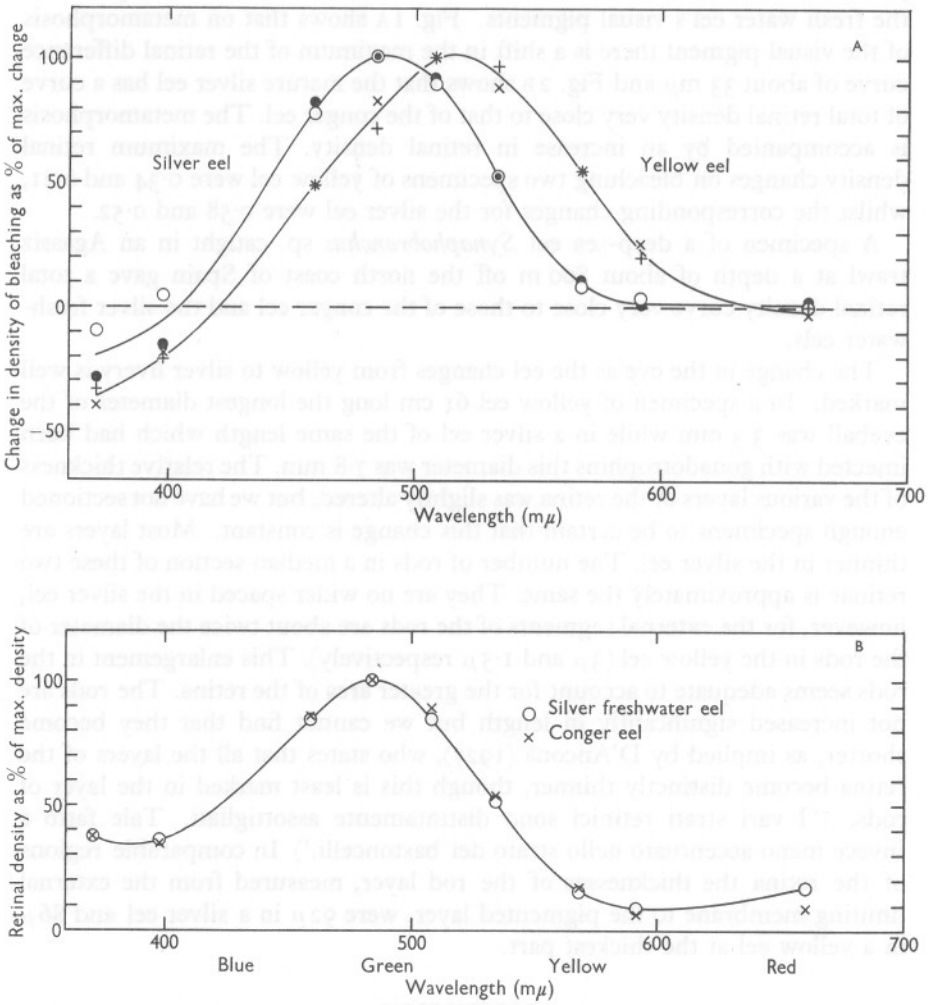

Fig. 1. A, *Anguilla anguilla*: immature (yellow) eels and mature (silver) eels. Spectral curves of difference in density between unbleached dark adapted retinae and the same retinae an hour after bleaching their photosensitive pigments with strong white light. B, *Conger conger* and mature (silver) eels (*Anguilla anguilla*). Spectral curves of densities of unbleached retinae with respect to an equal thickness of Ringer's solution.

course of this metamorphosis. Their results and those obtained here are in good accord.

Whilst the observations of D'Ancona on the histology of the eyes of yellow and silver eels are confirmed here, the deductions made from D'Ancona's observations by Bertin would seem to be false. The fraction of light incident on the retina absorbed by the retinal pigments is very high in the silver eel; after taking account of the shift in absorption curve the eye of the silver eel is more efficient than that of the yellow eel in usefully absorbing light striking the retina.

Despite the great change in calcium metabolism there is no change in the absorption of light by the crystalline lens on metamorphosis (Denton, E. J. & Warren, F. J. unpublished observation), but in size the lens and the pupil increase even more than does the eye itself.

For a silver and a yellow eel looking at the same small source of light at the same distance, the total light thrown on to the silver eel's retina will be greater (because of the *absolutely* larger pupil), the brightness of the silver eel's retinal image will be greater (because of the *relatively* larger pupil), and the fraction of light absorbed by the retinal photosensitive pigments will be greater (because of the higher retinal density of pigment).

We are very grateful to Mr A. C. G. Best for making the histological preparations for us.

We are indebted to the Royal Society for a scientific grant-in-aid, and to Organon Laboratories Limited for a gift of gonadotrophic hormones.

SUMMARY

European eels, *Anguilla anguilla* (L), while they retain the immature 'yellow' livery, have purplish coloured retinae, close in colour to those of freshwater fish. The purple colour is that of photosensitive pigments.

When an eel assumes the 'silver' livery of approaching maturity, in preparation for the deep-sea transatlantic migration to the breeding grounds off the Bermudas, the eye enlarges and the retina changes to a golden colour, like that of the photosensitive chrysopsins of deep-sea fish. The maximum of absorption shifts by about 33 mμ towards the shorter wavelength end of the spectrum and the final total retinal density curve of the silver eel is almost identical with that of the conger eel, *Conger conger* (L), and of a deep-sea eel, *Synaphobranchus* sp. This change of pigment takes place even before the fish leaves fresh water.

The larger eye and the relatively even larger pupil of the silver eel make it a more efficient light-collecting organ, whilst the total retinal density of photosensitive pigment is higher in the silver than the yellow eel and the retina will therefore be more efficient in usefully absorbing the light incident on it.

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THE GROWTH STAGES OF THE LOPHOPHORE OF THE BRACHIOPODS *PLATIDIA DAVIDSONI* (EUDES DESLONGCHAMPS) AND *P. ANOMIOIDES* (PHILIPPI), WITH NOTES ON THE FEEDING MECHANISM

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From the Plymouth Laboratory

(Text-figs. 1–23)

The lophophore of *Platidia*, as illustrated in most memoirs and text-books, bears little resemblance to its appearance in life, no doubt because such illustrations and the accompanying descriptions were based on dried specimens. The lophophore of *Platidia* has been considered to be of a peculiar sigmoid type, differing from that of any other known lophophore. The dredging by R.V. 'Sarsia' of three species of the genus in recent years has afforded the opportunity of figuring the lophophore in its natural state, and the working out of its growth stages in *P. davidsoni* and *P. anomioides*: these were previously unknown for any species of *Platidia*. The third species, a new one, is described separately (Atkins, 1959).

Although *P. anomioides* (Philippi) is the type species of the genus, *P. davidsoni* (Eudes Deslongchamps) is considered first as it was the first to be dredged by R.V. 'Sarsia' and work on it was ready for publication when *P. anomioides* was obtained in May 1958.

All figures have been drawn with the aid of a camera lucida.

PLATIDIA DAVIDSONI (EUDES DESLONGCHAMPS)

A species of *Platidia* dredged by R.V. 'Sarsia' from off Penmarch and the north coast of Spain is evidently *P. davidsoni* (E. Deslongchamps) as it agrees with the description of that species by Eudes Deslongchamps (1855) in having 'small spinous asperities' on the outer surface of the ventral valve, although these are often confined to a submarginal zone, and in some individuals apparently worn and indistinguishable. Fischer (1872, 1873) noted of this species that 'elle porte quelquefois des aspérités assez nombreuses'. The brachial support agrees with the figures accompanying E. Deslongchamps's paper, but not with his description. There appears to be some confusion over its actual state. In his description of his new species, *Morrisia* (= *Platidia*) *davidsoni*, E. Deslongchamps (1855) described the 'apophysary system consisting of two lamellae originating at the base of the sockets, and

united to a small elevated process or septum which arises from near the centre of the valve'. In the accompanying figure (pl. x, fig. 20, *c*, *d*) prongs at the apex of the septum are described as 'broken lamellae attached to the summit of the septum'. The prongs were evidently considered to be part of the descending and not of the ascending branches. It may be surmised that he found the branches as figured but assumed that they had been broken.

Fischer in 1872 and again in 1873 said of the brachial apparatus 'que nous n'avons pu obtenir entier, pas plus que M. Deslongchamps'.

Davidson in 1887 (p. 155) stated: 'Interior of the dorsal valve not completely known. Short cylindrical processes project into the interior of the shell from a little under each angle of the wide semicircular foramen, and from about the middle of the bottom of the valve arises a thickened pillar-shaped process or septum, curved toward the hinge, and forked at its extremity'. On the following page he mentioned that 'in *Platydia davidsoni* these principal stems, in the specimens examined by M. E. Deslongchamps, Dr Fischer, and myself, were either broken or absent; so that to ascertain their real condition more specimens will have to be examined hereafter'. Curiously enough Fischer & Oehlert in 1891 stated briefly 'appareil brachial comme dans le *P. anomioides*' and figured the brachial support as being exactly the same (pl. viii, fig. 15*b*, *c*) with the descending branches complete. It is difficult to understand their failure to mention that in previous descriptions by one of them (Fischer, 1872, 1873) and by Davidson (1887) the descending branches were described as either broken or absent.

The difference in the brachial support of the 'Sarsia' specimens and those of Fischer & Oehlert (1891) would not seem to be a size difference: their specimens had a length of 6 mm and width of 6·5 mm, whilst of my two largest *P. davidsoni*, one was 7·8 mm long and 7·2 mm wide and the other 7 mm long and 8 mm wide. In the 'Sarsia' specimens there is no doubt that the brachial support is as described and figured by Davidson in 1887. The absence of descending branches joined to the septum is not due to the fracture of extremely delicate branches in animals allowed to rot in sea water and then the remains blown out of the shell with a pipette. In a specimen 5·4 mm long and 6·9 mm wide which was sectioned, there is no indication of lateral outgrowths from the septal pillar other than the forked processes at the apex. In brachial valves with lophophore intact cleared in cedar wood oil or oil of winter green the same state of development was found.

It is not impossible that better development of the brachial support may occur in local varieties. However, as previous to Fischer & Oehlert's 1891 paper all authors had agreed that the descending branches in this species were either incomplete or broken, it would appear that their 'Travailleur' and 'Talisman' specimens need re-examination.

Platidia davidsoni was dredged in some numbers by R.V. 'Sarsia' in February and July 1956 and in June 1957 from a small area of yellow coral,

Dendrophyllia cornigera Lamarck, off the Point of Penmarch at a depth of 45 to 48 fathoms. Two individuals, one 4·2 mm long and 6 mm wide and the other 2·7 mm long and 3·4 mm wide, were taken attached to a very large species of oyster off the north coast of Spain in position 43° 42′ N., 3° 58′ W. at a depth of 220 fathoms.

In the Penmarch area the *Platidia* were attached to the dead region of the growing coral and to the brachiopods *Terebratulina retusa* and *Megerlia truncata*, themselves fixed to the coral. They generally occurred on the lower brachial valves of the brachiopods in no definite position. Four *P. davidsoni* of shell length 0·8 to 2·7 mm were attached to the brachial valve of an adult *Megerlia*.

An occasional individual was found standing more or less erect on its hinge, with organisms encrusting both valves, but generally, when the animal is not feeding, the lower, brachial valve is closely applied to the substratum and when this has sharp irregularities the valve may be almost punctured. The brachial valve is thinner than the ventral, is generally approximately flat, but may be concave on coral. When situated where a slender side branch of coral arises the shell may show a well-marked artificial sulcus (see Fig. 11) where it extends on to the side branch.

The shell of *P. davidsoni* is frequently irregular in shape, owing to the irregularities of the coral and to the proximity of other growth. Occasionally when attached to the valve of another brachiopod the shell may be regular; an example was one near the anterior edge of the brachial valve of a *Terebratulina* and facing in the same direction. It was subcircular, 6 mm long and 7 mm wide, and regularly domed: half of its ventral valve was encrusted by a polyzoan. Irregularity in shell shape is accompanied by asymmetry in varying degree of the lophophore and sometimes by that of the gonad.

The mantle edge is produced into tiny lobes, and bears setae; in small individuals they reached a length of 0·6 mm.

Two spots of carmine pigment are present, probably in connexion with the preoesophageal ganglion. These pigment spots are difficult to distinguish, being masked by spicules: in some individuals they appear to be absent. They could not be found in *P. anomioides* and in a new species of *Platidia* (Atkins, 1959), both of which were taken in deep water. Carmine spots have also been found by me in certain other brachiopods.

From one *P. davidsoni*, 5·4 mm long, 6·9 mm wide, sectioned, with small gonad, it would seem that this species is hermaphrodite: the gonad was mostly male, with tailed sperm in the posterior region, but with a few small ova. From examination of entire specimens, however, it appears that ovaries and testes develop at different times, so that the animal appears dioecious. The ripe ovaries are dark orange and visible through the semi-transparent shell; the entire animal is orange tinted. The testes are of a less dark and more pinkish orange than the ovaries. *P. davidsoni* in the laboratory tanks retained their colour for about a month, but had lost much of it, especially from the

filaments, after 2 months, possibly as a result of semi-starvation. Other brachiopods so far known to be hermaphrodite are *Argyrotheca* (see Senn, 1934) and *Pumilus antiquatus* (Atkins, 1958).

The gonads of *P. davidsoni* were large in February, June and July; specimens were not obtained at other times of the year.

GROWTH STAGES OF THE LOPHOPHORE AND ITS SUPPORT

During development the lophophore passes through the usual growth stages, trocholophous, schizolophous and zygolophous, culminating in a somewhat modified plectolophe.

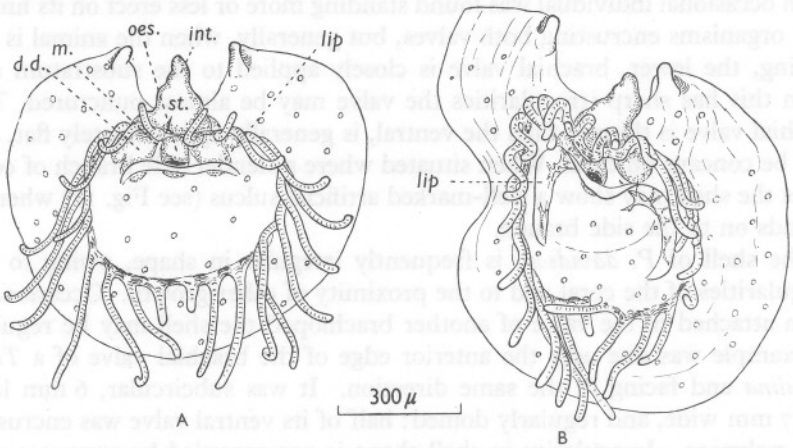

Fig. 1. *Platidia davidsoni*. Brachial valves of specimens of shell length 0·8 mm (A) and 1·0 mm (B) with trocholophes, to show the growth of the lip of the food groove (*lip*) in front of the mouth (*m.*): drawn living. In both individuals filaments are in single series. Spicules are present where indicated in the filaments and brachial membrane. Mantle caecae shown. In this and following figures mantle setae have been omitted. *d.d.*, digestive diverticulum; *int.*, intestine; *m.*, mouth; *oes.*, oesophagus; *st.*, stomach.

The trocholophous lophophore is of the broad-based terebratellacean type. The smallest individual obtained, of shell length 0·8 mm and width 0·9 mm, had the lophophore in this stage: the lophophoral ridge was a complete circle. Eleven filaments were present on the left and twelve on the right (Fig. 1A). These were set low on the mantle, except for those behind the mouth which arose from the body. The lip of the food groove extended but a short distance on each side of the mouth. Spicules were present in the filaments and at their bases, but not elsewhere.

An unusually long-stalked, irregularly shaped individual of some 1 mm diameter, in the late trocholophous stage, had 14 pairs of filaments in single series: a few on the right were abnormally short. The lip had extended much further than in the smaller individual and two pairs of spicules were present in the brachial membrane (Fig. 1B). These two specimens shown in Fig. 1 illustrate clearly the

manner of growth of the lip of the food groove by lateral growth from a small preoral lobe, and not as an invagination of the rapid extension of the region between the latest formed filaments of the trocholophe (see Williams, 1956, for use of term) as described by Percival (1944) in *Terebratella inconspicua*.

At a shell length of 1·4 mm and width of 1·5 mm the lophophore was very slightly indented anteriorly: seventeen pairs of long filaments with ridged frontal surfaces were present in single series, and two pairs of minute buds. The lip of the food groove had now extended to the bases of the last long filament on each side. The number of spicules in the brachial membrane was two on one side and one on the other, so that some variation in the time of formation of these spicules evidently occurs.

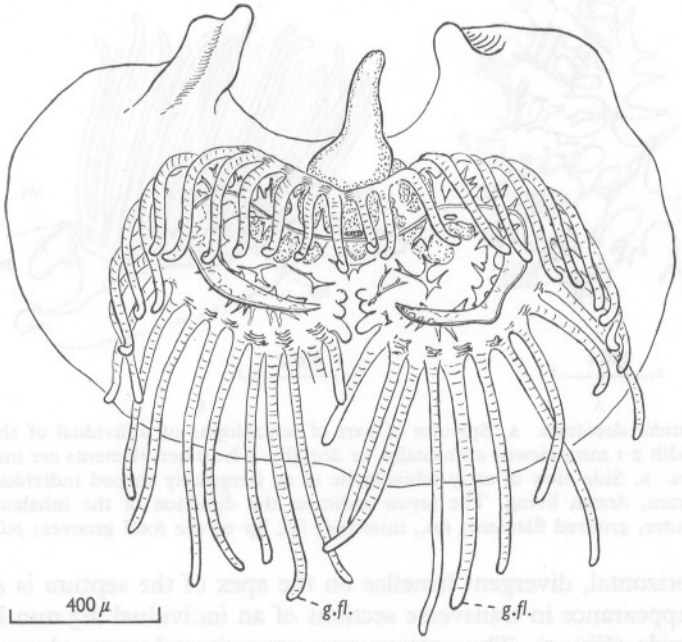

Fig. 2. *Platidia davidsoni*, of shell length 1·4 mm, width 1·7 mm. Brachial valve with early schizolophe, drawn living. Differentiation into a double series of filaments had begun, the first outer grooved filament on each side is indicated (*g.fl.*). The filaments behind the mouth are almost erect. The spicules supporting the lophophore have increased in size and numbers.

At a shell length of 1·4 mm and width of 1·7 mm the lophophore was early schizolophous with twenty-one pairs of long filaments and in addition three pairs of minute buds (Fig. 2). Differentiation of filaments had begun with three outer grooved filaments on the right and two on the left anteriorly. The spicules in the brachial membrane had increased in size and complexity.

The arrangement of the spicules at the base of the lophophore in an individual 1·8 mm long is shown in Fig. 3 A. At this size no septum could be distinguished in a valve with lophophore in position.

The trocholophe and early schizolophe are bell-shaped in the feeding position, the filaments are directed upwards and outwards (Fig. 3B): it is only in the contracted state that they are directed inwards.

A more advanced schizolophous stage of shell length 2·0 mm and width 2·3 mm is shown in Fig. 4A, and the appearance looking down into the gaping shell of a similar stage in Fig. 4B. The brachial skeleton first appears at about this size in the form of a low septum, with tiny divergent lamellae, having the appearance in ventral view of a small transverse boss. That it represents small,

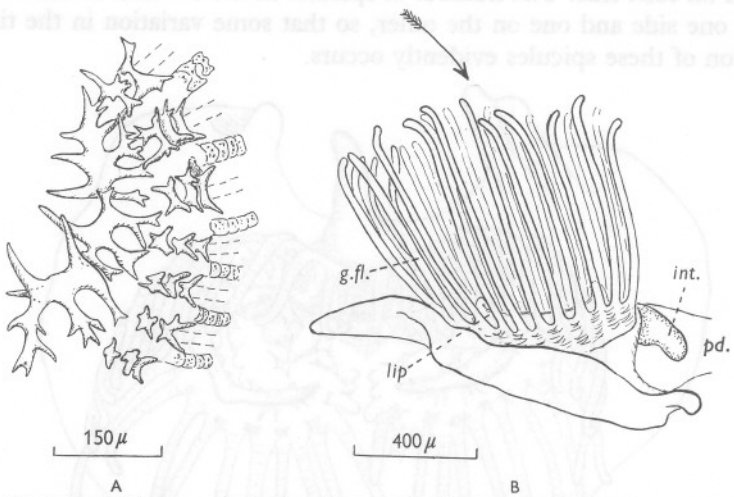

Fig. 3. *Platidia davidsoni*. A. Spicules of part of schizolophe of individual of shell length 1·8 mm, width 2·1 mm, viewed abfrontally, or dorsally. The inner filaments are indicated by broken lines. B. Side view of early schizolophe of an irregularly shaped individual of shell length 1·8 mm, drawn living. The arrow indicates the direction of the inhalant current. *g.fl.*, first outer, grooved filament; *int.*, intestine; *lip*, lip of the food grooves; *pd.*, pedicle.

almost horizontal, divergent lamellae on the apex of the septum is apparent from its appearance in transverse sections of an individual 2·3 mm long and 2·9 mm wide (Fig. 5). The septum was approximately 200 μ long and the conjoined bases of the lamellae 80 μ long antero-posteriorly, judging from the number of sections involved. The septum with the lamellae support the growing region of the lophophore and raise it above the valve floor, so that the brachial membrane slopes toward the mantle margins. At this stage the concavity formed by the upper surfaces of the lamellae is occupied by supporting substance similar to that present in the filaments. The two sections figured (Fig. 5) show the relation of the filaments to the mantle. Both small and great brachial canals are present at this stage.

The early zygolophous stage occurs between a shell length of 2·7 and 3·2 mm. At the smaller size the inner side of the lateral arms had not yet begun to be deflected, while at the larger size this inclination had begun (Fig. 6).

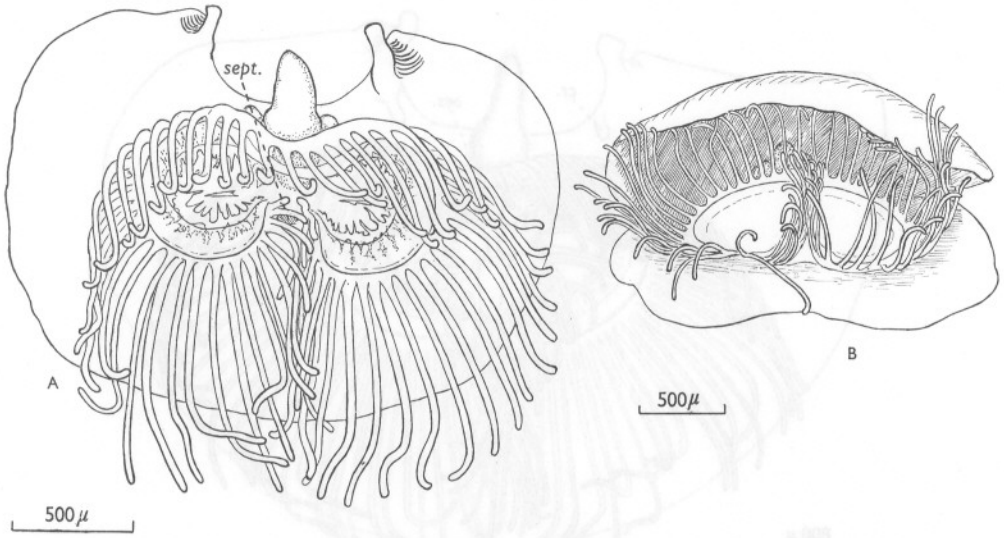

Fig. 4. *Platidia davidsoni*. A. Specimen of shell length 2·0 mm, width 2·3 mm: brachial valve with schizolophe, drawn living. The filaments behind the mouth are almost erect; a septum is present. Only the larger spicules are shown. B. Specimen of shell length 2·2 mm, width 2·3 mm: view looking down into the shell, drawn living, but narcotized.

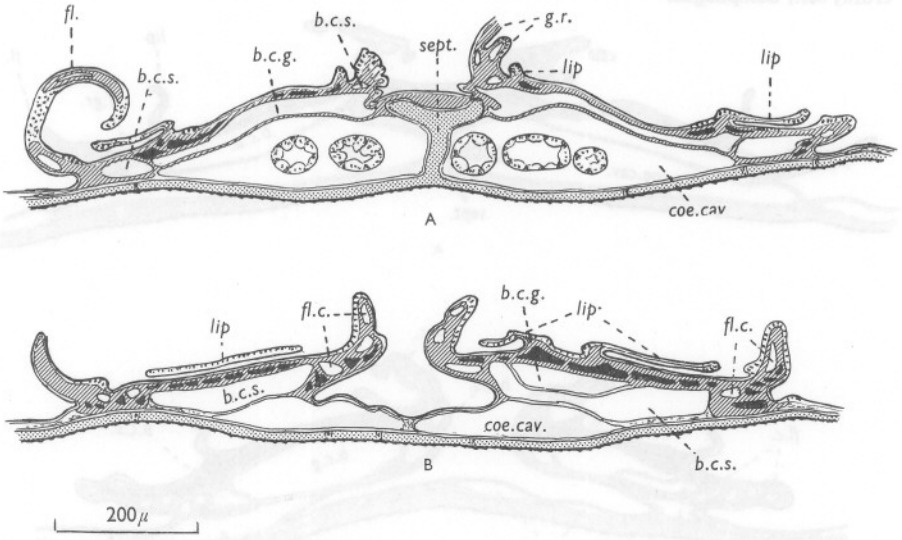

Fig. 5. *Platidia davidsoni*, of shell length 2·3 mm, width 2·9 mm. Transverse sections through the brachial valve with schizolophe: (A) through the septum (*sept.*) with its divergent lamellae, and the twin growing regions of the lophophore; (B) through the anterior region of the lophophore, slightly oblique. On the right through the anterior recurvature of the small brachial canal; on the left slightly more anterior, so that the great brachial canal is absent. *b.c.g.*, great and *b.c.s.*, small brachial canals; *coe.cav.* coelomic cavity; *fl.*, filament; *fl.c.*, filamentar canal; *g.r.*, growing region of right side; *lip*, lip of food groove. Spaces formerly occupied by spicules shown black; supporting substance shown hatched.

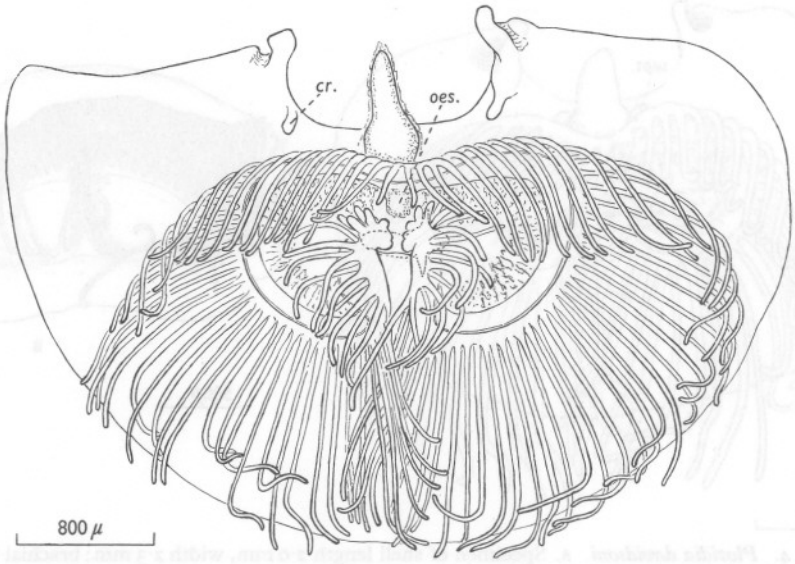

Fig. 6. *Platidia davidsoni*, of shell length 3·2 mm, width 4·6 mm. Brachial valve with zygolophe; the inner sides of the lateral arms have begun to turn outwards. Drawn living: brachial support, indicated by broken lines, added after clearing in cedar wood oil. *cr.*, crura; *oes.*, oesophagus.

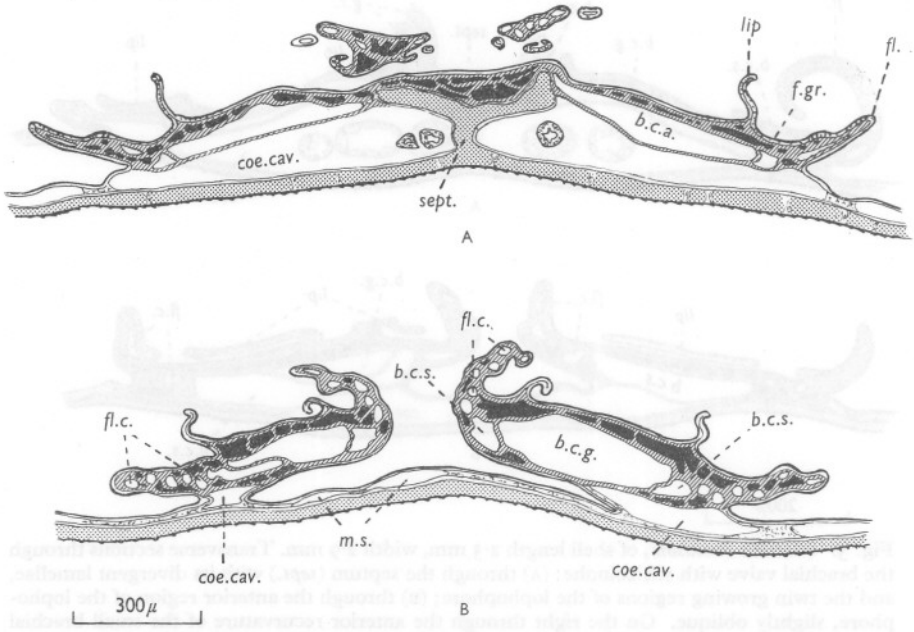

Fig. 7. *Platidia davidsoni*, of shell length 3·1 mm, width 4·1 mm. Transverse sections through the brachial valve and early zygolophe of a slightly later stage than shown in Fig. 6: (A) through the septum (*sept.*) and its divergent lamellae, (B) near the anterior end of the lophophore. The two lateral arms face ventrally, but slope slightly toward the mantle margins. The lateral arms are beginning to separate from the mantle anteriorly. *f.gr.*, food groove; *m.s.*, mantle sinus; other lettering as in Fig. 5.

A specimen 3·1 mm long and 4·1 mm wide was sectioned: the sections illustrated (Fig. 7) show the almost horizontal lamellae at the crest of the septum. The lophophore is being gradually raised above the valve floor, not only by the septum and its lamellae, but also by the lateral extension and increase in size of the coelomic cavity (Fig. 7A). More anterior to the section figured (Fig. 7B) the lophophore is free from the valve floor for a very short distance. At this size crura have begun to develop (Fig. 6). The brachial

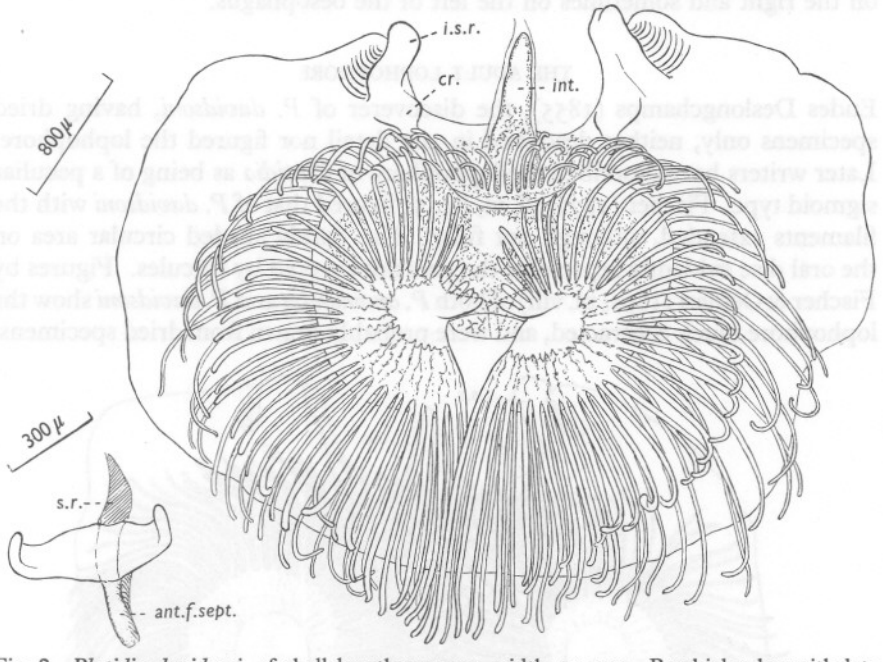

Fig. 8. *Platidia davidsoni*, of shell length 3·7 mm, width 4·4 mm. Brachial valve with late zygolophe, drawn living. Brachial support, indicated by dotted lines, added after clearing in cedar wood oil. Inset septum and divergent lamellae enlarged. *ant.f.sept.*, anterior face of septum; *cr.*, crura; *int.*, intestine; *i.s.r.*, inner socket ridge; *s.r.*, low septal ridge.

support of an individual of greater length (3·5 mm), but lesser width (3·2 mm) is shown in Fig. 12A, B: the septal pillar is continued posteriorly as a low ridge almost to the edge of the foramen. The posterior prolongation of the septal pillar is variable in development, for in the larger shell to be described it extended only a short distance (Fig. 8).

The late zygolophous stage occurred in an individual 3·7 mm long and 4·4 mm wide (Fig. 8). It appears to be of the normal type, except that the reflected portion of the lateral arms does not reach as far posteriorly as in most genera with plectolophes in the adult. The septum still bears what appear to be broad divergent lamellae, and these are produced on their outer ends into small ventrally curved processes (Fig. 8, inset). Possibly the latter are

rudiments of a transverse band, or it may be that the lamellae are undergoing transformation into the curved prongs or short ascending branches of the adult. The divergent lamellae resemble those in immature *Kraussina rubra* (Elliott, 1949) and in the adult *Pumilus antiquatus* (Atkins, 1958), but are set at a much wider angle to each other, being almost horizontal, and are borne on a high septal pillar. Crura are still short at this size.

It may be noted that the low posterior end of the septum sometimes passes on the right and sometimes on the left of the oesophagus.

THE ADULT LOPHOPHORE

Eudes Deslongchamps (1855), the discoverer of *P. davidsoni*, having dried specimens only, neither described in any detail nor figured the lophophore. Later writers have described the lophophore of *Platidia* as being of a peculiar sigmoid type. Fischer (1872, pl. vi, fig. 5) figured that of *P. davidsoni* with the filaments extended, although not fully. The darkly shaded circular area on the oral disc evidently represents the part not covered by spicules. Figures by Fischer & Oehlert (1891, pl. viii) of both *P. anomioides* and *P. davidsoni* show the lophophore much contracted, and were probably drawn from dried specimens.

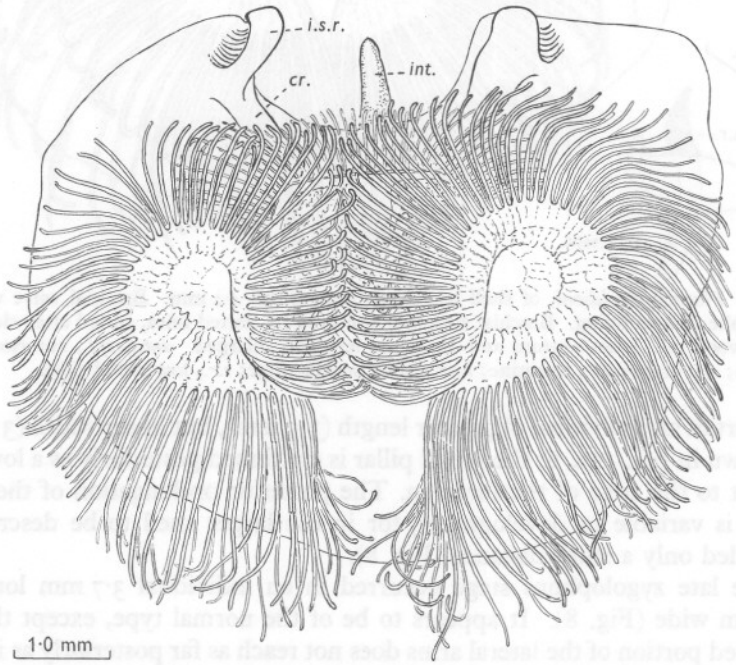

Fig. 9. *Platidia davidsoni*, of shell length 6·2 mm, width 7·0 mm. Brachial valve with fully adult plectolophe, drawn living. The spiral arm consists of one short coil. The brachial support added after clearing in cedar wood oil, but not clearly indicated. *cr.*, crura; *int.*, intestine; *i.s.r.*, inner socket ridge.

The adult lophophore of *P. davidsoni* as seen in the living animal is a somewhat modified plectolophe with a short spiral arm of little more than one coil (Fig. 9). This arm is held well away from the brachial valve by the septal pillar and the body (Figs. 10, 11). In the normally feeding animal the appearance is of a broad plectolophous lophophore.

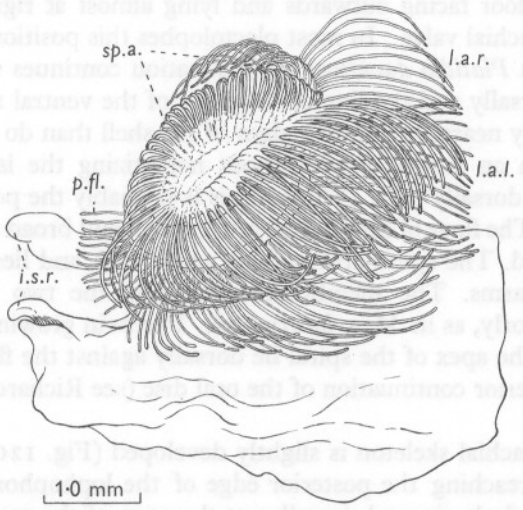

Fig. 10. *Platidia davidsoni*, of shell length 5·5 mm, width 7·0 mm; shell irregular. Side view of plectolophe, drawn after narcotizing, fixing and clearing in cedar wood oil. *i.s.r.*, inner socket ridge; *l.a.l.*, left and *l.a.r.*, right lateral arm; *p.fl.*, filaments behind mouth; *sp.a.*, spiral arm.

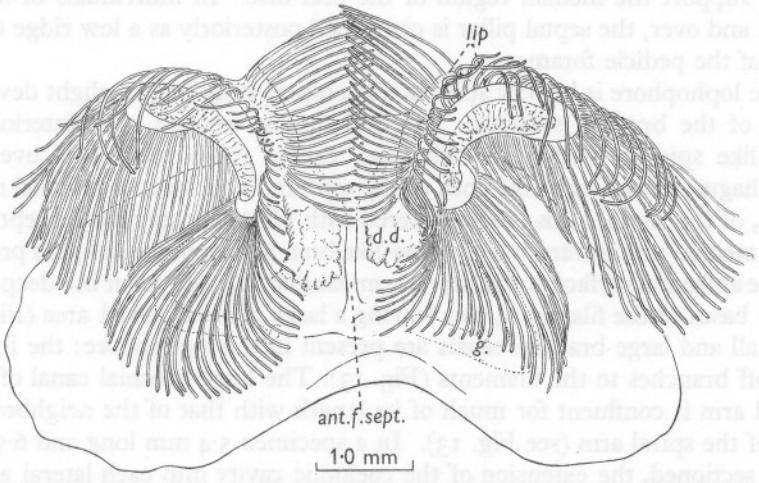

Fig. 11. *Platidia davidsoni*. Anterior view of brachial valve and plectolophe, the ventral side only of the spiral arm shown. Same individual as in Fig. 10, but drawn living. Shell irregular with artificial sulcus caused by the surface of attachment. *ant.f.sept.*, anterior face of septum; *d.d.*, digestive diverticulum; *g.*, gonad; *lip*, lip of food groove.

In the schizolophous stage, as Morse (1871, p. 420–1) noted in *Terebratulina septentrionalis*, and as probably in this stage in all brachiopods, the brachial membrane, or floor of the lateral arms, faces ventrally, and is almost parallel with the floor of the brachial valve, although raised to a varying degree medianly. As the zygolophous stage approaches, the lateral arms become deflected, the floor facing outwards and lying almost at right angles to the plane of the brachial valve. In most plectolophes this position is more or less retained, but in *Platidia davidsoni* the inclination continues so that the floor partly faces dorsally and the line of the bases of the ventral row of filaments lies considerably nearer the lateral edges of the shell than do the bases of the dorsal row. In an animal fixed without narcotizing the lateral arms face almost entirely dorsally (Fig. 13 E) and this is probably the position when the shell is closed. The floor of each lateral arm is short and broad and its posterior edge is incurved. The spiral arm is short and broad, and lies largely ventral to the lateral arms. The membrane connecting the two sides is deeply embayed anteriorly, as in *Megerlia truncata*. The twin growing regions of the lophophore at the apex of the spiral lie dorsally against the floor of this arm, which is an anterior continuation of the oral disc (see Richards, 1952, for use of term).

The adult brachial skeleton is slightly developed (Fig. 12 C, D). The crura are short, not reaching the posterior edge of the lophophore (Figs. 9, 10). The broad, nearly horizontal, lamellae at the apex of the septal pillar of the young stages of the lophophore have changed into the prongs or short ascending branches of the adult and curve around the sides of the oesophagus. They support the median region of the oral disc. In individuals of length 4 mm and over, the septal pillar is continued posteriorly as a low ridge to the edge of the pedicle foramen.

The lophophore is heavily spiculated, compensating for the slight development of the brachial skeleton. The oral disc is covered with interlocking plate-like spicules with some windows, except for a small area over the oesophagus, extending to the apex of the septum. The floor, or brachial membrane, of the lateral arms is also covered with plate-like spicules, except for a small median area toward which spine-like branches from the spicules project. On the abfrontal surface of the lateral arms similar spicules occur in a deep band at the bases of the filaments, but leaving a large median naked area (Fig. 9).

Small and large brachial canals are present in the lophophore: the former give off branches to the filaments (Fig. 13). The large brachial canal of each lateral arm is confluent for much of its length with that of the neighbouring part of the spiral arm (see Fig. 13). In a specimen 5·4 mm long and 6·9 mm wide, sectioned, the extension of the coelomic cavity into each lateral arm—known as the brachial pouch—was exceedingly short (Fig. 13 C).

A 'blood' vessel is present in the usual position within the small brachial canal and a branch is given off to each filament.

The development of muscle fibres in the walls of the canals is slight.

The principal (*n.p.*) and external (*n.ext.*) nerves of the lophophores are clearly discernible, while the secondary nerve (*n.sec.*) is difficult to distinguish. At the magnification of the section drawn (Fig. 13F) no more than the position of the nerves can be indicated.

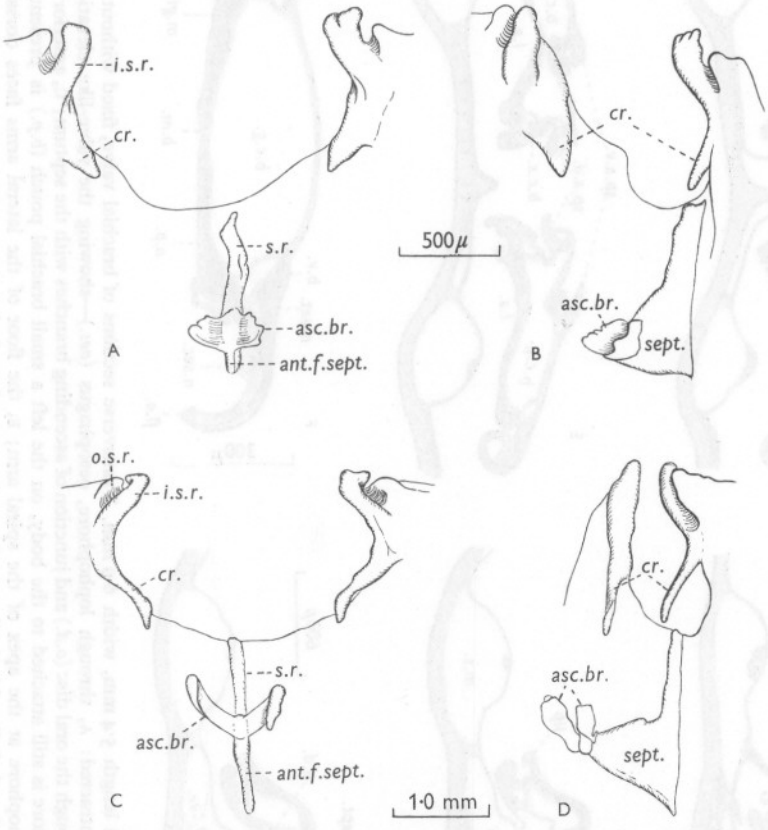

Fig. 12. *Platidia davidsoni*. Brachial support of: A and B, individual of shell length 3·5 mm, width 3·2 mm; C and D, individual of shell length 6·6 mm, width 8·4 mm. A and C ventra views; B and D lateral views. *ant.f.sept.*, anterior face of septal pillar; *asc.br.*, ascending branch; *cr.*, crura; *i.s.r.*, inner, and *o.s.r.*, outer socket ridges; *s.r.*, septal ridge; *sept.*, septum.

The distribution of the mucous gland cells on the lophophore is similar to that in other plectolophes. The abfrontal band below the filaments—in the exhalant chamber—is narrow, but the cells are deep. A narrow band of deep gland cells is present on the brachial membrane at the base of the lip of the food groove (Fig. 13F). Scattered mucous cells occur in the walls, including the lip, of the food groove.

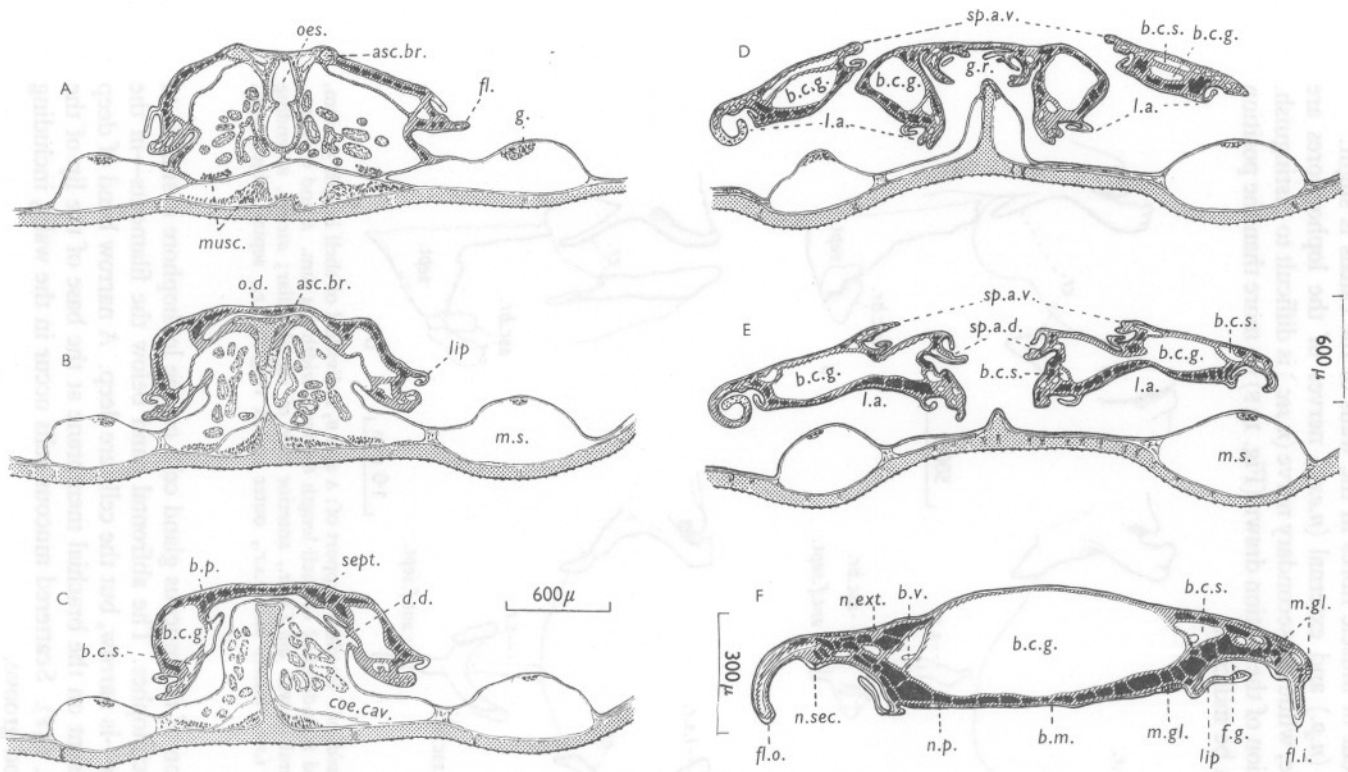

Fig. 13. *Platidia davidsoni*, of shell length 5·4 mm, width 6·9 mm. Transverse sections of brachial valve, fixed without being narcotized and therefore with plectolophe contracted: A, through lophophore, oesophagus (*oes.*)—showing the valve-like elevation of the wall—and the ascending branches; B, through the oral disc (*o.d.*) and junction of ascending branches with the septum; C, anterior to the ascending branches—on the right the lophophore is still attached to the body, on the left a small brachial pouch (*b.p.*) is present; D, through the growing regions (*g.r.*) of the lophophore at the apex of the spiral arm; E, the floor of the lateral arms faces dorsally; F, transverse section of lateral arm in position in closed shell, with the brachial membrane or floor facing the brachial or dorsal valve. *asc.br.*, ascending branches; *b.c.g.*, great, and *b.c.s.*, small brachial canals; *b.m.*, brachial membrane; *b.v.*, 'blood' vessel; *coe.cav.*, coelomic cavity; *d.d.*, digestive diverticula; *fl.*, filament; *fl.i.*, inner and *fl.o.*, outer filaments and bases; *f.g.*, food groove; *g.*, gonad; *l.a.*, lateral arm; *lip*, lip of food groove; *m.gl.*, mucous gland cells; *m.s.*, mantle sinus; *musc.*, muscle; *n.ext.*, external; *n.p.*, principal; and *n.sec.*, secondary nerves; *sept.*, septum; *sp.a.d.*, dorsal and *sp.a.v.*, ventral side of spiral arm. Spaces formerly occupied by spicules shown black: supporting substances shown hatched.

The filaments are arranged in a double alternating series of inner filaments, with ridged frontal surfaces, and outer filaments with grooved frontal surfaces, but behind the mouth some sixteen or seventeen pairs are in single series and of the ridged type. Spicules are present in both types of filament. They are broad transverse bands, granulated and somewhat irregular in outline, present abfrontally within the tube of supporting substance and curving around the sides of the filaments (Figs. 14, 15). The supporting substance in brachiopods was described as semi-cartilagenous by Hancock (1858), but according to Prenant (1928) working on *Terebratulina retusa* (=*caput-serpentis*) it is more nearly like collagen: he preferred to call it simply 'substance de soutien'.

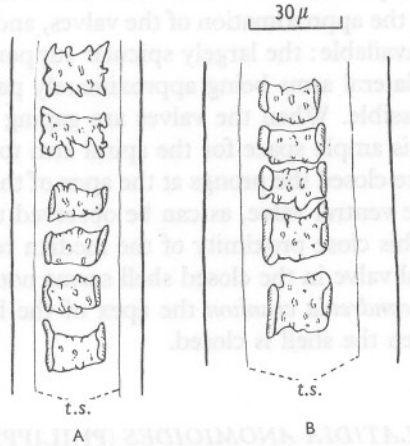

Fig. 14. *Platidia davidsoni*. Spicules in two adjacent filaments at the same distance from the food groove, viewed from the frontal surface. A, an inner filament, with ridged frontal surface; B, an outer filament, with grooved frontal surface. *t.s.*, tube of supporting substance.

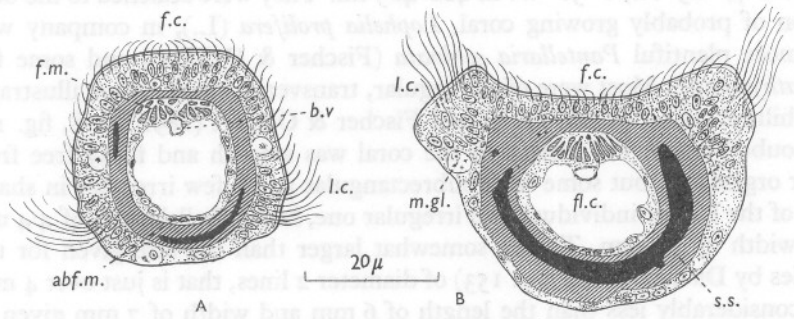

Fig. 15. *Platidia davidsoni*. Transverse sections of A, inner filament, with ridged frontal surface; B, outer filament, with grooved frontal surface. *abf.m.*, abfrontal muscles; *b.v.*, 'blood' vessel; *f.c.*, frontal cilia; *fl.c.*, filamentar canal; *f.m.*, frontal group of muscles; *l.c.*, lateral cilia; *m.gl.*, mucous gland cell; *s.s.*, supporting substance. Spaces formerly occupied by spicules shown black. Frontal cilia not shown at their full length, as they beat along the filament.

Longitudinal muscle fibres are present in the walls of the filamentar canal, especially well developed in a striated frontal group and to a lesser extent abfrontally (Fig. 15); the latter appear to be smooth.

The structure of the lophophore of *Platidia* is peculiarly adapted to the shallow mantle cavity of the closed shell. In separating and closing the valves of a detached living animal it is possible to see something of the normal movements of the lophophore. As the valves are closed the anterior ends of the side arms approach each other in the mid-line and the whole lophophore appears to be flattened by the approximation of the valves. As the valves are separated the lophophore is raised, although under these conditions the filaments remain tightly coiled. It would seem that it is so constructed that it can be flattened by the approximation of the valves, and fitted into the small dorso-ventral space available: the largely spicular support of the lophophore, and the floor of the lateral arms being approximately parallel with the valve floor making this possible. When the valves are gaping widely, as naturally when feeding, there is ample space for the spiral arm to expand.

When the valves are closed the prongs at the apex of the septal pillar almost touch the floor of the ventral valve, as can be observed through the foramen of an empty shell. This close proximity of the median region of the brachial support to the ventral valve in the closed shell seems not unusual in brachiopods. In young *Macandrevia cranium* the apex of the hood almost touches the pedicle valve when the shell is closed.

PLATIDIA ANOMIOIDES (PHILIPPI)

On 13 May 1958, over sixty *P. anomioides* from 1·1 to 4·6 mm long were dredged by R.V. 'Sarsia' somewhat to the south-east of La Chapelle Bank in position 47° 25′ N., 6° 30′ W. in 400–405 fm. They were attached to the dead region of probably growing coral, *Lophelia prolifera* (L.), in company with the more plentiful *Pantellaria echinata* (Fischer & Oehlert), and some few *Megathyris* sp.[1] Most were of the regular, transversely oval, shape illustrated by Philippi (1844, pl. 18, fig. 9) and Fischer & Oehlert (1891, pl. 8, fig. 14), no doubt because the surface of the coral was smooth and fairly free from other organisms, but some were subrectangular and a few irregular in shape. One of the largest individuals, an irregular one, had a shell length of 4·4 mm and width of 5·0 mm. This is somewhat larger than the size given for this species by Davidson (1887, p. 153) of diameter 2 lines, that is just over 4 mm, but considerably less than the length of 6 mm and width of 7 mm given by Fischer & Oehlert (1891, p. 95). Massy (1925) records a maximum size of *ca.* 5 × 6 mm of specimens taken on *Lophohelia* (= *Lophelia*) off the south-west of Ireland. The young are occasionally rather longer than broad, but with

[1] Bivalves on the coral were few.

growth tend to become as wide or wider than long. The mantle margin is furnished with fairly short setae, as in *P. davidsoni*.

The numbers of *P. anomioides* obtained has allowed of the working out of the growth stages of the lophophore, and in particular of the brachial support, which is considerably further developed than in *P. davidsoni*.

THE GROWTH STAGES OF THE LOPHOPHORE AND ITS SUPPORT

The lophophore of *P. anomioides* unfortunately did not expand well after separation of the valves; stovaine failed to give good results and magnesium chloride did not always act well.

The lophophore passes through the growth stages described for *P. davidsoni*. The filaments appear to be generally longer than in that species—compare, for instance, Figs. 3B and 16 and Figs. 9 and 21—and a greater number are in single series behind the mouth, some 25 or 26 pairs as compared with 16 or 17 pairs in *P. davidsoni*.

The lophophore is trocholophous (Fig. 16) up to a shell length of about 1·6 mm: it then becomes slightly indented in the mid-line anteriorly. A minute triangular septum and short crura are present. The individual figured (Fig. 17), of shell length 1·8 mm and width 1·9 mm, had the lophophore poorly expanded, but clearly shows the relation of the septum to the anterior median invagination. All the filaments were in a single row and were spiculated: spicules were also present in a wide band at their bases. Fig. 18 shows the characteristic arrangement of a large spicule on each side of the septum, the two converging anteriorly. At a diameter of some 2 mm the crura were longer than shown in Fig. 17, and the triangular septum somewhat higher, but as yet not bifurcated (Fig. 23A). Minute projections were present at its apex at a shell length of 2·3 mm and width 2·5 mm (Fig. 20A).

The late schizolophous stage was found at a diameter of 2·5 mm: the inner side of the side arms or lobes had begun to turn outwards, this stage corresponding to that figured for *P. davidsoni* at a length of 3·2 mm (see Fig. 6). The crura were short and reached to just behind the lophophore; crural processes were absent. The apex of the septum was forked; anterior ends of the descending branches if present must have been short as they were not distinguishable in the uncleared animal. It would appear that in this individual the lophophore was somewhat retarded in development as the zygolophous stage occurred in three individuals of length 2·4 mm, width 2·8 mm (Fig. 19); length 2·6 mm, width 2·9 mm; and length 2·6 mm, width 2·7 mm. In the first two of these the twin-growing regions of the lophophore were close together, in the last they were separated. In all three crural processes were present, although short: the posterior ends of the descending branches were either short or not yet formed; the anterior ends were present and longest in the third specimen. The ascending branches at the apex of the septum were best developed in the second specimen. At a length and width of of 3·3 mm

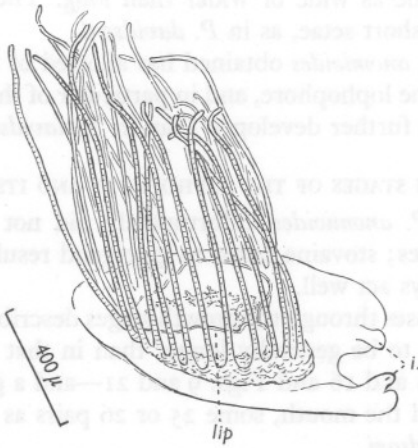

Fig. 16. *Platidia anomioides*, shell length 1·2 mm, width 1·3 mm. Side view of brachial valve with trochophe, drawn narcotized. Spicules indicated, except in filaments of the far side. *i.s.r.*, inner socket ridge; *lip*, lip of food groove.

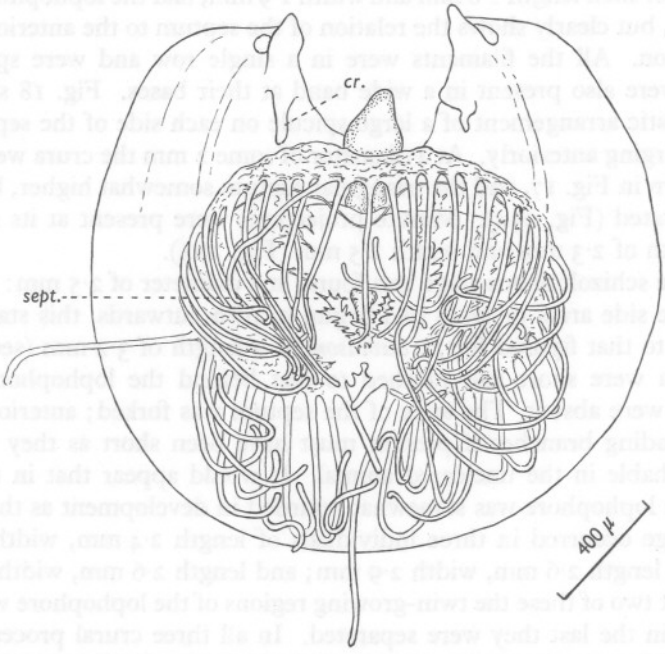

Fig. 17. *Platidia anomioides*, shell length 1·8 mm, width 1·9 mm. Brachial valve with early schizolophe, drawn unsuccessfully narcotized. It shows the relation of the septum (*sept.*) to the anterior median invagination of the lophophore. *cr.*, crura, *sept.*, septum.

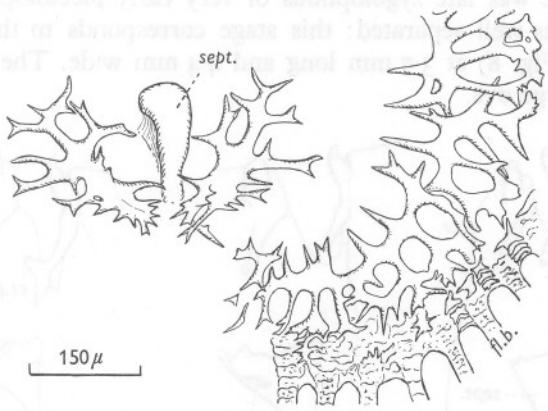

Fig. 18. *Platidia anomioides*, of length 1·9 mm, width 2·2 mm. Spicules of part of schizolophe viewed ventrally. The large spicules, one on each side of the septum (*sept.*) are to be noted. *fl.b.*, bases of filaments in single series at this stage.

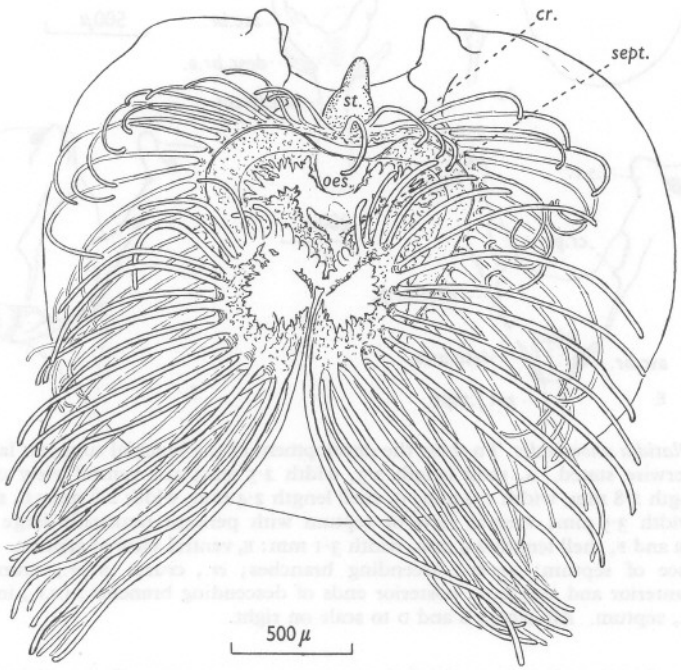

Fig. 19. *Platidia anomioides*, of length 2·4 mm, width 2·8 mm. Brachial valve with zygolophe, the twin growing regions close together: drawn narcotized. *cr.*, crura; *oes.*, oesophagus; *sept.*, septum, with ascending branches; *st.*, stomach.

the lophophore was late zygolophous or very early plectolophous with the growing regions well separated: this stage corresponds to that figured for *P. davidsoni* (Fig. 8) at 3·7 mm long and 4·4 mm wide. The animal was a female with large ova.

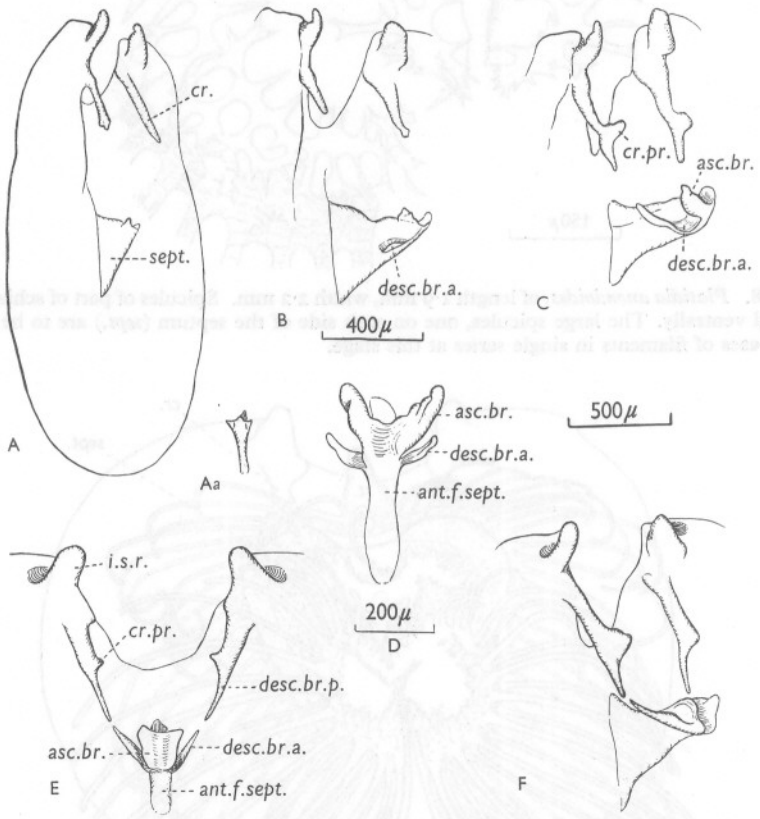

Fig. 20. *Platidia anomioides*. To show the development of the brachial support: lateral views unless otherwise stated. A, shell length 2·3, width 2·5 mm; A*a*, ventral view of septum; B, shell length 2·8 mm, width 2·9 mm; C, shell length 2·4 mm, width 2·8 mm; D, shell length 2·9 mm, width 3·5 mm; ventral view of septum with perhaps unusually large ascending branches; E and F, shell length 2·9 mm, width 3·1 mm: E, ventral view of septum. *ant.f.sept.*, anterior face of septum; *asc.br.*, ascending branches; *cr.*, crura; *cr.pr.*, crural process, *desc.br.a.*, anterior and *desc.br.p.*, posterior ends of descending branches; *i.s.r.*, inner socket ridge; *sept.*, septum. All except B and D to scale on right.

As fine details of the brachial support are not easily discernible in valves in which the flesh is present, they will be described from those in which it had been removed. The anterior ends of the descending branches had begun to grow from the septum in an individual of shell length 2·8 mm and width 2·9 mm (Fig. 20B). The crura were short and crural processes absent. In one

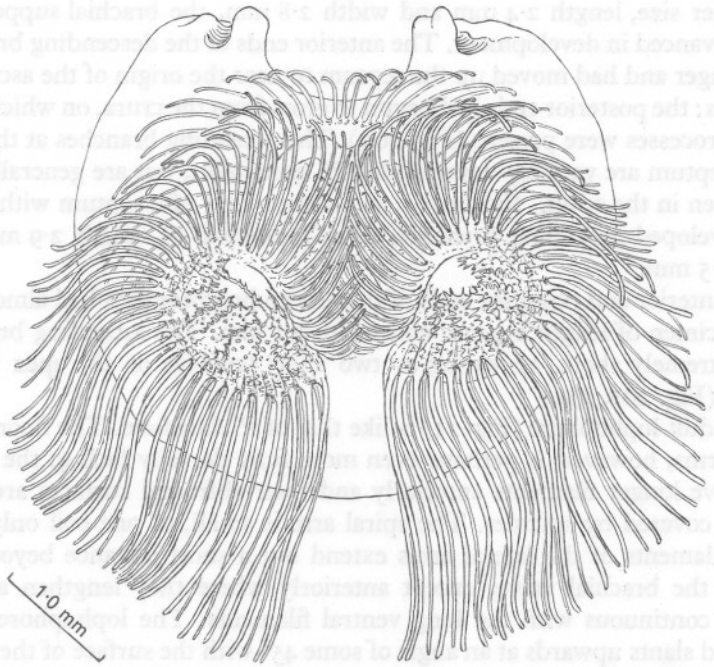

Fig. 21. *Platidia anomioides*, of shell length 4·6 mm, width 4·4 mm. Brachial valve with plectolophe, drawn living and narcotized.

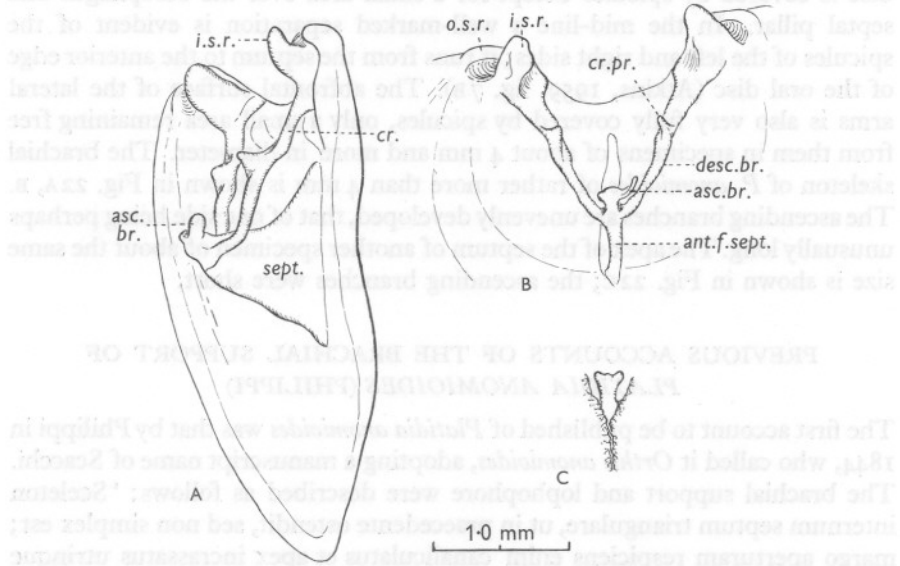

Fig. 22. *Platidia anomioides*, of shell length and width approximately 4 mm. A, side view of brachial valve; B, ventral view of brachial support, with the ascending branches unequally developed; C, ventral view of the septum of another individual of about the same size. *o.s.r.*, outer socket ridge; other lettering as in Fig. 20.

of smaller size, length 2·4 mm and width 2·8 mm, the brachial support was more advanced in development. The anterior ends of the descending branches were longer and had moved up the septum to near the origin of the ascending branches: the posterior ends had begun to grow from the crura, on which short crural processes were present (Fig. 20C). The ascending branches at the apex of the septum are variably developed in *P. anomioides*, but are generally very short even in the adult. Fig. 20D is an anterior view of a septum with rather well-developed ascending branches of an individual of length 2·9 mm and width 3·5 mm.

The anterior and posterior ends of the descending branches had almost met in a specimen of length 2·9 mm and width 3·1 mm. The ascending branches were extremely short, appearing as two short lamellae on the apex of the septum (Fig. 20E, F).

The adult lophophore (Fig. 21) is like that of *P. davidsoni*. The floor of the lateral arms, however, is perhaps even more fully dorsally facing: the lateral arms have longer filaments anteriorly and their abfrontal surfaces are more entirely covered by spicules. The spiral arm is small, of one coil only. The dorsal filaments of the lateral arms extend but a short distance beyond the edge of the brachial valve, except anteriorly where they lengthen as they become continuous with the long ventral filaments. The lophophore when expanded slants upwards at an angle of some 45° with the surface of the dorsal valve, so that it is raised high above the valve anteriorly. This anterior upward tilting of the lophophore is found also in *P. davidsoni* (see Fig. 10). The oral disc is covered by spicules except for a small area over the oesophagus and septal pillar. In the mid-line a well-marked separation is evident of the spicules of the left and right sides; it runs from the septum to the anterior edge of the oral disc (Atkins, 1959, fig. 7B). The abfrontal surface of the lateral arms is also very fully covered by spicules, only a small area remaining free from them in specimens of about 4 mm and more in diameter. The brachial skeleton of *P. anomioides* of rather more than 4 mm is shown in Fig. 22A, B. The ascending branches are unevenly developed, that of one side being perhaps unusually long. The apex of the septum of another specimen of about the same size is shown in Fig. 22C; the ascending branches were short.

PREVIOUS ACCOUNTS OF THE BRACHIAL SUPPORT OF *PLATIDIA ANOMIOIDES* (PHILIPPI)

The first account to be published of *Platidia anomioides* was that by Philippi in 1844, who called it *Orthis anomioides*, adopting a manuscript name of Scacchi. The brachial support and lophophore were described as follows: 'Sceleton internum septum triangulare, ut in praecedente ostendit, sed non simplex est; margo aperturam respiciens enim canaliculatus et apex incrassatus utrinque bicarinatus, inter carinas foveolatus est. Brachia circulos perfectos describunt,

cirrosque externe gerunt'. No mention was made of descending branches. The length of the shell was given as $1\frac{3}{4}'''$, and the width as $2'''$.

In January 1852 Costa gave the name *Platidia* to the genus of which *P. anomioides* was the type and only species. Davidson unaware of this, in May 1852*a* (p. 371) gave the name *Morrisia* to the genus and described 'the apophysary system consisting of two branches, originating at the base of the dental sockets, and united to a small elevated process arising from the centre of the valve'. As the type of the genus he gave *M. seminulum*. One of the accompanying figures appears to show two minute horns at the apex of the septum, although these are not mentioned in the text. The other figure shows the lophophore 'with two subspiral or *sigmoid* arms' and the filaments quite well extended: a spiral arm, however, is not shown. It was apparently drawn from a dried specimen (see Davidson, 1887, p. 153). The above description of the lophophore and its support was repeated under the name *Morrisia anomioides* by Davidson (1852*c*) in the same year in the *Proc. Zool. Soc.*

In 1887 (p. 153) Davidson's description was as follows: 'in the interior of the dorsal valve the loop is not reflected. The converging principal lamellae are found attached first to the hinge-plate, and then to a small pillar-shaped median vertical septum'. The accompanying figure (1887, pl. 21, fig. 18) shows no horns on the septum.

Fischer & Oehlert (1891, p. 94) described and figured the brachial support as more fully developed than in any previous account. They said: 'De la base de ces apophyses fovéales s'élèvant presque verticalement deux cruras longs et grêles, limités par deux fines pointes crurales, au delà desquelles les branches descendantes, minces et ténues, vont en convergeant rejoindre un pilier septal très élevé, auquel elles se soudent vers les trois quarts de sa hauteur. Le pilier est constitué par une lamelle triangulaire remontant jusqu'au bord de l'échancrure; cette lamelle, peu épaisse, est arquée vers l'arrière et légèrement renflée au sommet, qui se termine par deux pointes divergentes courtes et assez massives, supportant la membrane brachiale médiane'.

It is most probable from the appearance of the shell and pedicle opening that Philippi's *P. anomioides* is the same shell as now goes under that name, although his description of the brachial support, without descending branches, would apply to *P. davidsoni*. Philippi's specimen of *P. anomioides*, about 3·5 mm long and about 4 mm wide, is of a size to have the descending branches complete if they had not been broken.

THE IDENTITY OF *TEREBRATULA SEMINULUM* PHILIPPI 1836

Philippi in 1836 published a short account with figures (pl. vi, fig. 15) of a small shell which he called *Terebratula seminulum*. His description is as follows: 'Testa circa $1'''$ longa, totidem lata, mox exacte orbicularis, mox transversa, mox ovata, in fronte saepe emarginata, vid. fig. *b*, *d*, *e*, *f*, semper

compressa, densissime punctata. Apertura incompleta, v. fig. 15*d*; deltidium non vidi. Sceleton internum simplicissimum, a lamella triangulari versus frontem declivi formatum, v. fig. *a* ubi a latere inspectum est. Brachia versus cardinem connata seriem ciliarum simplicem, orbicularem antice interruptam exhibent v. f. *b*. Color testae albidus'.

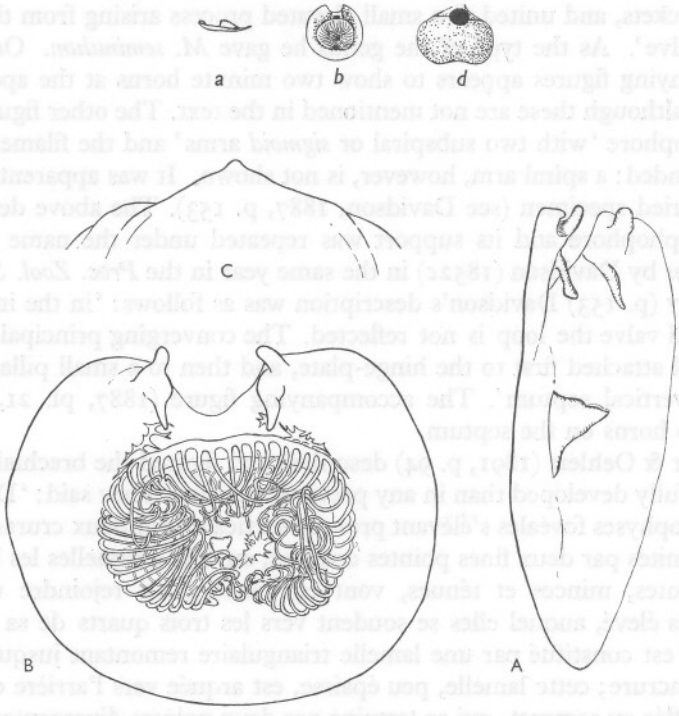

Fig. 23. A, B, C, *Platidia anomioides* of diameter 2 mm: A, side view of brachial valve; B, brachial valve with contracted schizolophe; C, beak of shell viewed ventrally (B and C are of a second individual). *a*, *b*, *d*. *Terebratula seminulum* Philippi of diameter 1 line, after Philippi's fig. 15*a*, *b*, *d*, for comparison with *Platidia anomioides* of the same size.

There has been argument as to whether *T. seminulum* is a *Platidia* or an *Argyrotheca* (=*Argiope*). In 1844 (p. 69) Philippi in describing *Orthis neapolitana* Scacchi (now *Argyrotheca cordata*) said 'cfr. vol. 1, p. 97, t. 6, f. 15 nomine Tereb. seminuli'. This possibly accounts for Davidson's (1852*b*, p. 514) statement in corrections to his paper earlier in the same volume (1852*a*, pp. 361–77) that 'the name *seminulum* was intended by Philippi for an *Argiope*, although his figure may have been taken from more than one shell'. In his paper (1852*a*) Davidson had evidently described and figured the *Platidia anomioides* of Philippi under the name *Morrisia seminulum* Philippi, and in 1921 (p. 332) Dall called it *Platidia seminula*, the generic name

Platidia having been proposed for the genus by Costa in January 1852, a few months earlier than Davidson's name of *Morrisia*.

Fischer & Oehlert (1891, p. 97) considered not only that *Platidia anomioides* and *Terebratula seminulum* were distinct, but that the latter probably belonged to a different generic group, perhaps to *Cistella* (= *Argyrotheca*): their opinion was apparently based on the form of the lophophore. Thomson (1927, p. 218) said that *Platidia anomioides* 'has been confused by Davidson and Dall (1921) with *Terebratula seminulum* Philippi, 1836, a species of similar external form referable to the genus *Amphithyris*'. Thomson (p. 216) separated *Terebratula seminulum* from *Platidia anomioides* because 'of the distinct character of the lophophore'. He had apparently temporarily overlooked the fact that as far as was known all the more highly organized lophophores pass through a schizolophous stage—the type of lophophore depicted by Philippi for *Terebratula seminulum*—and there was no reason to assume that *Platidia anomioides* was an exception, or that *Terebratula seminulum* seen by Philippi was necessarily in an adult state at a diameter of 1 line, that is approximately 2 mm.

Jeffreys (1878, p. 411) mentioned that according to Seguenza the young of *Platidia anomioides* is the *Terebratula seminulum* of Philippi, and this is probably what it is. *Platidia anomioides* at a shell length of about 2 mm closely resembles in shell form, triangular septum (Fig. 23A) and schizolophous lophophore (shown contracted in Fig. 23B) the figures by Philippi (1836, pl. 6, fig. 15*a*, *b*, *d*), reproduced in Fig. 23*a*, *b*, *d*, of *Terebratula seminulum* from Sicily of the same size. He clearly shows the amphithyrid foramen, not present in the genus *Argyrotheca*. The identity of the shell he figured in pl. 6, fig. 15*e*, *f*, *g*, is uncertain: it appears too elongated for even a young *Platidia*.

Unless Philippi's specimens of *Terebratula seminulum* are in existence and can be examined to determine without any doubt that they are the young of *Platidia anomioides*, then it seems best to leave that name undisturbed.

FURTHER REMARKS ON LOPHOPHORES

The brachial support is in a more advanced state in adult *Platidia anomioides* than in adult *P. davidsoni*, in that the descending branches are present and complete in the former and absent in the latter. But on the other hand the ascending branches are larger in *P. davidsoni* than in *P. anomioides*. In *P. anomioides* the descending branches, although complete, reach only to the centre of the oral disc, leaving the lateral arms unsupported except by spicules. This arrangement no doubt allows of the packing away of the lophophore in the constricted space available when the shell is closed.

The ascending branches or divergent lamellae of immature *P. davidsoni* are reminiscent of those of immature *Kraussina rubra* (Elliott, 1949) and of adult *Pumilus antiquatus* (Atkins, 1958) but differ in that they are almost horizontal and the septal pillar which bears them is considerably higher than

in the two other species. Moreover, *Platidia* differs widely from the Kraussinidae in shell shape and beak characters.

Beecher (1893) gave among the diagnostic characters of the Terebratellidae King emend. 'cirri directed inwardly during larval stages', in contrast to the Terebratulidae Gray in which it was said 'cirri directed outwards in larval stages', that is in stages when the lophophore is either trocholophous or early schizolophous. Thomson (1927, pp. 180, 202) followed Beecher in making this supposed difference between the direction of the cirri or filaments in young stages one of the chief diagnostic differences between the two families, and this has been repeated by later workers.

Beecher's figures of the trocholophous and early schizolophous stages of *Dallinella* (= *Terebratalia*) *obsoleta* (1893, pl. ii, figs. 10, 11, 12) were, he stated (1895, in the legends on p. 398), 'drawn from specimens which had been dried and afterwards expanded by soaking in water, and then stained and prepared for mounting. The original proportions and relations of the parts may be therefore somewhat altered'.

In the contracted state as when the valves of the living animal are first separated, or the animal is preserved without narcotizing, the filaments in the trocholophous and early schizolophous stages in terebratellaceans are as shown by Beecher, but when the animal is feeding with the shell gaping and lophophore expanded the filaments are directed ventrally and outwards, as may be seen from the figures of *Platidia davidsoni*, and *P. anomioides* accompanying this paper and from those of *Pumilus antiquatus* (Atkins, 1958). This has also been found to be so in *Argyrotheca cordata*, *Megathyris detruncata*, *Pantellaria echinata*, *Terebratalia transversa* and *Terebratella inconspicua*, and no doubt occurs also in *Macandrevia cranium* but unfortunately the very young of this species have so far only been seen preserved. Accounts are in preparation of the growth stages of most of these species and also of those of certain other brachiopods.

THE CILIARY FEEDING MECHANISM OF *PLATIDIA*

Work on the ciliary feeding mechanism of *Platidia* was done on *P. davidsoni*, which, being dredged from only 45 to 48 fm, survived well in the laboratory tanks. After separating the valves, the lophophore soon expanded and in one, perhaps exceptional, instance remained in good condition for 10 days at temperatures of 13° to 15·6° C, with the lateral cilia beating rapidly with a good metachronal wave. This species was found to narcotize easily with stovaine one drop of 1% stovaine being added to a watch-glass of sea water at intervals. *P. anomioides*, dredged from 400 to 405 fathoms was on the contrary difficult to deal with.

P. davidsoni usually, although not always, lifts the shell at an angle from the substratum, so that it is raised 1 to 2 mm anteriorly, preparatory to opening

the valves, uncoiling the filaments, ready for feeding. It can also shift the shell a little sideways in spite of its very short stalk.

In a normally feeding animal the valves gape fairly widely to an angle of 45° or more. A large specimen of some 6 mm in length was seen to have an anterior gape of 3 to 3·5 mm, and the lower, dorsal, valve was lifted from the substratum about 2 mm in front.

The lophophore as seen through the gape has the appearance of a plectolophe, but the short spiral arm in the expanded state is almost entirely ventral to the lateral arms. The dorsal filaments of the lateral arms extend to the edge of the dorsal valve: the ventral filaments usually appear to hang down toward the lower, dorsal valve—that is they do not touch on the edge of the ventral mantle as in other brachiopods observed—so that the inhalant current is drawn in somewhat dorsally and the exhalant current leaves the shell over a wider area than in most brachiopods with plectolophous lophophores. The correct position of the filaments cannot be shown in an opened animal.

The filaments on opposite sides of the short spiral arm either touch at their tips, interdigitate, or a slight space is left between the tips, which then appear to touch on the ventral mantle.

The ciliation of the lophophore and the mantle

The body of the lophophore is entirely ciliated—except possibly for mucous cells—as indicated by the movement of particles.

On the filaments the ciliation is in three main tracts, a frontal and paired lateral tracts.

The frontal cilia (*f.c.*, Fig. 15) are about 20 μ long. They appeared to be all alike, as seen in life across the frontal surface, when an inner filament with ridged frontal surface was bent sharply outwards. These cilia, as in other brachiopods examined, seem to be capable of reversing the direction of their beat (Atkins, 1956, 1958).

The lateral, current-producing, cilia (*l.c.*, Fig. 15) are some 30 μ long. They beat across the length of the filaments from the frontal to the abfrontal surface. The metachronal wave is of the type termed dexioplectic (Knight-Jones, 1954).

Sparse abfrontal cilia occur but do not appear to be effective, as no current could be demonstrated.

The ciliary currents

On the outer abfrontal surfaces of the lateral and spiral arms currents pass toward the bases of the filaments, although no abfrontal currents on the latter could be demonstrated.

The floor, or brachial membrane, of the lateral arms has currents passing toward the median line and posteriorly in the direction of the mouth.

On the posterior and lateral regions of the large oral disc currents are directed toward the food groove. On the anterior region of the disc they are anterior in direction and particles pass off into the exhalant current.

The general direction of the currents is anteriorly on the ventral mantle. Over the middle region of the valve, that is lying to the inner side of the gonads, currents pass into an anteriorly directed current in the mid line. To the outer side of the gonads currents pass somewhat laterally and anteriorly into a submarginal anteriorly directed current. In fact over the gonads currents pass in opposite directions, toward the mid line and laterally. Currents on the dorsal mantle are similar in direction.

On the anterior body wall currents on each side of the septal pillar pass dorsally and anteriorly, and when no exhalant current is evident particles collect at the base of the septal pillar. This material would no doubt be lifted into the strong exhalant current when this is working.

In the young stages of the lophophore, trocholophous and early schizolophous, the inhalant current produced by the lateral cilia on the filaments, passes into the bell-shaped lophophore (Fig. 3B) and escapes between the filaments all around as previously described in *Terebratulina retusa* and *Pumilus antiquatus* (Atkins, 1956, 1958). As the invagination of the schizolophe deepens the inhalant current becomes divided into two and a narrow excurrent channel is present between the two lobes of the schizolophe, as in the adult *Pumilus*.

As in plectolophes generally the inhalant currents are lateral and paired and the exhalant single and median.

Platidia davidsoni was unusual in that the lateral cilia continued beating with a good metachronal wave for several days after separation of the valves. This allowed of some observations being made on them. If a filament is suddenly coiled, while the laterals are beating, they slow or stop, and as the filament is uncoiled they begin beating again. When the laterals are active there are no momentary intermissions, such as occur in lamellibranchs several times in a minute (Lucas, 1931, pp. 157–8; Atkins, 1936, pp. 295–6), although they may stop for varying periods on some filaments or parts of filaments. The lateral cilia of brachiopods will evidently remain stationary for considerable periods, for at times animals will gape without detectable currents entering or leaving the shell cavity.

On the frontal surfaces of the filaments particles are conveyed by the cilia either toward the base and eventually to the mouth, or toward the tip to be rejected to the outside of the shell, according to the size and quantity provided (Atkins, 1956).

My thanks are due to the Captain and crew of R.V. 'Sarsia' who dredged the *Platidia* and to those members of the scientific staff, particularly to

Dr A. J. Southward and Mr G. R. Foster, who were in charge of the scientific work and took care of the brachiopods for me.

Mr G. F. Elliott kindly read the manuscript. A grant from the Browne Fund of the Royal Society and a London University table made the work possible.

SUMMARY

Platidia davidsoni and *P. anomioides* dredged by R.V. 'Sarsia' have been examined living. The adult lophophore in both is shown to be a somewhat modified plectolophe, the spiral arm short with but one coil. In *P. anomioides* the brachial support consists of complete descending branches, growing from both crura and septum, and very short ascending branches arising from the apex of the septal pillar. The whole apparatus reaches only to the centre of the oral disc. In *P. davidsoni* the brachial support is much reduced: descending branches are absent; ascending branches, however, are larger than in *P. anomioides*. In both the main support of the lophophore is by spicules.

Full series of growth stages of the lophophore and its support of both species are described and figured for the first time. The growth of the lip of the food groove by extension of a small preoral lobe is described. The structure of the lophophore of *P. davidsoni* has been investigated by sectioning.

It is suggested that the *Terebratula seminulum* of Philippi 1836 is an immature stage of *Platidia anomioides*.

The value as a diagnostic character between terebratulaceans and terebratellaceans of 'filaments directed outwards' and 'filaments directed inwards up to the schizolophous stage' is commented on.

The ciliary feeding mechanism of *P. davidsoni* is briefly described.

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A NEW SPECIES OF *PLATIDIA* (BRACHIOPODA) FROM THE LA CHAPELLE BANK REGION

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From the Plymouth Laboratory

(Text-figs. 1–8)

A new species of *Platidia* (Brachiopoda, Platidiidae) was dredged by R.V. 'Sarsia' in November 1956 in the La Chapelle Bank region, attached to the dead part of the coral *Anisopsammia rostrata* (Pourtales).[1] Eight entire specimens and two smashed were dredged at position 47° 30′ N., 7° 20′ W. at a depth of 870 to 970 fathoms, and one at position 47° 38′ N., 7° 28′ W. at 710 to 750 fathoms. All, except the two smallest, were a reddish brown, the coloration being due to a deposit of manganese oxide: the natural colour is a yellowish white. The dead coral was almost black with the same deposit (see Southward, 1958, p. 644).

Some individuals were transversely oval, others somewhat rectangular and irregular in shape, according to the surface of attachment (Fig. 1). The *Anisopsammia* was fairly free of encrusting organisms but the polyps are closely spaced and therefore apt to interfere with the regular spreading of the closely attached *Platidia*.

The new species of *Platidia* was difficult to deal with. As it was from deep water it was brought back in a refrigerator at a temperature of 5°–7° C: specimens then went into laboratory tank water of 13° C. It has been found that brachiopods generally cannot withstand sudden changes of temperature, and it was this change in temperature which no doubt adversely affected the specimens, most of which showed separation of the cells of the epithelium of the filaments after a few days. Those opened the day after arrival in the laboratory did not extend the filaments on the anterior region of the lateral arms, although the posterior and lateral filaments and those on the posterior extremities of the lateral arms expanded well. This continued contraction of the filaments of the anterior region of the arms may be dependent in some way on the fact that the arms remained depressed and did not raise themselves as they do under similar conditions in *P. davidsoni* and *P. anomioides*. Attempts were made to narcotize the animals with 1% stovaine and with 7% magnesium chloride, a drop added at intervals to a small dish or watch glass of sea water. The latter acted rather the better, but results were not good. The specimen with most expanded lophophore is shown in Fig. 5: it is not

[1] Identified by Dr A. J. Southward.

fully expanded. This specimen left in cedar wood oil for a few months suffered severe deterioration, the tissue becoming extremely brittle, and fragmenting.

All figures were drawn with the aid of a camera lucida.

Description **Platidia annulata** sp.nov.

The general shape of the shell is that typical of the genus *Platidia* (Fig. 1, A, B). The pedicle is short, and the dorsal or brachial valve is closely applied to the substratum; it is generally approximately flat, while the ventral valve is gently domed. So far as can be judged by the few specimens obtained, this is a small species. The three largest individuals had the following measurements: (*a*) length 4·7 mm, width 4·2 mm; (*b*) length 4·2 mm, width 4·3 mm; (*c*) length 3·7 mm, width 4·7 mm. This is approximately the size of *P. anomioides* (Philippi) found to the south-east of the La Chapelle Bank area (Atkins, 1959).

The test is smooth, with growth lines discernible, and is conspicuously punctate. As in *P. anomioides* and *P. davidsoni* the punctae appear to be smaller on the dorsal than on the ventral valve, probably because the shell is thinner. The beak is very short, rostrum apicate, foramen amphithyrid. The deltidial plates are narrow. The pedicle collar is short, sessile and not as conspicuous as in *P. anomioides* and *P. davidsoni*. Running anteriorly from the pedicle collar is a slight median elevation. The hinge teeth have very feeble dental plates as in the other two species. Fig. 2 shows the beak region at three sizes.

In the dorsal valve the inner socket ridges are prominent; the crural bases arise from them. A high septal pillar is present posteriorly. In adults the pillar is continued posteriorly by a septum gradually decreasing in height to a mere ridge on the foraminal margin. The crura are long, the crural processes short, but distinct. The descending branches are quite stout for the size of the shell and widen broadly at their insertion high on the septum, up which they run obliquely to become attached to the sides of the ring formed by the ascending branches. The tips of the short ascending branches are connected by a transverse bar, so that a ring is formed over the septum (Fig. 3). The brachial support is thus more completely developed than in any other species of *Platidia* described, but in spite of this the descending branches reach only to the centre of the oral disc.

The lophophore may be considered a modified plectolophe with an extremely small spiral arm, or even as a modified zugolophe (Fig. 5): it is possible that if *P. annulata* grows to a larger size than seen so far, the spiral arm may also be correspondingly developed. A greater area of the ventral surface of the oral disc is free from spicules than in either *P. anomioides* or *P. davidsoni*: they are present over an area anterior to the transverse bar of the loop (Figs. 5, 7A).

P. annulata is especially noticeable for the long, closely set mantle setae, reaching a length of at least 2 mm; considerably longer than those of *P. anomioides* and *P. davidsoni*. The setae in the specimens seen were dark and iridescent, but this was probably due to a deposit present also on the shells

The flesh of specimens was pale coloured: this may have been because the gonads were not fully developed.

As alcohol, neutral formalin and cedar wood oil have severally caused deterioration of the few specimens obtained, no single one has been chosen as the holotype. The adult specimens which may be considered as syntypes

have been deposited in the British Museum (Natural History) and given the following numbers: ZB. 2910–16, all at 870 to 970 fm.; ZB. 2917 at 710–15 fm.

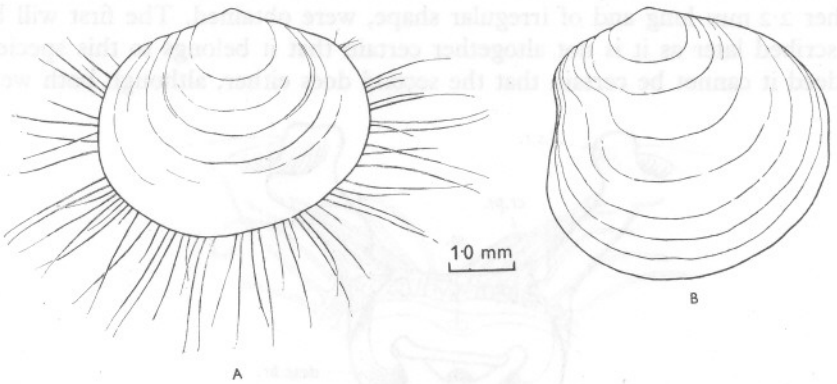

Fig. 1. *Platidia annulata*. A, specimen of regular, transversely oval, shape; mantle setae shown: shell length 3·5 mm, width 4·2 mm. B, specimen of irregular shape; mantle setae omitted: shell length 4·2 mm, width 4·3 mm.

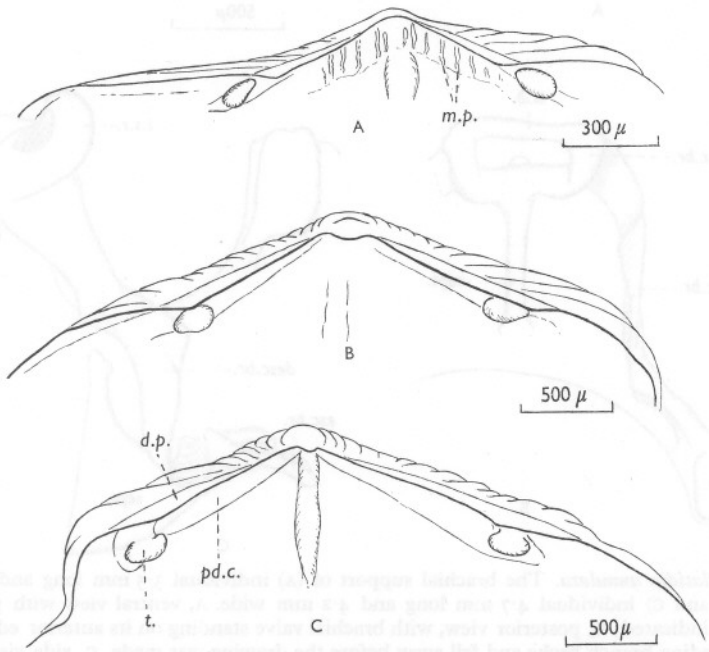

Fig. 2. *Platidia annulata*. Beaks of three individuals of different size. A, length 2·2 mm, width 2·4 mm; B, length 4·2 mm, width 4·3 mm; C, length 4·7 mm, width 4·2 mm. *d.p.*, deltidial plate; *pd.c.*, sessile pedicle collar; *m.p.*, mantle pits in pedicle collar; *t.*, tooth.

THE ADULT LOPHOPHORE

Material for the study of the growth stages of the lophophore was not available. Two small specimens, one 2·1 mm long and 2·2 mm wide, and the other 2·2 mm long and of irregular shape, were obtained. The first will be described later as it is not altogether certain that it belongs to this species, indeed it cannot be certain that the second does either, although both were

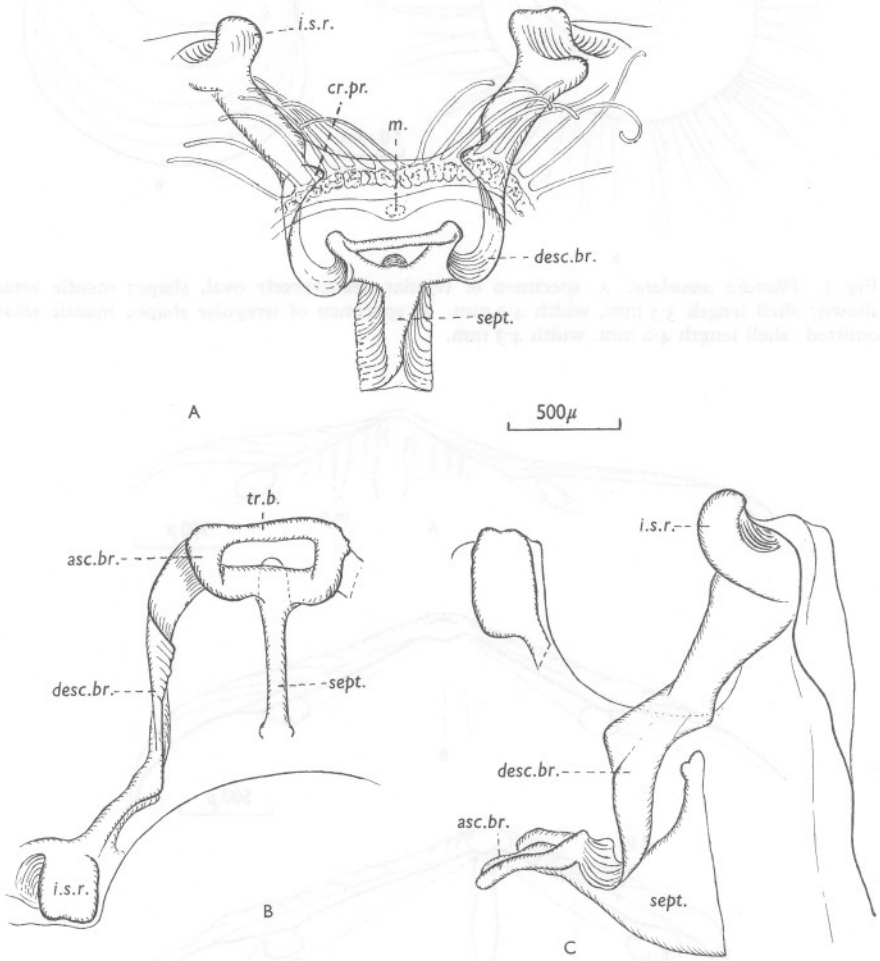

Fig. 3. *Platidia annulata*. The brachial support of (A) individual 3·5 mm long and 4·2 mm wide; (B and C) individual 4·7 mm long and 4·2 mm wide. A, ventral view with posterior filaments indicated; B, posterior view, with brachial valve standing on its anterior edge. The left descending branch broke and fell away before the drawing was made. C, side view of the same. *asc.br.*, ascending branch; *cr.pr.*, crural process; *desc.br.*, descending branch; *i.s.r.*, inner socket ridge; *m.*, position of mouth covered by lip; *tr.b.*, transverse band of the loop; *sept.*, septum.

found in the haul which contained the adults. The second specimen was an empty shell although still attached to the coral; it had probably died since collection. The septal pillar was high, not triangular, with minute triangular prongs at the apex. Crura and crural processes were present; descending branches from the crura were short and their anterior ends were wanting (Fig. 4). In *P. davidsoni* at a corresponding size the septum is low, with almost horizontal lamellae at its apex: crura are absent (Atkins, 1959).

Fig. 4. *Platidia annulata*. Brachial support of immature individual of irregular shell shape; length 2·2 mm. *asc.br.*, ascending branch; *cr.pr.*, crural process; *desc.br.*, descending branch; *i.s.r.*, inner socket ridge; *sept.*, septum.

P. anomioides at about this size has the septum a broadly based triangle, and although long crura are present, descending branches have not yet grown from them. At a slightly larger size, however, the septum may become taller and less triangular in shape (Atkins, 1959).

The largest individual of *P. annulata* obtained has a shell length of 4·7 mm and width of 4·2 mm. At this size the lophophore was in about the same condition as in the individual figured (Fig. 5) of length 3·5 mm and width 4·2 mm; there was little development of the spiral arm and the recurved portion of the lateral arms was short.

Some eighteen to twenty pairs of filaments behind the mouth are in single series and have ridged frontal surfaces.

In the adult the descending branches, although complete, reach only to the centre of the oral disc, and together with the septum, ascending branches and transverse bar support no more than the posterior region of the lophophore to about the centre of the oral disc (see Figs. 5, 6). The individual of which the lophophore is figured (Fig. 5) has a wide base to the septal pillar, the anterior face of which is somewhat asymmetrical (Fig. 3A).

In *P. annulata* a lesser area of the oral disc is covered with spicules than in either *P. anomioides* or *P. davidsoni* as may be seen from Fig. 7.[1] A band at the bases of the filaments, narrow behind the mouth, widens laterally as it passes on the outer side of the descending branches into the lateral arms (Fig. 5). The abfrontal surfaces of these are almost covered with large spicules, only a small central area in each being free. The floor of the lateral arms, or

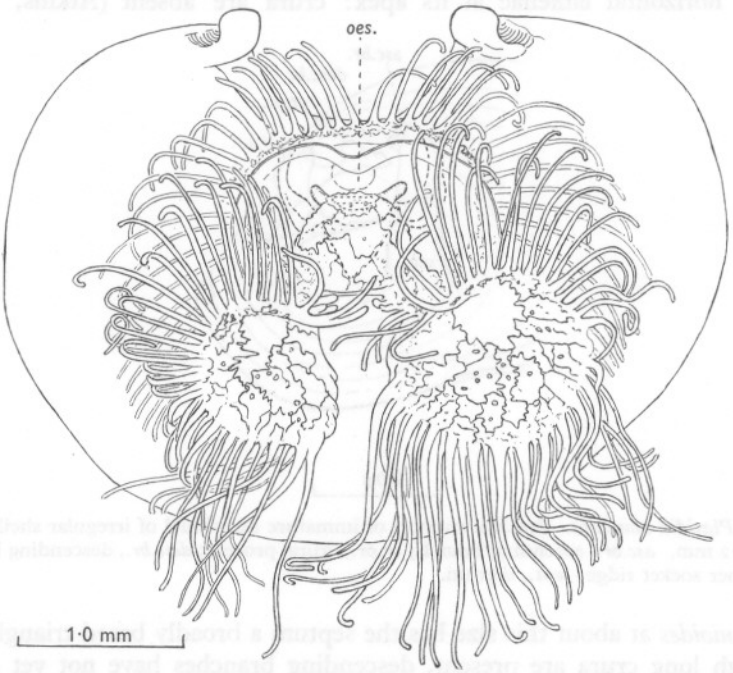

Fig. 5. *Platidia annulata*. Shell length 3·5 mm, width 4·2 mm. Brachial or dorsal valve with the lophophore not fully expanded: drawn narcotized. Brachial support, indicated by broken lines, added after clearing in cedar wood oil. *oes.*, position of oesophagus.

brachial membrane, seems to be without spicules, except perhaps for a narrow band at the bases of the filaments. A ventral area of spicules beginning at the transverse band extends to the anterior edge of the oral disc; laterally it joins the bands just described.

The outer filaments with grooved frontal surfaces are heavily spiculated, the inner ones, with ridged frontal surfaces less so. The spicules are broad bands with granulated surface such as are present in the filaments of the other two species.

The lips of the food groove are without spicules.

[1] In larger specimens of *P. anomioides* an even smaller area of the oral disc is left naked than shown in the figure.

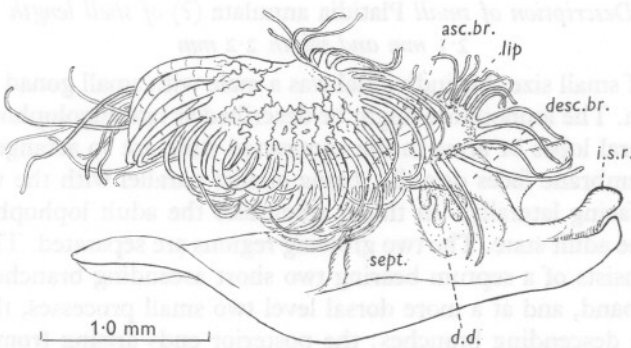

Fig. 6. *Platidia annulata*. Same individual as in Fig. 5 shown in side view to show position of the lophophore with regard to the descending branches and the septal pillar. The lophophore is somewhat depressed and contracted anteriorly. *asc.br.*, ascending branch; *d.d.*, digestive diverticula; *desc.br.*, descending branch; *i.s.r.*, inner socket ridge; *lip*, lip of food groove; *sept.*, septum.

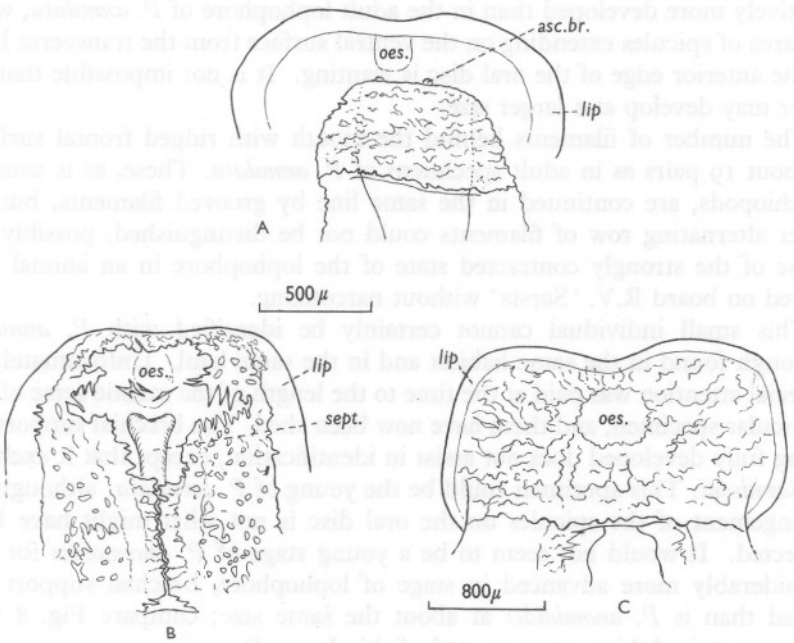

Fig. 7. Oral discs to show the distribution of spicules on the ventral surface of A, *Platidia annulata* of shell length 4·2 mm, width 4·3 mm; B, *P. anomioides* of shell length 3·9 mm, width 4·1 mm (at a larger size an even smaller area of the disc is naked); C, *P. davidsoni* of shell length 6·5 mm, width 8·1 mm. *asc.br.*, tip of ascending branch; *lip*, lip of food groove; *oes.*, position of oesophagus; *sept.*, septum. A and B are drawn to the same scale.

Description of small Platidia annulata (?) *of shell length 2·1 mm and width 2·2 mm*

Although of small size this individual was a male with small gonad containing tailed sperm. The lophophore might be described as late zugolophous (Fig. 8), but the lateral lobes or arms in the contracted state are so arranged that the brachial membrane faces dorsally, being almost parallel with the valve floor, instead of facing laterally. In this it resembles the adult lophophore and is almost in the adult state. The two growing regions are separated. The brachial support consists of a septum bearing two short ascending branches, without transverse band, and at a more dorsal level two small processes, the anterior ends of the descending branches: the posterior ends arising from the crura are short. The descending branches thus arise from both crura and septum as in *P. anomioides* (Atkins, 1959). It may be assumed that the brachial support is not yet fully formed.

On the oral disc a band of spicules, narrow behind the mouth, widens as it passes on either side of the septum into the lateral arms. This band seems relatively more developed than in the adult lophophore of *P. annulata*, while the area of spicules extending on the ventral surface from the transverse band to the anterior edge of the oral disc is wanting. It is not impossible that the latter may develop at a larger size.

The number of filaments behind the mouth with ridged frontal surfaces is about 19 pairs as in adult specimens of *P. annulata*. These, as is usual in brachiopods, are continued in the same line by grooved filaments, but the inner alternating row of filaments could not be distinguished, possibly because of the strongly contracted state of the lophophore in an animal preserved on board R.V. 'Sarsia' without narcotizing.

This small individual cannot certainly be identified with *P. annulata* although found in the same habitat and in the same haul. Unfortunately no especial attention was paid at the time to the length of the mantle setae of this particular specimen, and these have now been shed. The brachial support not being fully developed does not assist in identification, except that it excludes *P. davidsoni*. This specimen could be the young of *P. annulata*: although the arrangement of the spicules on the oral disc is not what might have been expected. It would not seem to be a young stage of *P. anomioides* for it is considerably more advanced in stage of lophophore, brachial support and gonad than is *P. anomioides* at about the same size; compare Fig. 8 with Fig. 23A, B in Atkins, 1959 (p. 126 of this Journal).

REMARKS

Perhaps the characters by which *P. annulata* is most easily separated from *P. anomioides* and *P. davidsoni* are (1) the loop over the septum (Fig. 3); (2) the small area of the oral disc covered by spicules (Figs. 5, 7); and (3) the long

mantle setae up to at least 2 mm long (Fig. 1). There is also a difference in the number of filaments in single series behind the mouth: in *P. annulata* the number is 18 to 20 pairs, in *P. anomioides* 25 to 26 pairs, and in *P. davidsoni* 16 to 17 pairs (Atkins, 1959).

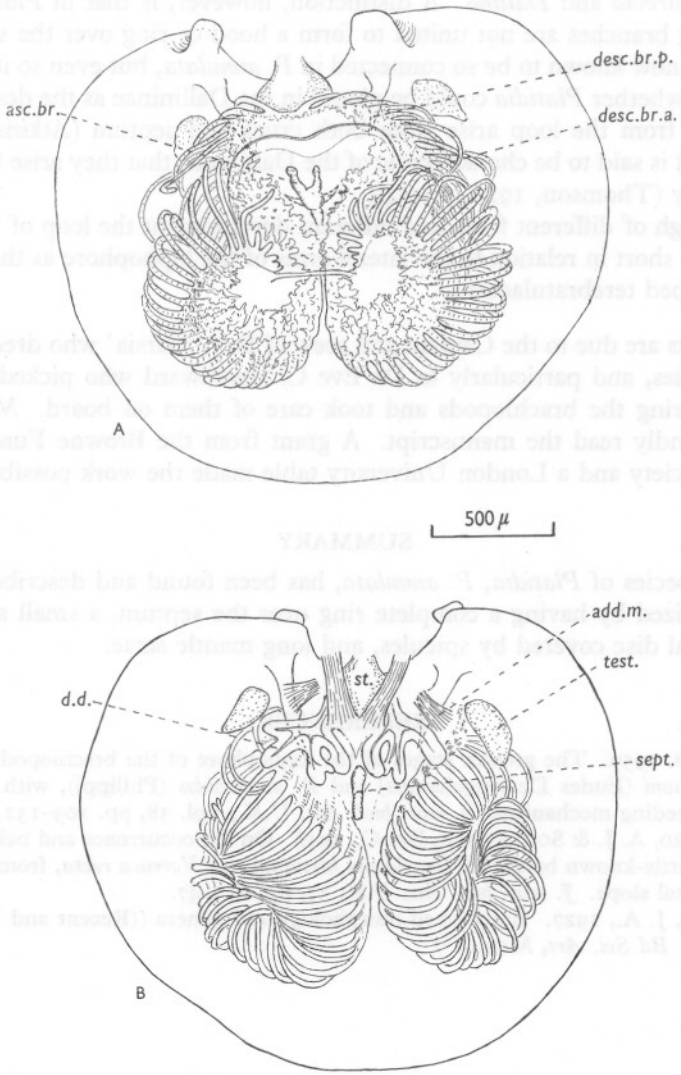

Fig. 8. *Platidia annulata* (?): shell length 2·1 mm, width 2·2 mm. Brachial valve with lophophore. A, ventral view: the distance apart of the two growing regions is to be noted. B, dorsal view of lophophore and body seen through the shell after staining and clearing in cedar wood oil. *add.m.*, adductor muscle; *asc.br.*, ascending branch; *d.d.*, digestive diverticula; *desc.br.a.*, anterior, and *desc.br.p.*, posterior ends of descending branch; *sept.*, septum; *st.*, stomach; *test.*, testis.

The umbonal region of *P. annulata* (Fig. 2) resembles that of *P. anomioides* more than that of *P. davidsoni*.

Thomson (1927, p. 219) remarked that 'Beecher placed the genus (i.e. *Platidia*) in the Dallininae, comparing the loop with the earliest loop stages of *Macandrevia* and *Dallina*. A distinction, however, is that in *Platidia* the ascending branches are not united to form a hood or ring over the septum.' They are now known to be so connected in *P. annulata*, but even so it is most doubtful whether *Platidia* could be placed in the Dallininae as the descending branches from the loop arise from both crura and septum (Atkins, 1959), whereas it is said to be characteristic of the Dallininae that they arise from the crura only (Thomson, 1927, p. 234).

Although of different form and different development the loop of *P. annulata* is as short in relation to the lateral arms of the lophophore as that of the short-looped terebratulaceans.

My thanks are due to the Captain and crew of R.V. 'Sarsia' who dredged the new species, and particularly to Dr Eve C. Southward who picked out the coral bearing the brachiopods and took care of them on board. Mr G. F. Elliott kindly read the manuscript. A grant from the Browne Fund of the Royal Society and a London University table made the work possible.

SUMMARY

A new species of *Platidia*, *P. annulata*, has been found and described. It is characterized by having a complete ring over the septum, a small area only of the oral disc covered by spicules, and long mantle setae.

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MOVEMENT RECEPTORS IN DECAPOD CRUSTACEA

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(With Text-figures 1–3)

The sense organ of *Carcinus maenas* located in the joint between the dactylo- and propodite possesses several types of sense cells (Wiersma & Boettiger, 1958). The most interesting types react to unidirectional displacement of the dactylopodite with equal sensitivity over the total possible arc of movement. Velocity has little influence on the discharges of the movement fibres since the maximum rate of firing is reached at a speed which is relatively little faster than the threshold. Fibres with marked differences in threshold are present for both extension and flexion. Other units in the organ react like conventional stretch receptors and give continuous discharges as long as the joint is near one of the extreme positions. Again different units are present for extension and for flexion. These position fibres are on the whole smaller than the movement fibres and their cell bodies have a more peripheral location in the organ.

Organs similar to this PD-organ of *Carcinus* are known to be present in other joints and in other species (Alexandrowicz, 1958, and personal communication). The purpose of the present investigation was to determine their functions and particularly to find out whether they possess movement receptors.

METHODS AND MATERIAL

Unit analysis of fibres reacting to manipulation of specific joints was made by preparing single fibres or small bundles according to the methods described elsewhere (Wiersma & Boettiger, 1958). In this investigation all fibres were prepared from the nerve or nerves in the meropodite. As it was not the purpose to study the relation between speed of movement and the discharge rate in the movement fibres, but merely to demonstrate their presence or absence, manual manipulation of the joints sufficed. For registration purposes a simple mechanical device was used which correlated the movements of the carpo-dactylopodite joint with the displacement of the second beam of a Cossor oscilloscope. For this purpose the knob controlling the vertical position of this beam was replaced by a brass pulley over which a thread without end

[1] John Simon Guggenheim Memorial Fellow.

was looped twice. The lower thread was similarly looped over the propodite at a convenient distance from the joint and continued to a pulley located on the other side of the preparation and then back to the brass pulley. By adjusting the tension in the thread and the place of the loop around the propodite, it was possible to establish a satisfactory relation between the vertical displacement of the beam and the maximum arc of movement of the joint. Since the brass knob was moved by hand, the displacement was not smooth, with resulting irregularities in the discharges, especially from the most sensitive movement receptors. But the method permitted clear distinction between the properties of most fibres.

In many preparations the nerve fibre bundles from which proprioceptive responses were obtained were subsequently traced to the organs from which they originated. To this end staining with methylene blue and additional exposure of the nerve bundles and organs were used.

The animals investigated were *Carcinus maenas*, *Maia squinado*, *Eupagurus bernhardus*, *Homarus vulgaris* and *Palinurus vulgaris*. The experiments on the latter four species were performed at Plymouth. In each animal the organs of the walking legs were investigated. Sea water was used as a physiological solution. For *Maia* a special solution was also tried, but no noticeable difference was observed, possibly because each experiment continued for at most two hours.

RESULTS

The PD-organs of various species

A comparison of the responses from the PD-organs of the other species with those of *Carcinus*, described elsewhere (Wiersma & Boettiger, 1958), shows that they are greatly similar. In all cases a small bundle of nerve fibres can be isolated in the meropodite, containing axons responding to different manipulations of the joint. In *Palinurus*, especially, fibres in another bundle also respond. It could be shown that these responses do not originate in the organ but from sense cells of hairs located on the distal part of the propodite, which are bent by the dactylopodite when it nears the extreme flexed position. These hairs form only part of the cluster present and on touch the signals in their fibres do not differ from those which are not stimulated when the dactylopodite is bent. It seems therefore unlikely that they have a proprioceptive function.

The four main types of fibres, opening and closing movement fibres, opened and closed position fibres, were regularly obtained from the PD organs of all genera with the exception of *Homarus*. In the PD nerve bundle of the latter closed position fibres were usually absent. Since all but the fourth walking legs are either chelated or subchelated in this species, it seemed possible that the stop provided by the propodite might be responsible. Therefore the fourth leg, in which the dactylopodite can move through as

large an arc as in other genera, was especially used, but tonically firing closed position fibres were here as rare as in the other legs.

For a few preparations from different species, a count was made of the number and type of fibre which could be prepared from one PD nerve bundle. Because of damage such counts will not show the actual number of active units, but they will provide an approximation of the numerical relation of the different fibre types. In Table 1 the results are shown.

TABLE 1. NUMBERS OF REACTING AXONS PREPARED IN THE PD-NERVE BUNDLES OF VARIOUS SPECIES

	Movement		Position	
	Opener	Closer	Opened	Closed
Carcinus	4	5	6	3
Maia	4	4	1	1
Homarus	6	3	6	0
Palinurus	5	6	15	5

The large number of fibres obtained from *Palinurus* resulted from (1) individual fibres being relatively larger and thus more readily prepared, and (2) there being a larger number of nerve cells in the PD-organ than in the other genera. The number of movement fibres for the opposite directions seems about equal in all genera. These counts do not show that here, as in all other joint organs, the number of position fibres is larger than that of the movement fibres. This is due to the smaller size of the position fibres, which makes them harder to prepare, and explains why in the preparation of *Maia* presented only a single one for each class was found, since in *Maia* the nerve fibres are smaller than in other genera used.

By staining the organs with methylene blue, it was observed that the elastic strand, which is so distinct in *Carcinus*, is a much more diffuse structure, and that the cell bodies are spread farther apart. This feature and the fact that the nerve bundle close to the organ is enveloped in a strong sheath have prevented splitting of subbundles, which showed in *Carcinus* the localization of the different reaction types. Since in all organs the larger cells are located at the proximal end and the signals of movement fibres are regularly larger than those of position fibres it is likely that a similar distribution is present in all organs.

The proprioceptor organs in the carpo-propodite joint

In this joint at least two separate organs are present in all genera investigated. Information about their occurrence has been given by Alexandrowicz (1958).[1]

[1] Alexandrowicz (personal communication) has suggested that receptors belonging to this system might be designated by the first letters of the segments between which they are situated, viz. PD—the organ between the propodite and the dactylopodite, CP—that between the carpopodite and the propodite, etc. When two organs differing somewhat in their structure are present near to one another, as at the mero-carpopodite and carpo-propodite joints, they may be distinguished by numerals, viz. MC 1, MC 2 and CP 1, CP 2 respectively.

In *Carcinus* the organs were readily found, at first by tracing back to their origin the bundles in which proprioceptive impulses were present. CP 1 (Fig. 1A) runs from the tendon of the bender muscle (productor propoditis) to the joint membrane. CP 2 (Fig. 1B) originates on the tendon of the stretcher muscle (reductor propoditis) and bridges the joint, being attached to the inner wall of the propodite. In *Carcinus* a clear elastic strand is present in both; the one of CP 2 resembles that of the PD organ closely, but the strand of CP 1 is broader and flatter and its origin on the bender tendon less distinct.

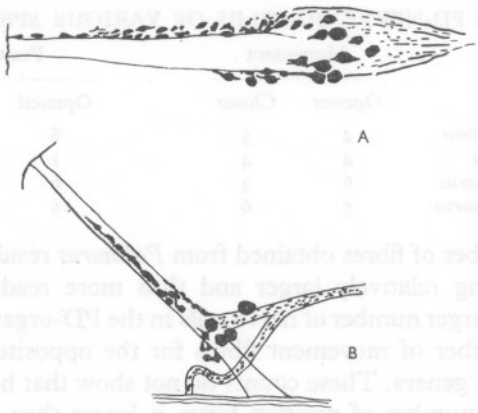

Fig. 1. *Carcinus maenas*. A, Carpo-propodite sense organ (CP 1), showing the arrangement of the nerve cells around the rather broad and proximally indefinite elastic strand. On the right the large cells of the proximal part, along the upper (outer) side the more peripheral continuation of small cells. After microphotograph of Rongalit methylene-blue stained preparation. B, CP 2 organ. Note the distinct elastic strand and the large nerve cells at the proximal end, which are in contrast to the peripheral smaller cells, loosely attached. Separate nerve branch disappears on the tendon of the stretcher muscle.

CP 1 has many more nerve cells than CP 2 and they are clearly arranged in two main rows, one on each side of the strand. The outer row continues farther peripherally than the inner, and in both there is a rather regular decrease in cell size towards the peripheral end. In CP 2 of *Carcinus* a remarkable feature is the location of the large cells at the proximal end, which are here only loosely connected to the elastic strand and sometimes a considerable distance from it.

In *Carcinus*, as in all other genera but *Palinurus*, the two nerve bundles from the two organs run well separated in the main nerve trunk in the meropodite. In *Palinurus* they often appeared to run close together, which prevented assigning them to each organ without subsequent tracing. In *Homarus* and *Eupagurus*, where a thicker and thinner nerve bundle are present, both CP bundles are located in the thicker nerve.

In all genera fibres reacting to unidirectional movement as a stimulus have been found in the nerve bundles of both CP 1 and CP 2. Regularly

several fibres differing in threshold but all indicating the same direction of movement are present in each bundle. Fig. 2A illustrates a rather sensitive movement fibre of *Homarus*. The most sensitive movement fibres are not suitable for recording since very slight changes in speed will greatly influence the discharges. In Fig. 2B medium sensitive movement fibres from *Maia* are shown, one for each direction, whereas insensitive fibres are represented by one from *Eupagurus* in Fig. 2C.

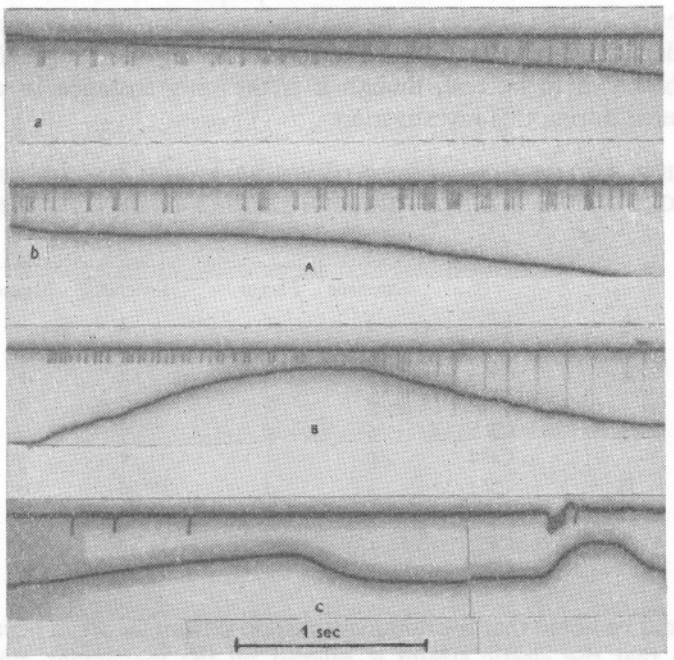

Fig. 2. A, response of sensitive flexor movement receptor from CP 1 of *Homarus*. *a*, start of the movement from complete extension; *b*, continuation to almost complete flexion. The irregularities in the discharge rate are mainly caused by those of the movement. B, a medium sensitive extensor and a flexor movement fibre from CP 1 of *Maia*, the first with the smaller signal discharging during a complete extension of the propodite, the second during flexion. C, insensitive extension movement fibre from CP 1 of *Eupagurus bernhardus*. Two complete extensor and flexor movements, the second faster. Note the limited number of impulses this fibre can maximally produce. Time-scale 1 sec. during one extension.

Besides movement fibres, position fibres are invariably present in both CP nerve bundles. These showed no properties other than those discussed for the PD-organ of *Carcinus* (Wiersma & Boettiger, 1958). Types which reacted only on position changes and types in which the frequency increased temporarily above that maintained during displacement were both noted.

In contrast to the PD-organ the CP-organs do not always respond to both movement directions. CP 1 resembles PD in this respect more than CP 2.

The latter may completely fail to respond to either movement or position in one direction, whereas CP 1 usually shows only a pronounced preference for one side. The CP-organs of *Carcinus* have been more closely studied in this respect but the phenomenon was present in all genera studied.

The dominant responses are extension for CP 1, flexion for CP 2. Large specimens invariably showed this preference for one direction, whereas in younger ones it was less pronounced though present. Counts made of the number of active fibres which could be prepared from the two bundles illustrate this feature (Table 2). In the last preparation of this table a reversal of the dominance appears, and subsequent tracing of the bundles to the organ showed it to be real, though it is the only instance in any genus encountered during this investigation.

TABLE 2. NUMBER OF ACTIVE UNITS PREPARED IN THE CP 1 AND CP 2 NERVE BUNDLES IN FIVE LEGS (A–E) OF *CARCINUS*

		Movement		Position	
		Extensor	Flexor	Extended	Flexed
A	CP 1	3	1	3	2
	CP 2	0	4	0	2
B	CP 1	4	0	3	1
	CP 2	0	5	0	2
C	CP 1	6	3	5	2
	CP 2	0	5	1	3
D	CP 1	4	0	6	0
	CP 2	1	4	0	5
E	CP 1	1	5	1	6
	CP 2	5	0	4	1

It should be noted that the dominant response from an organ occurs during the time that the elastic strand is relaxed by the movement, whereas the opposite might have been expected. That there was actual relaxation has been confirmed by studying the changes of exposed organs during the movements.

In several preparations, especially from *Palinurus*, fibres with a reaction to both movement and position were found. They did not occur in every preparation and were always accompanied by more conventional fibres. Sometimes there would be several of them in one bundle. Fig. 3A shows a type rather common in *Palinurus*, whereas Fig. 3B shows a rarer one for *Homarus*. As will be discussed, they may represent more or less abnormal sense cells. In *Eupagurus* a single fibre was found which reacted equally well to movement in either direction over the full range of the possible movement arc. This remarkable fibre is the only one so far encountered for which the name 'vibration fibre' would be appropriate.

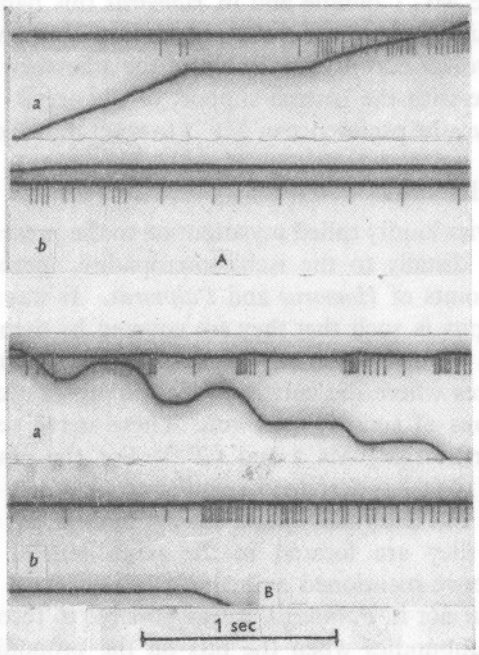

Fig. 3. A, receptor with intermediate properties from *Palinurus*. Insensitive to movement during the first part of the movement arc (*a*) it becomes quite sensitive for the second part and starts to respond to position though the maintained discharge rate remains low even in the extreme position (*b*). B, receptor with intermediate properties from *Homarus*. Movement sensitivity present throughout the arc from the extreme extended (*a*) to the extreme flexed position. In the latter it gives after the movement discharge a constant discharge at 20–25 impulses per sec. (*b*). The sections *a* and *b* are not continuous.

MC-receptors

For this joint there are again two main organs present, MC 1 which closely resembles CP 1 in structure and MC 2 which resembles CP 2. At least in *Carcinus* MC 1 is attached to the tendon of the accessory flexor muscle of the carpopodite (adductor carpi), and MC 2 is attached close to the tendon of the main flexor muscle, and, in contrast to MC 1, crosses the joint to be inserted on the inner side of the carpopodite. By exposing the nerve in the proximal part of the meropodite, leaving the distal part intact, a nerve bundle reacting to manipulation of the joint could be found for each organ. These bundles are widely separated. The bundle to MC 1 is easy to find as it usually leaves the main nerve trunk early in the meropodite.

In *Carcinus* the responses obtained from the nerve bundle of MC 2, as well as fibre analysis, showed that the organ typically, but not exclusively, signals joint flexion, whereas MC 1 has a preponderance of extensor movement and position fibres. In some preparations of *Carcinus*, no signals could be

obtained from the MC 1 bundle and in *Homarus* this happened often. The reason for such failure may be that the preparation of the nerve in the meropodite usually involves cutting the tendon of the accessory flexor muscle and hence interference with the natural support of the organ. In other genera, especially *Homarus*, the preference of MC 2 to react to flexion was also noted.

'*Slit sensilla*' *of* Homarus

Dr Alexandrowicz kindly called my attention to the presence of a number of pits, located just distally to the ischio-meropodite, mero-carpopodite and carpo-propodite joints of *Homarus* and *Palinurus*. It was observed that the location of these pits is such that they are covered by their joint membranes when the joint is moved maximally to the side on which they occur. The 'sensilla' are places where the cuticle is pierced by fine channels to which dendritic extensions of sensory cells run. These nerve cells are associated with those of Barth-organ, MC 2 and CP 2. For the crayfish, *Potamobius torrentium*, Barth (1934) has described a similar arrangement of the innervation of 'Sinneskegel', but externally these 22–23 sensilla do not appear to be distinct, though they are located in the same general area as the 'slit sensilla' of the above-mentioned animals.

In *Homarus*, but not in *Palinurus*, it was possible to record impulses from small prepared subbundles when the pits on the propodite were touched. The reacting nerve fibres did not run together with the CP 2 proprioceptor fibres, but formed part of a larger bundle consisting of fibres responsive to touch of hairs on the ventral and proximal aspect of the propodite. This bundle was located near the CP 2 bundle. By tracing the two bundles forward it was shown that the bundle of hair fibres had no connexion with the CP 2 nerve cells. This excludes the possibility that the CP 2 cells going to the pits are responsible for the discharges on touch. Since they might be chemoreceptors, distilled water, concentrated salt solutions and some organic material were applied to the pits, but no responses in either the CP 2 bundle or the hair fibre bundle were obtained. It therefore remains to be shown whether or not these cells of CP 2 are but part of the normal proprioceptor components of this organ.

From the location of the pits, it might be expected that responses would be obtained from them when they are being covered by the joint membrane. But in preparations in which touch with a brush resulted in responses, extension of the propodite at different rates, failed to do so. It is possible that under natural conditions stimulation takes place under these circumstances, as the membrane will then be more turgid through the blood pressure.

DISCUSSION

Notwithstanding the considerable differences in the structure of the proprioceptive sense organs in different joints and different genera, they all have sense cells perceiving unidirectional movement and cells responsive to position. This strongly indicates that the as yet unknown relations between the dendrites and the elastic fibres of the strand determine the function of the sense cell. For the sense organs as a whole a development to more compactly built organs may have taken place. For instance the PD-organ of the rock lobster with its many sense cells and indistinct elastic strand may represent a more primitive state than the PD-organ of *Carcinus*. Physiologically a similar perfection may be seen in that fibres influenced to a great extent by both movement and position are rare in crabs and frequent in the rock lobster.

In all genera the proprioceptors of the coxal region appear to be built much more precisely than those of the peripheral joints (Alexandrowicz & Whitear, 1957; Alexandrowicz, 1958). On the other hand, the number of sense cells in several of these organs is very small and thus a few units may transmit as detailed information as can be obtained from many of the peripheral organs. A reason for this difference may be seen in the fact that after autotomy the peripheral organs must be rebuilt. It has been observed that in regenerated legs the structure of the PD-organ can be noticeably different and that more fibres with intermediate types of responses are present. Therefore integration of many signals may be used to compensate for inaccuracy in single units.

It appears that the organs can become specialized for certain functions with ageing of the animal. This points to a functional degeneration of part of the sensory cells. How far a similar process may take place for all kinds of cells and explain the observed discrepancy between number of cell bodies and number of functionally reacting units remains to be determined.

The finding of movement sense in all groups of the Crustacea Decapoda Reptantia raises the question whether this sense is present in other Arthropoda. The available evidence strongly indicates this to be so. The responses obtained in the nerve bundles to the proprioceptive organs during the movement of joints in *Limulus* (see Pringle, 1956) and scorpions (Pringle, 1955) most likely originate in movement receptors. These impulses arise from large sense cells located internally, whereas smaller cells give rise to tonic discharges. According to Pringle the latter are homologous to campaniform sensilla of insects, whereas he mentions the possibility that the large cells may be homologous to the chordotonal organs. It may be that the crustacean joint organs are in a state in which these two sense organs are still combined and that the organs of the lobster represent a first stage in their divergence. It should be mentioned that in arachnoids the joint sense organs occur along the outer, upper side of the leg, whereas in Crustacea they are situated on the inner, lower side.

I am grateful to the Director and Staff of the Plymouth Laboratory for their co-operation and for their hospitality, and especially to Dr J. S. Alexandrowicz for the help he has given me in many ways. The experiments were carried out during my tenure of a visiting Professorship at the Department of Zoology, University of Cambridge. I want to thank Prof. Sir James Gray and Staff for their confidence.

SUMMARY

Sensory fibres responding exclusively to unidirectional movement of joints are present in representative species of all four groups of Crustacea Decapoda Reptantia: Palinura, Astacura, Anomura and Brachyura.

They arise from nerve cells located in sense organs in the region of the joints, which contain additional sense cells. The axons of all these cells form bundles in the main trunk from which single unit responses were obtained by preparation of single fibres or small subbundles.

Potentially each organ contains cells sensitive to unidirectional movement for both directions and tonic position fibres for each of the sides of the mid position. Cells with different thresholds are present in each of the four classes.

In certain organs, especially those of older animals, one or two of the four types of sense cells may be lacking.

Sense cells which share some properties of movement and position-sensitive ones are always present, but truly intermediate cells are relatively scarce, more so in higher forms (crabs) than in lower ones (rock lobsters).

The functional significance of some peculiar pits in the joint regions of *Homarus* is studied.

The presence of movement fibres in other Arthropods is discussed and some points relating to the possible homologies of proprioceptive sense organs in the legs of Arthropods are presented.

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EXPERIMENTS ON SOME EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON *GRACILARIA VERRUCOSA* (HUDSON) PAPENFUSS

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(Text-figs. 1–3)

At an early stage of an autecological study of *Gracilaria verrucosa* (Hudson) Papenfuss it seemed possible that the best growth of the plants occurred in places, such as the Achill Sound and the Church Island Channel in the Menai Straits, where, in the absence of heavy wave action, strong currents flowed over the plants. Experiments were carried out, in the sea, to investigate the effect of currents on the growth rate; the apparatus used and described here would probably be suitable for the investigation of current effects on other sedentary marine organisms.

These experiments also led to some observations on the effects of illumination on the pigmentation and growth rate of the plants which were supplemented by laboratory experiments. High intensity illumination in the laboratory also demonstrated positive phototropism in the plant.

FIELD EXPERIMENTS

Apparatus

The raft shown in Fig. 1 was designed and constructed in timber. Two of the four parallel compartments (*W* and *Y*) were open at the ends, top and bottom. The other two (*X* and *Z*) had pointed bow and stern sections closing them to the current and also perforated wooden bottoms which were shown, by trials, to be necessary to prevent turbulent upwelling when the raft was moored in a rapid current. The raft was moored astern of an anchored barge in the Menai Straits, both being free to swing with the tidal stream so that the raft faced constantly into the current. The tidal current in this part of the Straits reaches about 3 knots. To prevent the entry of floating weed and other debris, the open compartments were protected at both ends and bottom by $\frac{1}{2}$ in. mesh wire netting. Shrimp netting of $\frac{3}{8}$ in. mesh was lashed over the top to prevent floating matter being washed into the compartments by waves. The net also had the effect of shading the interior to some extent.

When first launched the raft floated with 10–12 cm freeboard; waterlogging of the wood later reduced this and eventually net floats had to be attached to

maintain a freeboard of 5–8 cm. Water entered rapidly through the perforated bottoms of the closed compartments. The accumulation of water-borne silt in these compartments demonstrated the movement of water in and out of them and that stagnation need not be feared.

In each compartment longitudinal battens were arranged to support four 'Tufnol' plastic bars. Two specimens plants were tied to each bar; thin nylon

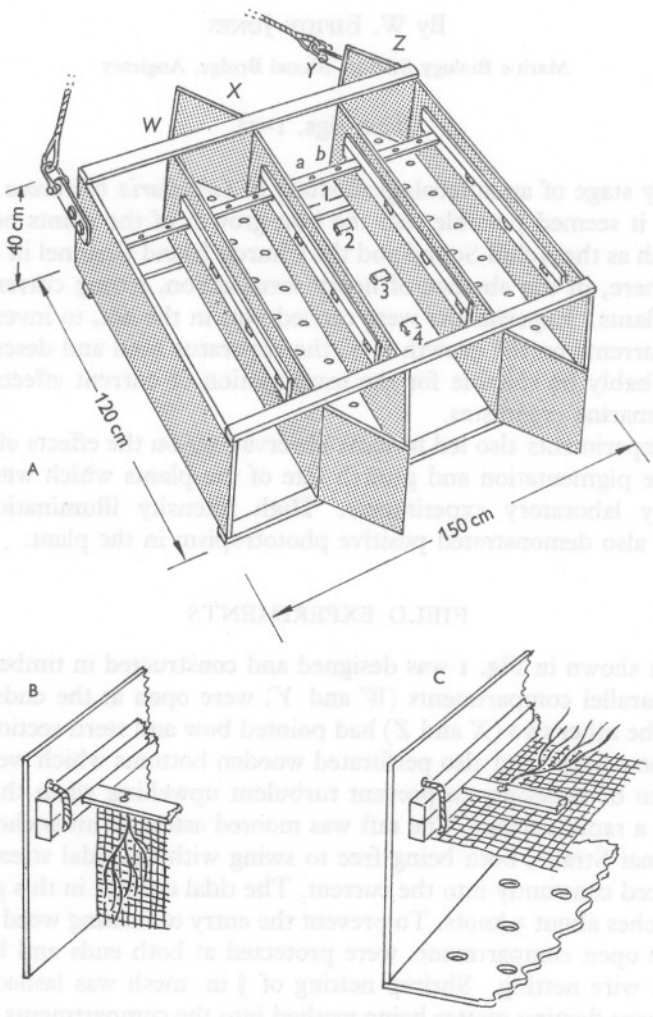

Fig. 1. A, raft used in experiments on the growth of *Gracilaria verrucosa*. Some structural members are omitted for clarity. The four compartments are lettered as shown for reference; the positions of the 'Tufnol' bars bearing the plants are shown in compartment *Y* and were similar in the others. B and C, modifications to compartments *W* and *Z* respectively as described in the text.

fishing gut proved to be the most satisfactory material for this purpose. The bars with the plants attached were removed periodically for examination.

The raft was used in this form during the first season's experiments.

Recording

The specimens used consisted either of a single branched axis with its individual holdfast or else a suitably sized clump of axes arising from part of an expanded holdfast of several seasons' growth. For convenience these specimens are hereafter referred to as 'plants'. The plants were weighed at the start of the experiment and subsequently at intervals of about 10 days. During the first season they were also photographed against a background ruled in 2 cm squares to investigate form changes.

Weighing was carried out with the plants suspended from the arm of a 0–1 g torsion balance so as to be completely submerged in sea water. This method avoided the uncertainty involved if the superficial moisture had to be removed before the plant was weighed in air and also reduced the risk of damage by desiccation during weighing. Although the weight measured was small, owing to the density of the plants being only a little greater than that of sea water, this method was found to be quick and reliable, provided care was taken to ensure that the plants did not touch the sides of the containing vessel or the water surface during weighing and that no air bubbles were trapped amongst the branches.

Results of the first season's experiments

The comparative increases in the fresh weight of a set of thirty-two plants, collected at Criccieth and grown on the raft from 25 June to 6 July 1954, are shown in Table 1. Fig. 1A shows the arrangement of the raft compartments and plant positions. It will be seen that while plants in the open compartments *W* and *Y* increased by about 62%, those in the closed compartments increased by only about 36%. These differences are statistically highly significant. Results in succeeding periods were similar, except where loss of plants or damage occurred.

Conclusions from the first season

It was obvious that growth was more rapid in those compartments open to the current, but it became evident that this was not necessarily due to the direct effect of the current itself. It was observed that the plants in the compartments open to the current lost their original dark red colour, changing to a light straw, while those in the still water compartments were not greatly changed. It is generally accepted that this loss of colour results from strong sunlight and occurs in many red algae in summer. The difference in pigmentation in the current and still water compartments presumably resulted from

TABLE 1. COMPARATIVE INCREASE IN WET WEIGHT OF PLANTS ON RAFT DURING PERIOD 25 JUNE–6 JULY 1954

The values given for the weights are the torsion balance scale deflexions. These are almost exactly one-third of the fresh weight in g.

	Plant	Weight 25. vi.	Weight 6. vii.	Gain	% gain
W. Open	1*a*	0·57	0·90	0·33	57·89
	b	0·46	0·81	0·35	76·09
	2*a*	0·77	1·51	0·74	96·10
	b	0·27	0·52	0·25	92·59
	3*a*	0·37	0·60	0·23	62·16
	b	0·30	0·03*	—	—
	4*a*	0·96	1·22	0·26	27·08
	b	0·79	0·97	0·18	22·70
		Mean gain 62·09 %			
X. Closed	5*a*	1·91	2·74	0·83	43·45
	b	0·13	0·24	0·11	86·61
	6*a*	2·43	2·86	0·43	17·69
	b	0·26	0·30	0·04	15·38
	7*a*	1·76	2·33	0·57	32·38
	b	0·47	0·68	0·21	44·68
	8*a*	2·28	2·81	0·53	23·45
	b	0·80	1·02	0·22	27·50
		Mean gain 36·14 %			
Y. Open	9*a*	0·50	0·90	0·40	80·00
	b	0·19	0·32	0·13	68·42
	10*a*	1·30	2·12	0·82	63·07
	b	0·25	0·45	0·20	80·00
	11*a*	0·89	1·40	0·51	57·30
	b	0·17	0·30	0·13	76·57
	12*a*	1·88	2·78	0·90	47·87
	b	0·36	0·44	0·08	22·22
		Mean gain 61·93 %			
Z. Closed	13*a*	2·02	2·88	0·86	42·57
	b	0·42	0·48	0·06	14·29
	14*a*	1·20	1·65	0·45	37·50
	b	0·57	0·77	0·20	35·09
	15*a*	0·77	1·02	0·25	32·47
	b	0·29	0·40	0·11	37·93
	16*a*	0·40	0·65	0·25	62·50
	b	0·19	0·25	0·06	31·57
		Mean gain 36·74 %			

Analysis of variance

Source of variation	Degree of freedom	Sum square	Mean square	Variance ratio	Probability
Current	1	5229·83	5229·83	11·3	1·0—0·1 %
Pairs of compartments	2	1·53	0·77	·0017	> 20 %
Replication	27	12532·81	464·17	1·0	> 20 %
Total	30				

* Plant damaged: in calculation this value taken as equal to mean of remaining plants in block I.

differences in illumination. The shading by the partitions caused some reduction in the amount of light reaching the lower parts of each compartment. Thus, where the current was flowing, the plants were trailed out horizontally, level with the tufnol bars, less than 10 cm below the water surface and so received all the light available at that level. In the closed compartments, on the other hand, the plants hung downwards most of the time and therefore received less light because of the shade cast by the partitions and the mutual shadow of their own fronds. Thus the results obtained might be due primarily to differences in illumination rather than conditions of current or still water. In the following season the experiment was redesigned to investigate this.

Modification of the apparatus

One closed compartment (*X*) was left unchanged. In the other (*Z*) a net was arranged horizontally below the tufnol bars so that the plants were held permanently spread level with them (Fig. 1 C). One open compartment (*Y*) was not altered; in the other (*W*) a series of nets was fitted, one behind each bar so as to prevent the plants being swept out horizontally by the current which, instead, kept them pressed against the nets in the hanging position (Fig. 1 B). As the currents flowed for only part of the day (on the flood and ebb) and as some movement of the free plants occurred in all but a flat calm, the new conditions meant that plants in compartment *Z* would obtain the most light and those in *W* the least.

Recording was carried out as before except that the plants were not regularly photographed and that a note was kept of the changes in their colour.

Results

Table 2 gives the results of these experiments. As the periods between successive weighings were not all of equal length, the weight increases are divided by the length of the period and presented as percentage increases in weight per day. The table includes the changes made in the position of the groups of plants after the first growth period (24 May–8 June), when those in the current compartments were exchanged with those in still water, and also shows the observed colour changes in the plants.

During the first growth period the plants in compartment *Z* (held horizontal in still water) and those in *Y* (free in current) showed an average daily increase in weight of 5·33 and 4·39% respectively. Those in compartment *X* (free in still water) and in *W* (held vertically in current) showed, respectively, 2·75 and 2·82% increase per day. Statistical analysis showed that the differences resulting from conditions of still water and current were not significant, but that the difference between the increase in the plants which received most light (in *Z* and *X*) and those which were shaded was highly significant.

TABLE 2. GROWTH OF *GRACILARIA VERRUCOSA* SHOWN AS PERCENTAGE INCREASE IN FRESH WEIGHT PER DAY IN CONDITIONS OF CURRENT AND STILL WATER, FULL LIGHT AND SHADE ON A RAFT DURING 1955

(1) Condition of plants on 24 May	(2) Compartment occupied 24 May–8 June	(3) % gain per day 24 May–8 June	(4) Condition of plants on 8 June	(5) Compartment to which transferred 8 June	(6) % gain per day 8 June–21 June	(7) Condition of plants on 21 June	(8) % gain per day 21 June–5 July	(9) Condition of plants on 5 July	(10) Condition of compartment on 5 July and treatment	(11) % gain per day 5 July–27 July	(12) Conditions of plants on 27 July
Fully pigmented	*Z* (held horizontal in still water)	5·86	All red colour lost	*W*	0·58	Some red colour regained	2·57	Red colour almost fully regained	Many filaments of algae on nets. Cleared 5 July	2·18	Fully pigmented
		1·91*			0·78		3·16			1·64	
		4·91			1·57		0·92			3·95	
		5·80			0·57		0·82			—	
		4·79			1·14		0·09*			—	
		4·86			—		3·18†			4·54	
		5·15			1·26		1·46			0·24*	
		6·20			1·21		1·56			—	
	Mean	5·33			1·01		2·02			3·08	
Fully pigmented	*Y* (free in current)	5·00	Red colour much reduced	*X*	3·00	Most red colour lost	2·10	Most red colour lost		—	Most red colour lost
		4·42			4·37		2·36			3·54	
		—			3·54†		2·35			—	
		—			4·95†		4·13			2·97	
		—			5·45†		3·31			2·98	
		—			4·00†		1·93			3·26	
		4·85			2·31		0·74			3·72	
		4·29			3·42		2·40			—	
	Mean	4·39			3·92		2·41			3·29	
Fully pigmented	*X* (free in still water)	3·85	Red colour slightly reduced	*Y*	2·97	Red colour greatly reduced	1·86	Red colour largely restored	Heavy growth of filamentous algae. Cleared 5 July	2·86	Red colour much reduced
		1·35			4·28		—			4·86	
		1·67			2·35		2·33			—	
		—			3·48		3·28			—	
		3·84			2·15		2·72			6·18	
		4·34			4·85		0·82			1·69	
		1·47			2·53		2·71			6·05	
		2·64			4·96		1·86			4·77	
	Mean	2·75			3·42		2·23			4·40	
Fully pigmented	*W* (held vertical in current)	4·10	Colour unaffected	*Z*	3·15	All red colour lost	2·55	All red colour lost		4·14	All red colour lost
		3·55			4·77		2·46			1·46	
		1·69			5·02		1·93			0·24*	
		1·33			4·58		2·26			2·82	
		2·56			5·04		2·29			2·52	
		3·66			4·86		2·85			2·55	
		0·46*			2·30		1·63			—	
		—			2·76†		4·86			1·82	
	Mean	2·82			4·06		2·60			2·71	

Notes. Each horizontal row concerns the same plants throughout the experiment.

* Damaged plants: not included in calculations.

† New plants introduced to replace casualties.

Conclusions

It appears from these results that the effect observed in the earlier experiment was only secondarily due to current and resulted from the better illumination received by the plants spread out by the flow of water. Later experiments were made in the laboratory on the direct effect of current.

The plants in compartment *Z*, being constantly in a horizontal position, probably received more light than those in *Y*, which were horizontal only when the tidal currents flowed. The growth rate in *Z* did appear, from its mean value of 5·33%, to be higher than that in *Y* (4·39%), but statistical analysis did not show the difference to be significant.

Causey, Prytherch, McCaskill, Humm & Wolf (1946) showed that unshaded *Gracilaria* reached its maximum growth rate at 60 cm below the surface without improvement at lesser depths. In the present experiment pronounced differences in growth occurred in plants within the upper 35 cm of water but, owing to shading, plants nearer the surface received very much more light than the lower ones. Measurement of the light reaching the plants with the raft afloat and the nets in position was not practicable. A Weston meter showed that when the raft was out of the water the shading effect of its sides reduced illumination at the bottom of the compartments to about one-eighth of that at the level of the tufnol bars. Thus, if plants at the latter level were receiving 25% of the incident light owing to loss at the water surface (Sverdrup, Johnson & Fleming, 1942), then, after allowing for the difference shown by the meter, the lower parts might receive about 3%.

Bleaching effects

During the first growth period (24 May–8 June) the plants in the two well-illuminated compartments changed colour from their original dark red to a light straw colour as the photolabile phycoerythrin was lost. The colour of the plants in the two shaded compartments was virtually unaltered.

After weighing at the end of the period (on 8 June) the plants were replaced in different compartments for the remainder of the experiment. These changes are shown in Table 2. They involved interchange of the plants from compartment *W* (current and shade) with those from *Z* (still water and good illumination) and a similar interchange between compartments *X* (plants hanging in still water) and *Y* (plants free in current).

In the next period (8–21 June) bleached plants in the 'shaded' compartment *W* showed a much lower growth rate than unbleached plants in the same compartment in the previous period, while the unbleached plants in the 'light' compartment *Z* showed a high rate comparable to that of the first period. During this and subsequent periods the plants in *W* regained their colour while, at the same time, their growth rate increased, the successive average values for the daily rise in fresh weight being 1·01, 2·02 and 3·08%.

The latter value was rather higher than that for unbleached plants in the same compartment during the first growth period but may have been erroneously high as damage and loss had reduced the numbers of plants in the compartment and adversely affected the replication. At the same time, in compartment *Z*, the plants became bleached while growing rapidly (4·06% per day) in the 8–21 June period and, in the subsequent periods, grew at lower rates of 2·60% and 2·71% per day. This rate was similar, incidentally, to that of fully pigmented plants in the shaded compartments.

Meanwhile, settlement of the raft as its timbers became waterlogged and the loss of the attached floats frequently resulted in its being virtually awash and this, while not greatly affecting plants in *W* and *Z*, greatly reduced the shading effect in compartment *X* owing to the plants in it being swayed by movements of the raft and the shipping of water. In fact a reverse shading effect occurred between compartments *X* and *Y* owing to the rapid growth of filamentous algae in the latter (open to current) which shaded the *Gracilaria* plants and slowed their growth. At the same time, the plants in *Y* regained their colour and when, on 5 July, the shading weed was removed, a period of rapid growth followed comparable to that during the first period (24 May–8 June) and in both cases resulting, presumably, from the full illumination of unbleached plants.

Before considering the final conclusions to be drawn from these results it is proposed to describe supplementary experiments carried out in the laboratory.

LABORATORY EXPERIMENTS

EXPERIMENTS ON THE EFFECTS OF WATER CURRENTS ON GROWTH RATE

As a check on the current/still water experiment plants were grown in 3 cm. diameter Pyrex glass tubes. Four tubes were used and supplied with sea water from the laboratory system via a constant head device. The outflow from each tube was controlled by means of a screw clip closing a rubber tube. The rate of flow from each tube was found by timing the collection of a measured volume from the outlet. To prevent any rise in temperature the tubes rested in a tray and tap water was directed on to each. A thermometer was placed in each tube and showed that no temperature differences occurred.

Weighed portions of a single plant, divided at its expanded basal holdfast, were placed in the tubes. They were grown for 9 days under constant, even illumination of 600 lux from daylight type fluorescent tubes and then weighed again.

Results

Table 3 gives the results obtained.

TABLE 3

Approx. rate of flow (ml./h)	Increase in fresh weight (%)
22	7·7
1,500	14·9
7,200	20·4
36,000	20·2

Conclusions

It appears that the growth rate increases with increasing flow up to about 7 l./h, after which, under the conditions of light and temperature prevailing here, further increase in the flow rate does not induce faster growth. These results must, of course, be treated with great caution owing to the lack of replication and the shortcomings of the apparatus, in which it was difficult to maintain a steady flow. However, a flow rate of 7 l./h is equivalent to a current of about 1 m/h through the tube, so that it seems that currents cannot be expected to have a direct effect on the growth rate in the field, even allowing for the higher light intensity which the plants would receive for part of the time under natural conditions. More movement of water would occur even in the calmest conditions and, in fact, it seems that current becomes a limiting factor only when the water moves so slowly as to be almost stagnant. This is in agreement with the observations of Gessner (1940) who showed that respiration and assimilation rates in *Fucus* spp. were retarded up to 50% in stagnant water, compared with water in a shaken vessel.

EXPERIMENTS ON EFFECTS OF HIGH INTENSITIES OF ILLUMINATION

The bleaching effect observed on the shore and in the raft experiments occurred under conditions of intense summer illumination. Confirmatory experiments in the laboratory therefore require the provision of light of the same order of intensity.

Apparatus

In these experiments, two Strand Electric pattern 23 N theatre spotlights were used. These employ 500 W projector bulbs in highly efficient spherical reflectors and have a lens system concentrating the light in an 11° cone. They were set up so as to shine on to a mirror, inclined at 45° to the horizontal, which deflected their beams downwards. (This was to allow the lamp filaments to burn in the correct vertical position.) At a total distance of 65 cm from the front lenses the light from both lamps coincided on an area about 20 cm in diameter and here there was placed a white enamel dish 5 cm deep, through which a constant stream of sea water was passed, without causing ripples on the surface. Although the lamps produced considerable heat it was found possible to prevent the temperature of the water in the dish rising

above its original level (that of the laboratory supply) by suitably adjusting the rate of flow.

The light intensity was not uniform over the whole of the illuminated area; in the brightest, central area the intensity of illumination was about 56,000 lux, as measured by a Weston meter with Invercone calibrated from a standard source. This value fell off away from the centre of the illuminated area and was of the order of 30,000–35,000 lux at the periphery. It must be borne in mind that the spectrum of the light from tungsten filaments is very different from normal daylight. The former is deficient in the ultra-violet and the shorter wavelengths of the visible spectrum. Thus, although in these experiments the measured intensities are comparable and the results similar, no quantitative correspondence should necessarily be expected between the results of the laboratory and field experiments.

Methods

Both mature plants and sporelings of *Gracilaria verrucosa* have been used. With the former it was intended to test the effect of increasing daily periods of intense illumination and at the same time to observe whether any photo-tropic response occurred. The latter phenomenon seemed likely from the observation of some forms assumed by the plant in the field. To prevent confusion of the results by the reflexion of the light upwards from the bottom of the dish and to hold the plants in a fixed position, they were attached by nylon thread to perforated 'Tufnol' plastic plates, each about 23×7 cm. so that no branches projected beyond the edges. When not under the bright light, the plants received constant illumination of about 500 lux from fluorescent lamps. In the first experiment three 'plants' were used, all parts of the same tetrasporic clump. The fresh weight of each was recorded before the experiment began and their colour checked against an arbitrary standard designed to show the change from complete bleaching to full pigmentation in eight numbered steps.

One of the plants was left in the dish under a constant illumination of 500 lux all the time to serve as a control, the others were given additional daily periods under the bright lights of 30 min and 1 h respectively for the first run of 12 days, these periods being increased in subsequent runs.

As only two plants could be accommodated under the lamps at once and as daily periods of 8 h were envisaged in the later stages, replication of this experiment was not practicable and this must detract from the reliability of the results.

Phototropism

At the end of the first run of 12 days the form of the control plant was unchanged. The branches of the other two, which had received respectively 6 and 12 h of strong illumination, were turned upwards towards the light

(Fig. 2), except where they were secured to the tufnol plates. After each weighing between runs these plants were turned over before being tied again to the plate; in each case the upward curvature was quickly re-established. Although appreciable growth of the control took place during the experiment, no upturning of its branches occurred. It may therefore be concluded: (i) The upturning is not due to gravity, since this factor affected all plants, including the control, equally. (ii) There is a pronounced positive phototropism in response to bright light of the order of full daylight but not, apparently, in response to lower intensities. As the lower intensities are sufficient to promote growth, it seems possible that the upturning is not so much the result of an auxin migration (its usual explanation in higher plants), which might be expected to occur under all intensities, but is a direct effect of the high light intensity, perhaps by speeding up growth of the more shaded and therefore less bleached lower side (see below). (iii) The response has been observed after as little as 3 h total intense illumination.

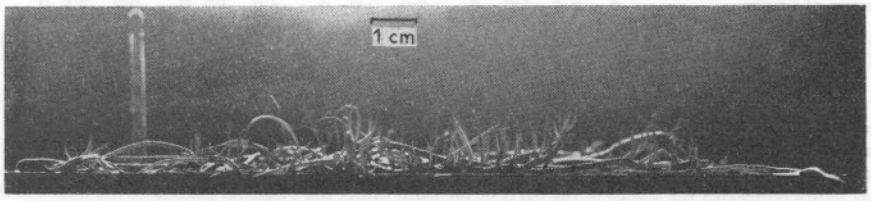

Fig. 2. Plant of *Gracilaria verrucosa* showing response to unidirectional illumination. Those branches which are not secured to the 'Tufnol' plate are turned upwards towards the incident light. The hooking over of the extreme tips of the branches was caused by desiccation during their photography. The scale line is 1 cm.

Changes in pigmentation and growth

The main changes observed and the length of the daily high light period in successive runs are shown in Table 4.

Pigmentation changes became noticeable during the second run, the parts of the plants under the brightest area of the field becoming lighter in colour, while the remainder in the less intense light lost less of their pigments. It was also noticed that the loss of pigment was, at this stage, restricted to the sides of the fronds facing the light, while the sides in contact with the tufnol plates were less affected. As the daily light period was increased, the bleaching effect became more marked until almost all the plant was bleached in each case. Little change in pigmentation occurred in the control. The temperature in both dishes throughout the experiment was maintained between 12·5° and 14·5° C.

During one run the control plant was placed on the white bottom of the dish and not on the tufnol plate. During this period a fourfold increase in

the growth rate occurred in the control compared with that in other periods, which may be attributed to the increased light obtained by reflexion upwards from the bottom of the dish and internal reflexion between this and the water surface. Normally most of the light passing the plant would be absorbed by the tufnol plate.

The effect of increasing daily illumination is shown in Fig. 3, which also indicates the state of pigmentation. It will be seen that there appears to be a direct relationship between the daily illumination and the increase in fresh weight as long as pigmentation is not greatly affected, but that after bleaching occurs the growth rate, so far as can be judged from the data available, does not rise very much with further increases in the period of illumination and falls

TABLE 4. GROWTH OF *GRACILARIA VERRUCOSA* WHEN SUBJECTED TO HIGH-INTENSITY ILLUMINATION

Duration of run...				17–29 May			29 May–9 June			9–18 June			18–29 June			29 June–9 July		
Plant...	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
Daily hours of bright light	—	—	—	0	0·5	1·0	0	2·0	3·0	0	5·0	4·0	0	6·0	2·5	0	8·0	8·0
% gain in fresh weight at end of run*	—	—	—	2·0	6·5	10·1	31·4†	20·1	29·0	7·7	25·9	23·6	8·8	33·3	15·5	3·0	19·8	20·3
Colour at‡ end of run	(17 May) 6	6	6	6	6	6	6	3–5	2–5	6	1–4	2–4	5–6	1–2	2–4	5–6	1–2	1–2

* Corrected to give equivalent for 12 days.

† Plant '*a*' not on tufnol plate during run 29 May–9 June—received better illumination than in other runs.

‡ Values given are according to arbitrary standard where 1 = bleached, 8 = very dark. Where two values are given the lower figure represents the colour of the parts of the plant under the brightest portion of the field and the higher one the remaining darker parts.

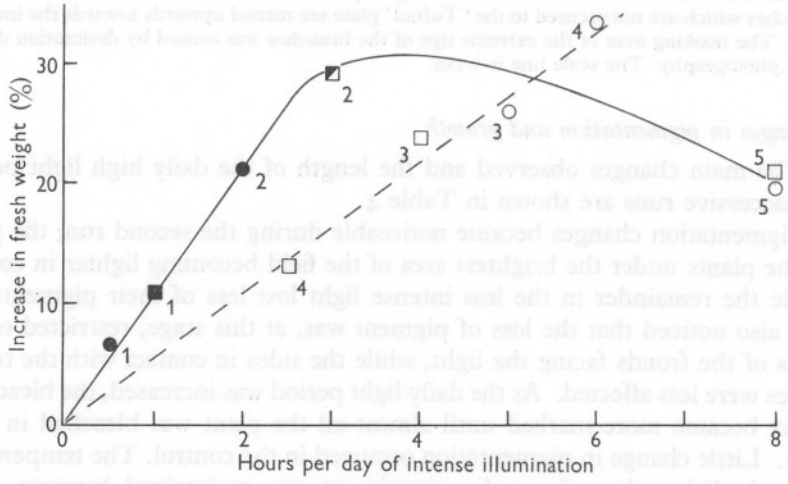

Fig. 3. The effect of increasing daily dosage of intense illumination on the growth and pigmentation of *Gracilaria verrucosa*. The numerals alongside each symbol indicate the consecutive periods of illumination. The vertical scale represents percentage increase in fresh weight in 12 days. Symbols: ●, 1st plant; ■, 2nd plant. Pigmentation: ■, fully pigmented; ◩, half bleached; □, fully bleached; — — —, growth in fully bleached condition.

appreciably when the daily dosage is raised to 8 h. The growth of plant '*c*' during the fourth run (18–29 June), when in the bleached condition, was only about half that obtainable in an equal period of illumination when unbleached. In fact the values of the percentage increases in weight of the plants in the bleached state, for periods of illumination up to 6 h, fall on a straight line whose slope is approximately half (actually 1:1·9) that for the unbleached plants, a value which agrees with the results of the raft experiments.

When the same lighting system was used in experiments on sporelings the results were very different. Sporelings at an early stage of development, up to 1 week old, grown from carpospores shed in the laboratory, were illuminated by the light for periods of up to 1·5 h daily. Although there was a slight initial increase in growth rate, the loss of phycoerythrin was very rapid and development ceased after a total of 4–5 h illumination. The sporelings did not recover from this treatment. Controls which received constant illumination of 400 lux grew normally and retained their colour.

GENERAL CONCLUSIONS AND DISCUSSION

The following conclusions may be drawn from the results of the experiments described here, bearing in mind that additional, more refined, experiments would be required to place them on a more exact quantitative basis.

(i) Phycoerythrin in living *Gracilaria verrucosa* disappears under the action of light intensities of the order of full daylight.

(ii) When the light is reduced, phycoerythrin is regenerated. In shade where the light intensity is approximately 12% of that just below the sea's surface, considerable regeneration occurs in ten days.

(iii) The bleaching effect does not appear to depend on unusually high temperature. In the laboratory it occurred at under 14·5° C and in the field the temperature was substantially the same (rising from 10° to 14° C), while both regeneration of pigments and their bleaching proceeded.

(iv) The growth rate of the plant, under all lighthing conditions so far observed, is lower in the bleached condition than when fully pigmented. At the low intensities under which phycoerythrin is regenerated unbleached plants grow from twice to three times as fast as bleached ones; at intensities high enough to cause bleaching, unbleached plants grow from 1·5 times to twice as fast as bleached plants.

The slower growth of bleached plants points to phycoerythrin being directly useful to the plant in its growth processes. This reinforces, in terms of the growth rate, what has been demonstrated by several workers in the measurement of assimilation rates in the Rhodophyceae. Wurmser & Ducleaux (1921) showed that the assimilation rates of *Rhodymenia* and *Chondrus* when red were twice as great as when green (i.e. bleached, presumably), a value which fits in well with the present results.

Although the loss of phycoerythrin reduces the growth rate of the plant this does not appear to be a serious difficulty in nature since bleaching is caused by the high summer illumination, and at these intensities the growth, even of bleached plants, is rapid. On open shores with clear water bleaching begins to be noticeable in late spring and early summer and it is at this time, when the light intensity is high but before the plants lose all their phycoerythrin, that growth is fastest. Later bleaching becomes more pronounced and the growth rate falls but the maximum size is reached in late summer when the plants are fully bleached.

The reduction in the growth rate of plants which have been intensely illuminated for a long daily period is also in agreement with previous work: Meyers & Burr (1940) showed that, in *Chlorella*, high light intensities (above 15,000 lux) reduced the rate of photosynthesis. The plants recovered from this high illumination, recovery being slower the longer the period of illumination and the higher the intensity, but at very high intensities permanent injury took place. In the case of sporeling material of *Gracilaria*, injury from which the sporelings do not recover occurs under intensities of the order of full daylight when this is received for 4–5 h. This can explain why plants of *Gracilaria* are not found in upshore pools where intensities of this order may be received for considerable periods every day in summer.

This work was carried out at the suggestion of Prof. L. Newton, whose encouragement and helpful comments I should like to acknowledge.

SUMMARY

A raft is described which permits experiments on the effect of current and still water on marine organisms. This has been used in experiments on *Gracilaria verrucosa* which, supplemented by laboratory experiments, show that, while there is no direct current effect on the growth, there is an indirect effect. This is an increase in the growth rate due to the better illumination of plants spread out by the current.

The bleaching of the thalli when illuminated by light of high intensity has been observed on the raft and demonstrated under tungsten spotlamps in the laboratory. It has been shown that the colour is regained when the light is reduced and that growth is from one and a half to three times as fast in unbleached plants as in those from which the phycoerythrin has gone. This difference between bleached and unbleached plants is less marked at high light intensities.

Positive phototropism of the branches of the plant has been demonstrated.

High light intensities have been found to have an adverse effect on mature plants only after prolonged illumination but to be quickly harmful to sporelings. It is suggested that this may limit the upshore distribution in pools.

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STUDIES ON MARINE FLAGELLATES

V. MORPHOLOGY AND MICROANATOMY OF *CHRYSOCHROMULINA STROBILUS* SP.NOV.

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(With total of 44 Figures in text and on Plates I–VIII)

CONTENTS

INTRODUCTION

The new species to be described here is very common in the English Channel, though like other members of this genus it is so fragile that it needs to be cultured to be effectively detected. This particular species has been under observation for some years, but publication has been deferred until sections of it could be made available. The observations involved in the taxonomic description have been based on two early isolates numbered 4 and 43 in the Plymouth collection. More recently, however, it has been encountered

frequently in routine sea-water samples brought into temporary culture to record the nanoplankton forms present, and we are therefore able for the first time to give tables of seasonal and depth distributions for the incidence of the species, at various stations. In Table 1 of Appendix (p. 187) its occurrences are listed, all being from water-bottle samples, except those taken on 23 August 1950 and 6 November 1957 (fine tow-net) and on 19 June 1957 (very fine tow-net). Table 2 (p. 188) gives densities at different depths sampled on one day at Hydrographic Station E 1.

The other technical methods involved are substantially as before except for minor variants in fixing and embedding procedures. As on previous occasions the electron micrographs of external morphology were carried out on the old Philips microscope in the Leeds Botany Department. A few of the high-power details, notably those on haptonema structure contained in Pl. VIII, were obtained on the Siemens Elmiskop I at the Rockefeller Institute which was made available during a 2-week visit at Christmas 1957. The remaining anatomical micrographs have been taken on the new Siemens Elmiskop I recently installed in the Leeds Botany Department by means of a grant from the Rockefeller Foundation.

Very grateful thanks are due to Dr K. R. Porter of the Rockefeller Institute for his unfailing courtesy and help during flying visits to his laboratory, also to the Rockefeller Foundation for removing the necessity for such visits. For help with the Latin diagnosis we have to thank Dr T. Christensen of Copenhagen. We have also to thank Miss I. Adams for assistance in the routine examination of samples, Mr F. G. C. Ryder for designing and building the special apparatus used for the growth of the very numerous temporary cultures from which distribution records have been obtained, Miss D. Ballantine (Mrs B. Hepper) for testing this organism for its possible toxicity to fish, Dr L. H. N. Cooper, Mr E. I. Butler, Dr T. J. Hart ('Discovery II'), Mr D. Vaux and Mr A. C. Burd ('Sir Lancelot') for the collection of sea-water samples.

FORMAL TAXONOMIC DIAGNOSIS

Chrysochromulina strobilus sp.nov. Parke & Manton

(Gr. *στρόβιλος*—a pirouette)

Motile cells showing considerable metaboly; dorsi-ventrally flattened, convex on the dorsal surface, flat or concave ventrally; when stationary or gliding slowly body saddle-shaped or appearing truncate-ovate in dorsal or ventral view; when swimming rapidly bell-shaped, obovoid or depressed-globose; 6–10 (exceptionally 5–12) μ in size. Two flagella and one haptonema arising fairly close together from the ventral surface, usually one-third cell length from rounded end in a centre line; flagella subequal to equal, very fine,

smooth, tapered to a small knob (E.M. observation), appearing homodynamic when cell moving rapidly and heterodynamic when cell moving slowly or stationary, 2–3 times body length; the haptonema capable of attaching along its whole length, half the thickness of the flagella, 12–18 (exceptionally 20) times the body length when fully extended, with a swollen tip and an internal structure of three concentric membranes surrounding a ring of six 'fibres'. The periplast, pectic in nature, showing a surface pattern of tightly packed angular 'cup' scales 0·15–0·2 μ in diameter; additional very thin, transparent, circular to oval, sculptured scales, 0·3–0·4 μ in diameter, with a pattern of radiating ridges, present beneath the 'cup' scales.

Cells uninucleate, no stigma. Chromatophores faintly striated on outer face, 2 or 4, occasionally 1 or none, golden brown; in cells of motile phase parietal, saucer-shaped to oblong, lacking an external pyrenoid but with a well-marked internal storage region; in non-motile phase pale gold and very finely lobed. Lipids and leucosin produced. Ejectile muciferous bodies small, distributed in peripheral cytoplasm, more numerous on dorsal and ventral surface of back of saddle but their position changing with the metaboly of the body. Nutrition phototrophic and/or phagotrophic. Non-toxic to fish.

In motile phase asexual reproduction by fission into two daughter-cells, usually of equal size; in non-motile phase by successive fission of amoeboid cells to produce 4 ovate daughter-cells with thin walls; motile phase liberated from walled daughter-cell through pore.

Habitat. The sea at position lat. N. 49° 21′, long. W. 04° 54′ (9 May 1950, type culture) at surface. Type culture (Plymouth no. 43) deposited with the Culture Collection of Algae and Protozoa, Cambridge.

Cellula in statu erratico satis metabola, depressa, dorso convexo, ventre plano vel cavo; dum quieta lenteve prolabens ephippioides seu a dorso vel ventre truncato-ovata visa; dum cito natans campanuliformis seu obovata seu depresse globularis; 6–10 (raro 5–12) μ longa. Flagella duo haptonemaque unicum in facie ventrali sat conferte inserta, plerumque mediana, tertia cellulae longitudinis parte ab apice rotundato remota; flagella paene vel plane aequalia, tenuissima, glabra, ad apices attenuata, nodulo quidque terminatum (per microscopium electronicum viso), cellula 2–3 plo longiora, inter motum citum homodynamica, inter lente movendum ut inter quietem heterodynamica visa; haptonema flagellis dimidio tenuius, extensum cellula 12–18 (raro –20) plo longius, apice incrassatum, in sectione transversa tres membranas tubiformes concentricas ostendens fibras 6 in orbem dispositas induentes, in tota longitudine adhaerendi potens. Periplastum pecticum, squamis dense angulate congestis, 0·15–0·2 μ diametro, marginibus adscendentibus, discis intus mucronato-incrassatis obtectum, alteris illis suppositis delicatulis, hyalinis, orbicularibus vel ovalibus, 0·3–0·4 μ diametro, costis radiantibus ornatis.

Nucleus unicus; stigma nullum. Chromatophora 2 vel 4, interdum unum vel nullum, fulva, in facie externa striatula, inter statum erraticum cellulae parietalia, catilliformia vel oblonga, pyrenoidibus externis carentia, sed regione penaria interna manifesta quidque instructum; inter statum sedentarium pallide aurea, subtilissime lobata. Synthemata lipoida et leucosinea. Corpora mucifera ejectilia parva, in strato

externo cytoplasmatis distributa, in facie dorsali et ventrali posterioris partis ephippii crebriora, inter metabolam situs mutantia.

Alga et phototropha et phagotropha seu alterutro solum victu alta; piscibus non venenosa.

Propagatio vegetativa in statu erratico bifissione effecta, cellulis filialibus plerumque aequalibus; in statu sedentario fissione iterata cellulae amoeboidis, cellulis filialibus 4, ovatis, parietibus subtilibus indutis, quaque earum cellulam erraticam per porum liberante.

Typus die 9. Maji 1950 in summo mari lat. bor. 49° 21′, long. occ. 04° 54′ lectus, in Plymouth Angliae sub numero 43 cultus, postea in vivario Cantabrigiensi depositus.

OBSERVATIONS WITH THE LIGHT MICROSCOPE

Description and behaviour of the living cell

Chrysochromulina strobilus (Figs. 1–12) is somewhat similar to *C. ephippium* and *C. alifera* (Parke, Manton & Clarke, 1956) in shape, size and in the behaviour of the flagella and haptonema when an individual is stationary or when slowly gliding; it also exhibits phagotrophism in common with all our species so far described.

It differs from *C. ephippium* and *C. alifera* in the position of origin of the flagella and haptonema (Fig. 8), the body attitude and the behaviour of the

Legends to Text-figs. 1–12

Chrysochromulina strobilus sp.nov.

(Figs. 1–7, × 1250; Figs. 8–12, × 5000)

Fig. 1. Cell anchored by fully extended haptonema which is bent and attaching only by swollen tip.

Fig. 2. Anchored saddle-shaped cell with flagella showing heterodynamic movement; haptonema attached along most of its length.

Fig. 3. Saddle-shaped cell gliding slowly with haptonema lying away from and in front of body.

Fig. 4. Early fission stage rotating slowly and moving with haptonema fully extended in front of body.

Fig. 5. Fission stage with four flagella and two haptonemata in attitude adopted for fairly rapid swimming.

Fig. 6. Individual swimming with flagella in the position characteristic for the species for fairly rapid movement; haptonema extended but coiled up on itself and trailing behind body.

Fig. 7. Individual gliding without rotating with flagella in position characteristic for the species during gliding movement.

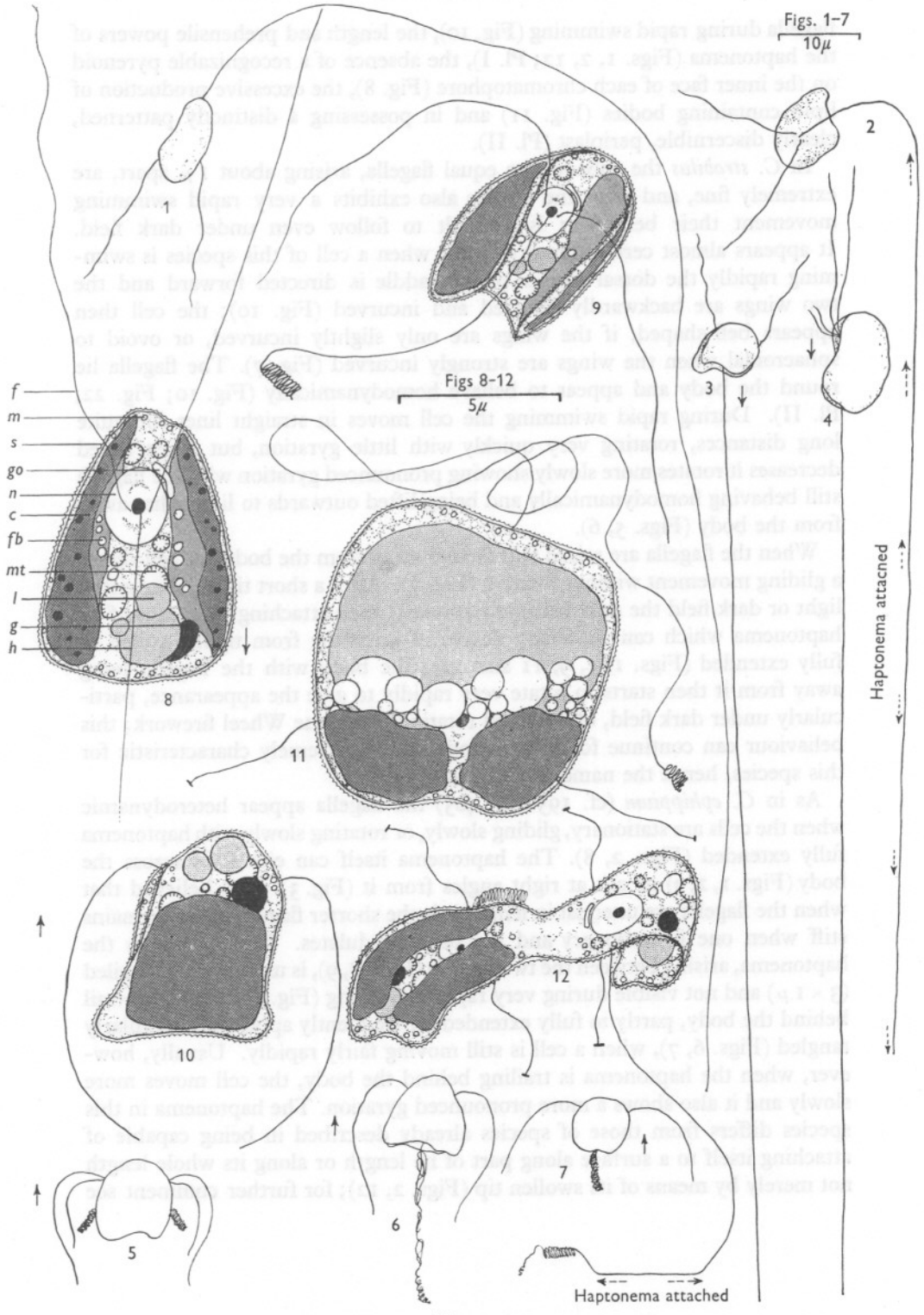
Fig. 8. Kite-shaped cell (ventral surface) moving slowly with haptonema fully extended in front of body, one flagellum slowly undulating, the other stiff or gently vibrating. *c*, chromatophore containing saturated lipid globules stained by Sudan Black; *f*, flagellum; *fb*, lipid globules; *g*, graphite; *go*, golgi; *h*, haptonema; *l*, leucosin vesicle; *m*, muciferous body; *mt*, mitochondrion; *n*, nucleus; *s*, 'cup'-shaped scale.

Fig. 9. Anchored cell with haptonema partly coiled and flagella lying out from body.

Fig. 10. Individual swimming with flagella and body in the position characteristic for the species during very rapid swimming.

Fig. 11. Cell containing numerous lipid globules and a large leucosin vesicle from a culture grown in strong light for 10 days; haptonema nearly fully extended, coiled on itself and attached only at tip.

Fig. 12. Late fission stage, one daughter-cell without chromatophores.


Figs. 1–7
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Figs 8–12
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Haptonema attacned
Haptonema attached

Figs. 1–12

flagella during rapid swimming (Fig. 10), the length and prehensile powers of the haptonema (Figs. 1, 2, 12; Pl. I), the absence of a recognizable pyrenoid on the inner face of each chromatophore (Fig. 8), the excessive production of lipid containing bodies (Fig. 11) and in possessing a distinctly patterned, clearly discernible, periplast (Pl. II).

In *C. strobilus* the subequal to equal flagella, arising about 1 μ apart, are extremely fine, and since the species also exhibits a very rapid swimming movement their behaviour is difficult to follow even under dark field. It appears almost certain, however, that when a cell of this species is swimming rapidly the dorsal surface of the saddle is directed forward and the two wings are backwardly directed and incurved (Fig. 10); the cell then appears bell-shaped, if the wings are only slightly incurved, or ovoid to sphaeroidal when the wings are strongly incurved (Fig. 7). The flagella lie round the body and appear to behave homodynamically (Fig. 10; Fig. 22, Pl. II). During rapid swimming the cell moves in straight lines for quite long distances, rotating very quickly with little gyration, but when speed decreases it rotates more slowly showing pronounced gyration with the flagella still behaving homodynamically and being lifted outwards to lie further away from the body (Figs. 5, 6).

When the flagella are raised still farther away from the body the cell shows a gliding movement without rotation (Fig. 7). After a short time under either light or dark field the cells become stationary, each attaching by means of its haptonema which can show any degree of uncoiling from tightly coiled to fully extended (Figs. 1, 2, 9, 11 and 12); the body with the flagella lying away from it then starts to rotate very rapidly to give the appearance, particularly under dark field, of a lighted rotating Catherine Wheel firework; this behaviour can continue for long periods and is extremely characteristic for this species, hence the name *C. strobilus*.

As in *C. ephippium* (cf. 1956, p. 405) the flagella appear heterodynamic when the cells are stationary, gliding slowly, or rotating slowly with haptonema fully extended (Figs. 2, 8). The haptonema itself can either lie across the body (Figs. 1, 2, 9) or out at right angles from it (Fig. 3). It is believed that when the flagella are unequal in length it is the shorter flagellum that remains stiff when one is stationary and the other undulates. In *C. strobilus* the haptonema, arising between the two flagella (Figs. 8, 9), is usually tightly coiled (3×1 μ) and not visible during very rapid swimming (Fig. 10) but it can trail behind the body, partly to fully extended, or frequently appearing irregularly tangled (Figs. 6, 7), when a cell is still moving fairly rapidly. Usually, however, when the haptonema is trailing behind the body, the cell moves more slowly and it also shows a more pronounced gyration. The haptonema in this species differs from those of species already described in being capable of attaching itself to a surface along part of its length or along its whole length not merely by means of its swollen tip (Figs. 2, 12); for further comment see

p. 177. In this species also it took a great deal of time and patience to obtain measurements of 100 fully extended haptonemata since a cell with a fully extended haptonema when brought into the light or dark field for measurement will immediately retract its haptonema and swim away. Although the species lacks an obvious stigma it shows a definite phototactic reaction.

In an actively growing culture 65% of the cells are between 6 and 9 μ in size and a culture at the peak of growth contains up to $\frac{1}{2}$ million cells per ml. Occasionally cells lacking chromatophores are seen in the stock cultures (Fig. 12), but in cultures treated with penicillin and streptomycin the colourless cells are not uncommon; they are usually smaller (4–6 μ) than those possessing chromatophores.

Colourless forms, undoubtedly belonging to this species, have also been recorded from sea-water samples as well as their frequent occurrence being recorded from mixed cultures grown from sea-water samples.

Phagotrophy occurs very frequently (Figs. 8, 12; Fig. 18, Pl. I; Fig. 35, Pl. VI), the cell ingesting graphite, bacteria and plant cells usually up to 4×3 μ but in a mixed culture set up from a sea-water sample a cell of *C. strobilus* was seen to have engulfed a 15 μ long Naviculoid diatom, but the ends of the diatom were sticking out of the body. Direct examination of sea-water samples has also shown that *C. strobilus* does exhibit phagotrophy under natural conditions.

Contents of the body

Unlike *C. chiton* (1958), there is no external pyrenoid attached to the inner face of the chromatophore in *C. strobilus* and the lamellae in the chromatophores are less obvious, but, as in *C. chiton*, saturated lipid globules are present between the lamellae of the outer face of the chromatophore. Additional globules of unsaturated lipid material are also present in the body, as in *C. chiton* (1958, p. 221), but in *C. strobilus* they are generally more numerous. In the cells from an actively growing culture of *C. strobilus* there are from 1 to 4 of these lipid globules (*ca.* 0·5 μ) lying near to or against the inner face of each chromatophore (Fig. 8; Fig. 28, Pl. III; Fig. 34, Pl. IV). As growth in a culture slows down or when a culture has been grown in strong light (112 ft.c.) for 10 days the number and size of these globules increases very greatly so that a cell can contain from 10 to 20 (Fig. 11), some measuring up to 1·5 μ in diameter. This great increase in lipid material in the cell may be due to low nitrogen content of the medium (see Fogg, 1956). A control culture grown in weak light (8 ft.c.) for the same period showed that the cells still had only 1 to 4 small globules to each chromatophore.

All lipid globules stain orange to orange red with Sudan IV but only those free in the body react with osmium tetroxide becoming yellowish brown in the centre and dark brown or black on the outside. Using an unpublished

method for the staining of phospholipids given to one of us (M.P.) by Dr G. Y. Kennedy of Sheffield University the following results were obtained. The small globules between the lamellae of the outer face of the chromatophores gave a reaction for lipids of the 'cephalin' group whereas the larger globules free in the body (originating from the inner storage face of the chromatophore?) sometimes gave a staining characteristic for lecithins in the centre while a layer round the outside of the globule gave a reaction for cephalins. Two or three fairly small vesicles of leucosin are generally present in this species, lying in the body usually towards the non-flagellar end of the saddle. When a cell is moving rapidly, however, the leucosin can frequently be seen pushed to the centre of the dorsal surface and forming a slight bulge in the front of the cell while the chromatophores are drawn back into the wings (Fig. 10). The cells which showed a great increase in the number and size of the lipid globules after being grown in very strong light also showed the production of very large leucosin vesicles which sometimes filled nearly half the volume of the cell (Fig. 11).

The nucleus, ovoid and up to $3 \times 2\ \mu$ in size, lies towards the ventral surface of the saddle sometimes centrally in the body but more frequently excentrically, to the left of the centre when looking down on the ventral surface.

A dark bar-shaped body lying to one side of the nucleus and visible in the living cell stains up bright red with cresyl blue and as blue-green stripes with Janus green; this is almost certainly the golgi area (Figs. 8, 9, see p. 182 and Pls. V–VII). Four to six mitochondria can be distinguished by the use of Janus green; two or four, ($0{\cdot}5$–$0{\cdot}75\ \mu$), lie fairly close to the nucleus and two others, usually larger (1–$1{\cdot}5\ \mu$), lie towards the non-flagellar end of the saddle (Figs. 8, 9).

The muciferous bodies are small (*ca.* $0{\cdot}25\ \mu$) and not very conspicuous in this species (Fig. 8; Pl. V). They may be of a different structure to those described for other species (1955, 1956, 1958) since it is difficult to make them eject their contents even with the use of vital stains. *In situ* they stain a true clear blue round the outside with cresyl blue, but the contents do not appear to take up the stain. Most usually when ejection does occur with the use of dilute cresyl blue, the ejected mass appears to consist of two parts—a thicker part close to the body which becomes yellow to lime green and a much thinner mass which gradually balloons out from the thicker part and becomes a pale mauve colour; this suggests that the whole body may be ejected on a neck and that the thicker part is the organ itself—possibly not a natural procedure as the ejection is so difficult to obtain. Very occasionally, however, the ejection of short threads has been observed and, as in *C. ericina* (1956, p. 395), a small disk remains attached to the distal end of the thread.

When the cells are fixed with osmium tetroxide the contents shrink leaving the 'pellicle' or scale covering clearly visible; under high power it appears to

be covered by punctae. With cresyl blue and methylene blue the pellicle frequently bursts and the cell contents are extruded leaving the 'pellicle' practically complete (cf. *C. chiton*, 1958, and see p. 181).

Reproduction

Fission in the motile phase occurs as in *C. alifera* (1956, p. 413) and takes place most frequently in late afternoon (Figs. 4, 5, 12). Non-motile stages similar to those already described for other species (1955, 1956, 1958) are then produced. The large amoeboid and walled cells with very finely lobed chromatophores, as in *C. alifera* (1956), measure from 14×11 to $17 \times 12\ \mu$. The ovate to sphaeroidal daughter-cells have thin walls and finely lobed chromatophores and measure from 4×3 to $7 \times 5\ \mu$ in size. The partial but not the complete release of the motile stage from the walled daughter-cells has been observed.

OBSERVATIONS WITH THE ELECTRON MICROSCOPE—MORPHOLOGY

In addition to the observations already described from the light microscope, which include among others the measurement of relative length of the haptonema and its capacity, when alive, to become attached to a surface at any point along its length and not merely at the tip as in our previous species, the use of shadowcast whole mounts has added several significant facts by which this species is peculiar. One of these is the extreme elegance with which the haptonema uncoils, as this is expressed in dried specimens in a partly uncoiled condition. Several examples are included in Pl. I with greater detail of one of these in Fig. 27, Pl. II. The original coil itself is faintly visible in the undried cell of Fig. 18, Pl. I. The very regular configuration of two loops alternating to right and to left, often associated with the presence of apparent constrictions occurring at regular intervals along the haptonema, at first suggested to us that the whole organ might perhaps be ribbon-shaped rather than cylindrical and owe some of its properties to this cause. This suggestion is not borne out by sections, however, and therefore although in the dried condition the organ is undoubtedly flat, this flattening must in itself be attributed to the drying process. Nevertheless, it is possible that a tendency to become flattened may be greater in this than in any of our previous species, a circumstance which, if it were true, might explain the unusual ability of the haptonema to become attached throughout its length. For further discussion see p. 179.

Another peculiarity is the firmness with which the scales remain in position. In all our other species the scales have been so loosely attached both to each other and to the cell that they commonly litter the field either singly or in clusters which bear no relation to their original position. In this species

scales are only rarely encountered singly. With fresh material killed directly onto the formvar film (our usual method) the scales generally appear as compact uniform sheets often still in relation to the cell body (Figs. 22, 25, Pl. II), and with the component scales held in a very regular close-packed arrangement (Fig. 25) suggesting that they are partially embedded in some kind of a matrix, the whole forming a coherent pellicle-like mat which tends to behave as a unit. When cells are not killed in this way but treated in any other of our occasional procedures such as with iodine as a preliminary to stripping from glass, the scale-mat may cohere completely to the body surface and be undetectable (Fig. 23). In embedded material, on the other hand, pieces of 'scale-mat' with the scales still in position are abundant and easily recognized (for further details see p. 181); we may therefore be certain that the close-packing seen in whole mounts is here not accidental.

There are undoubtedly two types of scale present. This is not obvious from the surface view of a scale mat which (Fig. 25) generally shows only a compact and even array of small featureless scales with raised rims. But occasionally loose scales of slightly larger diameter and with faint surface striations are encountered (Figs. 25 (top right), 26). Once seen these can with care always be detected near sufficiently dismembered cells, but they are so very thin that it is never easy to determine their finer details. Nothing can be ascertained with certainty from whole mounts about their arrangement on the cell body.

OBSERVATIONS WITH THE ELECTRON MICROSCOPE—ANATOMY

The haptonema

The great length of this organ in our present species compared with *C. chiton* (1958) is at once revealed by the clusters of much more numerous component sections which can be encountered; compare, for example, Fig. 30, Pl. IV, with Pl. IV of our previous paper. Since the structure of this organ was the most important first object of inquiry and the only one for which the American microscope was used (cf. p. 170) it will be convenient to describe it first.

As may be seen at a glance in Fig. 30, Pl. IV, the haptonema here, as in our previous species, is only about half the width of a flagellum. The actual dimensions can be directly measured either in Fig. 30 or in several of those included in Pl. VIII, all of which indicate that, disregarding obvious distortions, the average width of cross-section is of the order of 0·2 μ. It should, however, perhaps be pointed out that higher magnifications than were achieved previously have been used for most of Pl. VIII and only the inset pictures on Fig. 39 are exactly comparable with some of those reproduced on Pl. IV of our previous paper.

Within the haptonema the salient anatomical features are comparable, though not identical, with those of *C. chiton*. As before, the most conspicuous

components are the three concentric membranes (using the term membrane rather loosely and without implications as to whether each is in fact single or compound) surrounding a ring of fibres (or tubes) and a central space. As before, the number of component fibres in the ring is extremely constant, having in this case been ascertained without any variation in thirteen specimens. It is, however, six and not seven as in the other species. Representative sections illustrating this number from three different cells are included in Pl. VIII (Figs. 39–41, Fig. 42 and Fig. 43 respectively), though the clearest individual section is doubtless that of Fig. 41. The diameter of each of the central fibres is of the order of 200–250 Å.

The three membranes of the haptonema wall are not all alike; the outermost one is undoubtedly compound. Its total thickness is rather less than 100 A, but when accurately cut a three-layered sub-structure consisting of two dense surface layers separated by a lighter central layer can be clearly resolved (see especially between the arrows in Figs. 41 and 40), the thickness of each of these components being of the order of 30 Å. or somewhat less. The other two membranes contained in the haptonema wall cannot be similarly resolved. They appear to be thinner than the outer triple membrane (see especially Fig. 41) and they are certainly more fragile since they often break under the action of the fixative (cf. Fig. 42). In so doing they frequently roll up and cease to be individually recognizable (see Fig. 39*c* and various parts of Fig. 40), an artifact which prevents effective discussion of the possible presence of an additional component which is not membranous. Nevertheless, certain sections (e.g. Fig. 43 uppermost LS) do suggest rather strongly that there may be a fibrous component in the haptonema wall arranged roughly at right angles to the longitudinal direction marked by the position of the central fibres. Further evidence will, however, be required before this component, if genuine, can be located with certainty.

A minor peculiarity which might perhaps be connected with the special properties referred to in the first paragraph of this section is that the central fibres seem less firmly attached to the innermost membrane than was the case in *C. chiton*. In our former species the union was so close that we were at first in doubt whether the fibres themselves were in fact thickenings or intuckings of the inner membrane and it was only in specimens considerably distended by 'blistering' that their separation could be clearly demonstrated (as in Fig. 42 here). In our present species it is the exception rather than the rule for the inner fibres to be found still touching the inner membrane, e.g. in insets *a* and *b* in Fig. 39. More usually, e.g. Figs. 41 and 43, the fibres are free from the membrane and are tending to become clustered together in the centre of the organ thus partially obliterating the cavity. Since it is an unavoidable condition of working with killed cells that we can only observe structure in relaxed coiled haptonemata and not in extended ones, it is impossible to know whether this difference from *C. chiton* is trivial or of functional significance.

The uppermost section included in the right-hand top corner of Fig. 39 perhaps represents the region of the thickened haptonema tip. It contains no interpretable structure except a solid centre surrounded by one membrane. If its nature had been more fully demonstrated, these observations would be important, but until they can be confirmed by additional, or by better, specimens we can only quote this one as possibly of this nature. We have no observations on the structure of the basal end of the haptonema.

Explanation of Plates I–IV

Chrysochromulina strobilus sp.nov.

I

Fig. 14. A cell dried on glass and photographed with the light microscope. × 1000.
Fig. 15. As Fig. 14, another cell. × 1000.
Fig. 16. Flagella and haptonema from the cell of Fig. 15 photographed by phase contrast. × 2000.
Fig. 17. The specimen of Figs. 15 and 16 after transfer to formvar, viewed with the low power of the electron microscope. Micrograph M 166.9, × 3000.
Fig. 18. A cell killed after ingesting graphite and photographed in a liquid mount under oil immersion; the central pellet of graphite and two lateral plastids appear dark, the coiled haptonema attached to the lower part of the body appears light. × 2000.
Fig. 19. As Fig. 14, another cell. × 1000.
Fig. 20. As Fig. 14, another cell. × 1000.
Fig. 21. The cell of Fig. 20 after transfer to the electron microscope. Micrograph M. 152.23, × 3000. For further details from this specimen see Fig. 25, Pl. II.

II

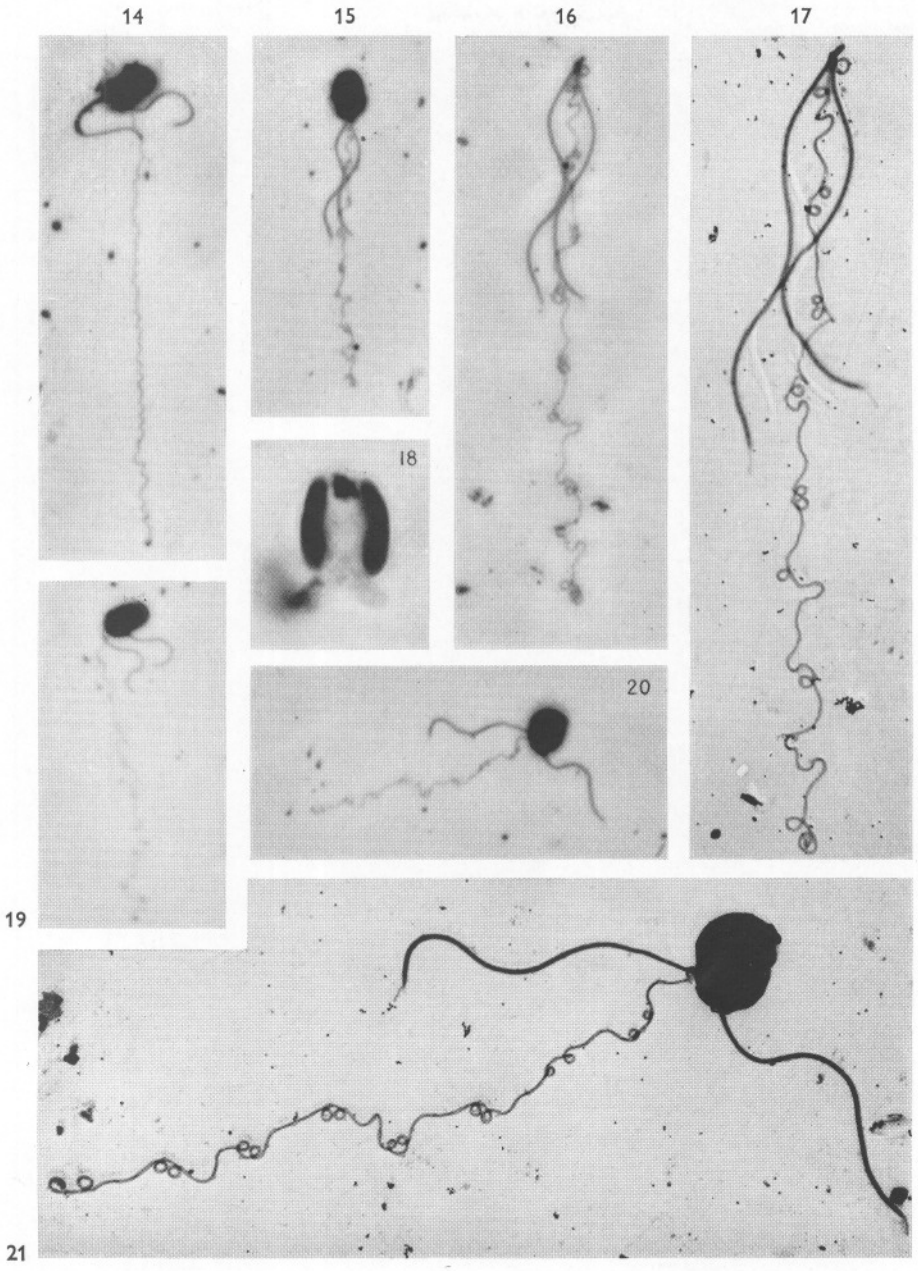
Fig. 22. A flattened cell seen with the electron microscope showing the layer of scales still in position outside the more opaque body. Micrograph M. 327.3, × 3000.
Fig. 23. Part of a cell with flattened appendages, stripped from a glass preparation. The partial decomposition of the haptonema has revealed a slender axis within translucent material (cf. with Fig. 27). × 10,000.
Fig. 24. Tip of a flagellum. M. 284.16, × 10,000.
Fig. 25. The edge of a scale-mat from a specimen comparable to that of Fig. 22, the cup-shaped scales still in position and apparently embedded in some amorphous material; two separate plate-scales appearing at the top of the figure. Micrograph M. 135.4, × 20,000.
Fig. 26. Free scales of the two types, the plate-scales in the upper part of the figure very transparent and difficult to record, the cup-shaped scales in the lower part of the figure projecting slightly from the surface of the mount. Micrograph M. 336.13, × 30,000.
Fig. 27. Tip of the haptonema of Fig. 21, more highly magnified, showing the swollen tip and configuration characteristic of uncoiling, in a less damaged specimen than that of Fig. 23. Micrograph M. 152.25, × 10,000.

III

Fig. 28. Section of a cell with scales on the surface, showing nucleus (*N*) 2 plastids (*P*), a flagellar base (*fb*), two black lipoid bodies and part of a third, mitochondria, golgi area and miscellaneous vesicles. Micrograph H. 1837, × 15,000.
Fig. 29. Surface of a similar cell with scales in position (for further details see Fig. 44, Pl. VIII). Micrograph H. 1733, × 30,000.

IV

Fig. 30. Section of a cell with related haptonema (*H*) and flagella (*f*) near two detached pieces of scale mat (*S*), one inverted with respect to the other. Micrograph H. 1830, × 15,000.
Fig. 31. Part of Fig. 30 to show details of the storage region in the plastid; arrows point to sections of paired tubes which traverse it. Micrograph H. 1831, × 30,000.



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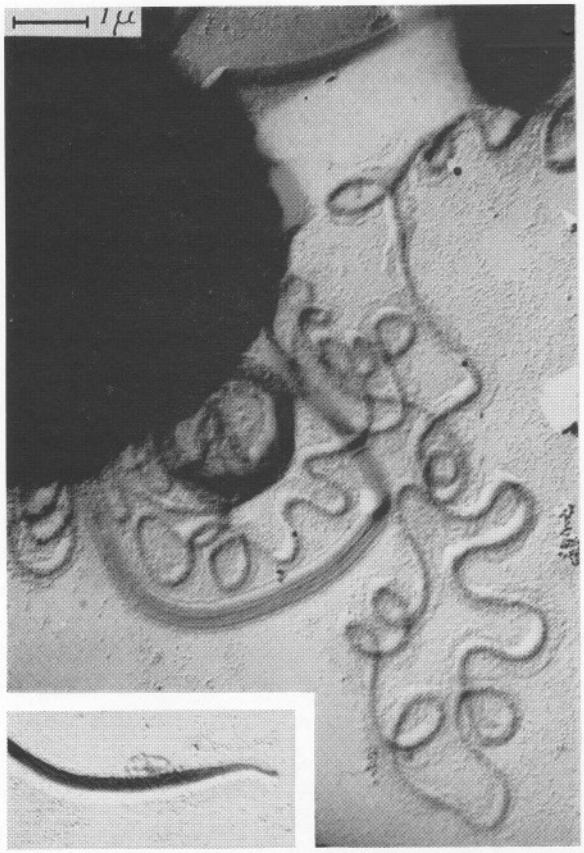

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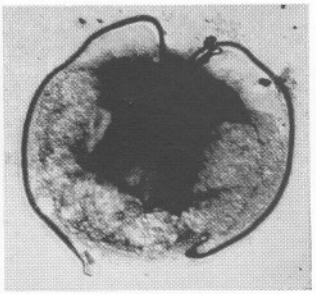

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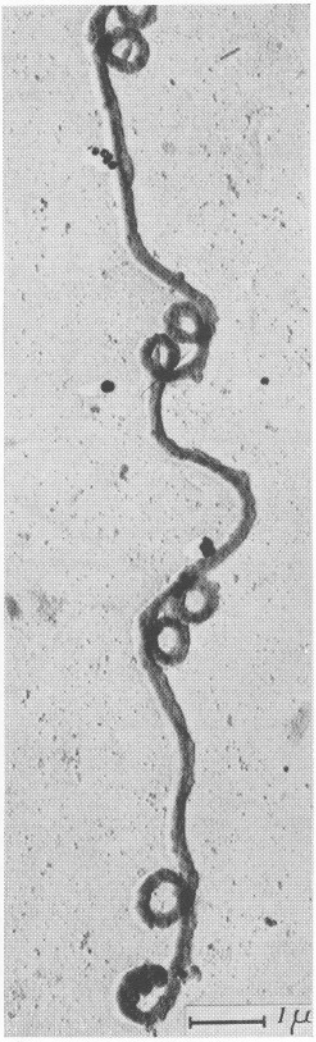

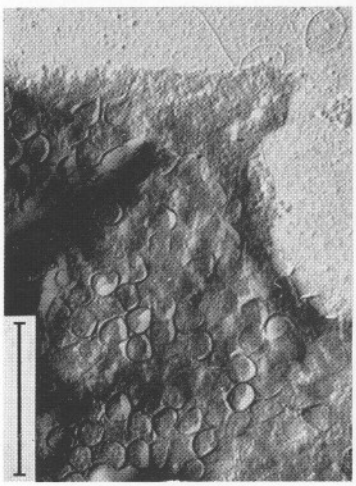

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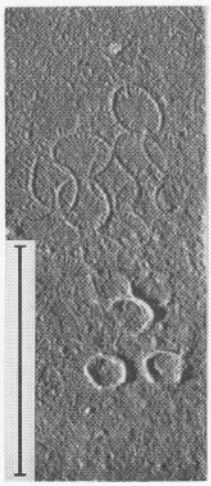

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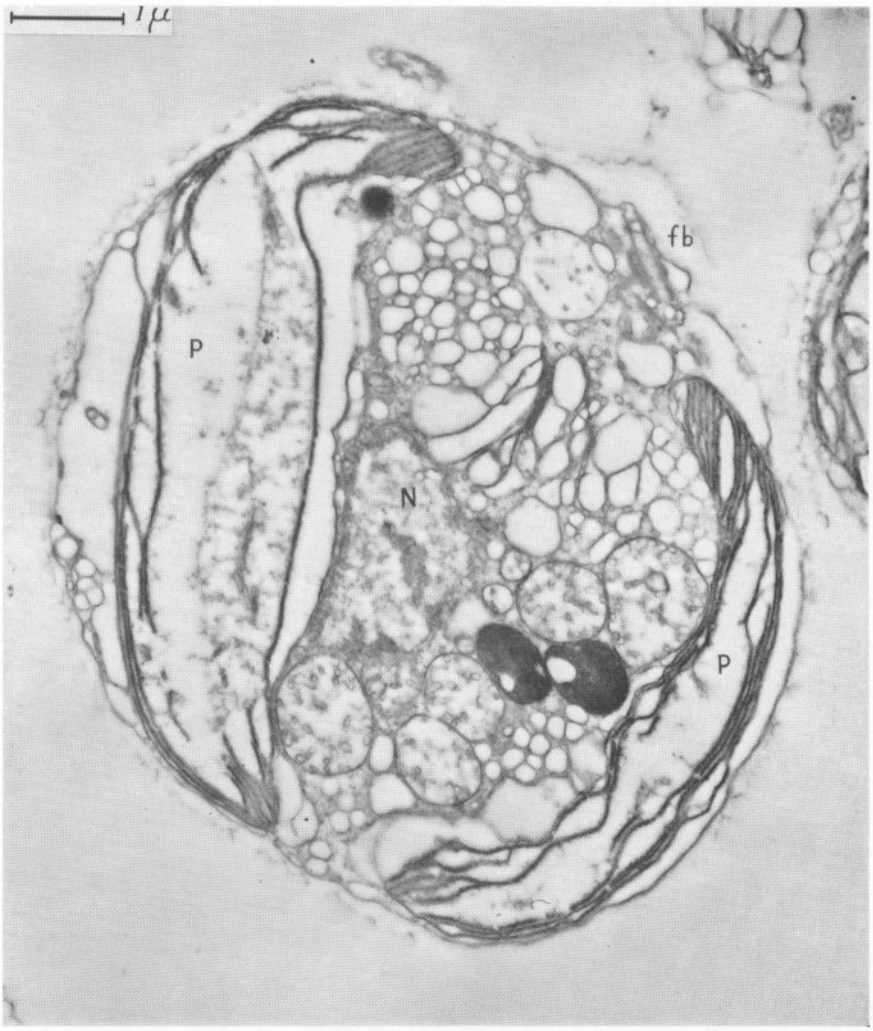

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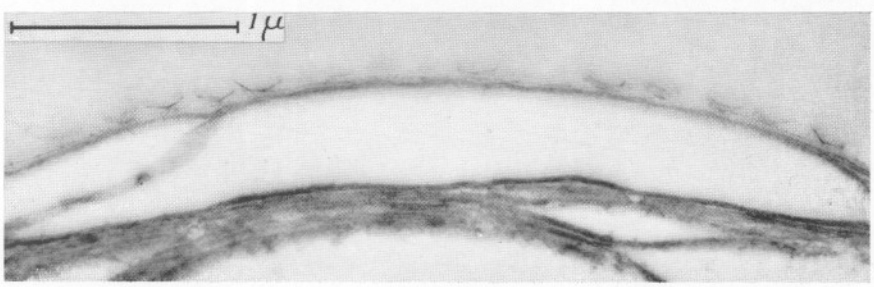

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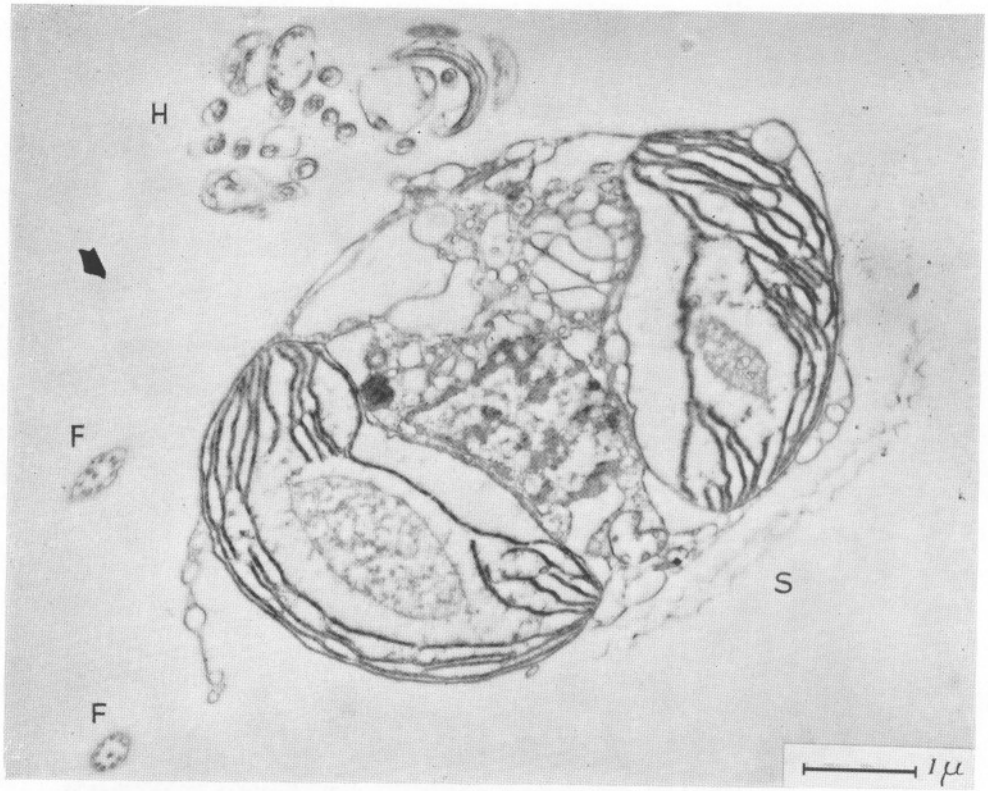

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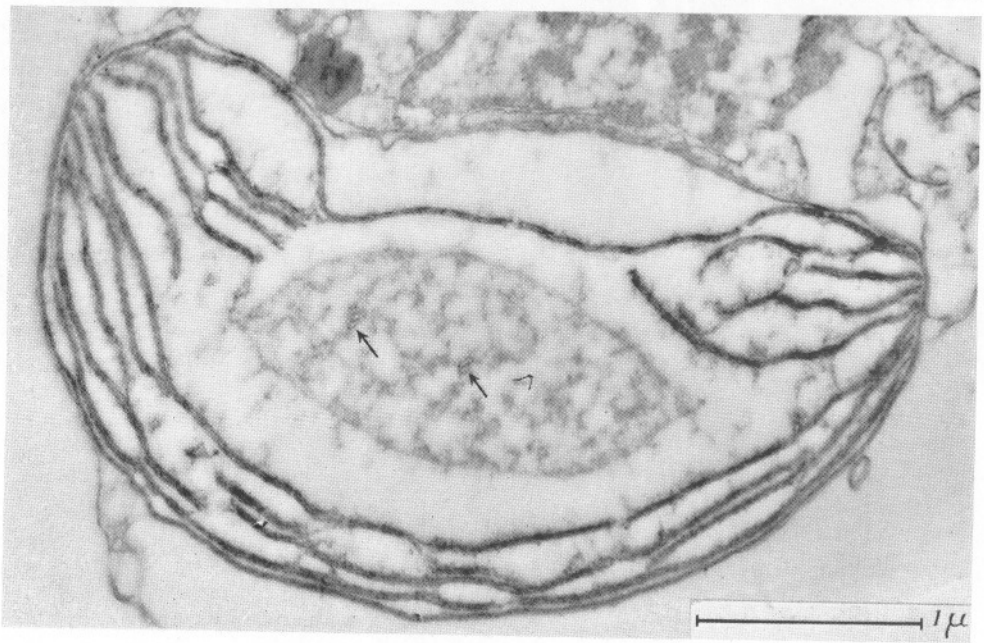

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The scales

Fig. 44, Pl. VIII (for explanatory diagram see Fig. 13), shows a section of scales in position on the body at a magnification comparable to that of the adjacent haptonema sections (i.e. 60,000 as in Figs. 42 and 43). The cup-shaped scales with conical thickened base are arranged in a very regular layer, as was to be expected from the external view. Beneath them are the plate scales, also in a single layer; each is a very delicate sheet with a slight central thickening and a rim projecting up from both surfaces like the edge of a coin. Other less highly magnified sections showing the scales still in position on the cell are contained in Pl. III and elsewhere.

Fig. 13. Diagram traced over a photographic print to show the arrangement of scales in Fig. 44, Pl. VIII, magnification of the diagram × 80,000.

Detached scales, still arranged in sheets, are common. Two such sheets, one inverted with respect to the other, are situated near the letter S on Fig. 30, Pl. IV. Neither can be directly related to the adjacent cell since the sheet nearest to the body surface is upside down with respect to it. When cut transversely the conical cup-scales, arranged side by side, produce an effect as of a delicate zig-zag line at this low power. The amorphous material partially investing the scales on dried material is no longer visible in sections but this is likely to be due to solution in the methacrylate since the regular array of scales in each sheet is undisturbed. This can be seen no less clearly when a sheet is cut tangentially as in the top corner (right) of Fig. 32, Pl. V. In such an aspect the scales appear circular with a central opaque area; there is again no sign of intercalary material between them but they are in exactly the same serial arrangement as in Fig. 25, Pl. II.

Beneath the scales is a membrane, as in *C. chiton*, and sometimes though not always a layer or layers of small vesicles. The diameter of these vesicles is of the same order as that of the scales. Since there were no superficial vesicles in *C. chiton* as small as this we may perhaps find this fact to be significant when developmental processes can be more seriously considered.

The internal organs

A glance at the low-power views of complete sections reproduced in Pls. III–V will sufficiently indicate the general positions of the more important body organs. The chromatophores, nucleus, mitochondria and food vacuole are labelled as such in Fig. 32, Pl. V. In addition the lipid bodies in the cell interior and the muciferous bodies on the surface are conspicuous by their

opacity, a property connected with their chemical effect on the osmic fixative. Leucosin vacuoles or equivalent spaces bounded by a membrane appear empty.

Some of these organs or organelles resemble those of *C. chiton* sufficiently closely to be passed over without further comment; the nucleus, mitochondria and food vacuole fall into this category. Differences of a fairly striking kind do nevertheless exist and since we are still without sufficient knowledge to be able to distinguish characters which may be of generic importance from others which only delimit taxa of a lower order, it will be necessary to enumerate differences as fully as possible. The following comments will therefore be restricted to this topic.

The pyrenoid

The most conspicuous difference between the internal organs of *C. chiton* and our present species concerns the pyrenoid. In *C. chiton* this was a subspherical body filled with dark contents and attached by a narrow neck to the inner face of a chromatophore. No such bodies can be detected in our present species. Instead there is an internal storage region within the chromatophore, often of considerable extent and containing similar dark contents. A good example is illustrated in Pl. IV and parts of others will be detectable elsewhere. The stored material is traversed by some highly characteristic narrow paired tubes which are almost certainly continuous with some of the lamellations of the pigmented part of the chromatophore although we have not on this occasion reproduced any micrographs illustrating this continuity. Examples of the tubes in question, cut in slightly oblique TS are indicated by arrows in Fig. 31, Pl. IV.

The flagellar bases

These have not been studied in great detail here but it is necessary to locate them before attention can be given to the organelle to be discussed in the next paragraph. They differ a little from the situation in *C. chiton* by the extreme obliquity with which they are inserted. This is clearly indicated in Fig. 28, Pl. III, where a flagellar base (fb) in almost median LS is lying almost parallel to the cell surface. This is a highly characteristic position and we have never encountered in this species the almost vertical orientation of flagella to the surface which was illustrated, for example, in Fig. 34, Pl. IX, of our previous paper. When both flagellar bases are contained in the same section they make a very obtuse angle with each other as in Fig. 34, Pl. VI.

Golgi

Immediately below the attachment of the flagellar bases is an area occupied by vesicles of the characteristic kind previously diagnosed as golgi. The golgi area is commonly bounded by the nucleus, mitochondria and chromatophores

on the sides towards the cell (e.g. Fig. 28, Pl. III and Fig. 32, Pl. V), though it is never separated from the flagellar bases by any of these organs, and it is not delimited by a membrane. When cut tangentially or merely grazed, only the compacted vesicles and traces of flattened paired membranes are visible (e.g. Figs. 28, 32). When cut more nearly centrally, however, a surprising complexity of structure is revealed. Pls. VI and VII are inserted to illustrate this.

In Pl. VI are two cells cut in planes approximately at right angles to each other but both passing through the central region of the golgi area. A more highly magnified view of one of these cells is reproduced in Fig. 38, Pl. VII, while the two upper figures on Pl. VII are similarly magnified views of two different sections from one specimen resembling Fig. 34 in plane of cutting. Pls. VI and VII thus illustrate the golgi structure in three different cells.

The central part of the golgi area is most easily interpreted as a cavity occupying the concave side of the strongly curved outer paired membranes (flattened cisternae) into which many of the inner paired membranes are budding off vesicles. These vesicles are commonly somewhat distorted and perhaps burst as a fixation artifact leaving numerous fragments of membrane distributed through colourless liquid. For further discussion see p. 185.

Muciferous bodies

The only additional details to add about these organelles are firstly that they are not very numerous. A section displaying as many as appear in Fig. 32, Pl. V, is an exception selected for reproduction for this reason; the more usual condition is as in the other plates in which these bodies are only encounted here and there or not at all. In structure they recall those of *C. chiton* though they may perhaps be simpler. There is no suggestion here of any obvious modification of the outer wall, an undischarged body merely projecting a little above the surface of the cell (Fig. 33) without other detectable structural features. The contents appear slightly darker than in our micrographs of *C. chiton*, but a minor difference in fixation procedure could perhaps explain this.

DISCUSSION

While the more obvious comparisons, namely those with *C. chiton* (Parke, Manton & Clarke, 1958), have already been made, a few general comments remain. It is clear that the structural differences recorded fall into two rather different categories. On the one hand there are clearly determined divergences as in the pyrenoids and numerical details within the haptonema, on the other are observations which could depend in part on fuller knowledge of our present species. It may be recalled that for our previous paper there was only very limited access to high resolution microscopes and the amount of material surveyed was in consequence severely restricted. We cannot therefore be quite

certain without further investigation of *C. chiton* whether, for example, the very peculiar structure encountered in the centre of the golgi area in our present species is actually absent from our previous one or whether we failed to detect it for the reason given.

Explanation of Plates V–VIII

Chrysochromulina strobilus sp.nov.

V

Fig. 32. Section of a cell to show muciferous bodies (black) in the outermost layer. In addition the nucleus (*N*), mitochondria (*m*), a food vacuole (*FV*), spaces which could have contained leucosin, golgi vesicles near the base of the appendage (uncertain whether this is a flagellum or a haptonema). Arrow in the top right-hand corner points to a scale mat seen in surface view; elsewhere scales in position on the body and sections of bacteria in the ground. Micrograph H. 1637, × 18,000.

Fig. 33. Part of the surface of a similar cell to show the way in which full muciferous bodies (dark) project above the cell surface. Micrograph H. 1969, × 20,000.

VI

Fig. 34. Section of a cell to show golgi structures between the two plastids (*P*), and below the flagellar bases (*fb*). In addition (dark) lipid bodies, mitochondria and vesicles. Micrograph H. 1706, × 15,000.

Fig. 35. A similar cell cut in a plane roughly at right angles to the preceding showing the nucleus (*N*), a large food vacuole (*FV*) and the golgi area immediately above it; for further details see Fig. 38, Pl. VII. Micrograph H. 1833, × 15,000.

VII

Figs. 36, 37. Two sections, some distance apart, of a cell cut somewhat as in Fig. 34, to show the structure of the golgi area when cut near its edges (Fig. 36) and more centrally (Fig. 37). Signs of the flagellar bases (*fb*) visible in Fig. 36. Two fat bodies and the edges of adjacent plastids, arranged as in Fig. 34 visible laterally (see especially Fig. 36), in addition several mitochondria (*m*) and scattered vesicles. Micrographs H. 1619 and H. 1624, × 25,000.

Fig. 38. Detail of the golgi area in Fig. 35 more highly magnified, lettering as in that figure. Micrograph H. 1834, × 25,000.

VIII

Fig. 39. General view of a haptonema with inset details of three component sections (a, b, c) from the places marked by the upper arrows; lower arrow a significant region for Figs. 40 and 41; *fb* a flagellar base on what is probably the subtending cell. Micrographs RS. 80, × 25,000, and RS. 378, × 50,000 (insets).

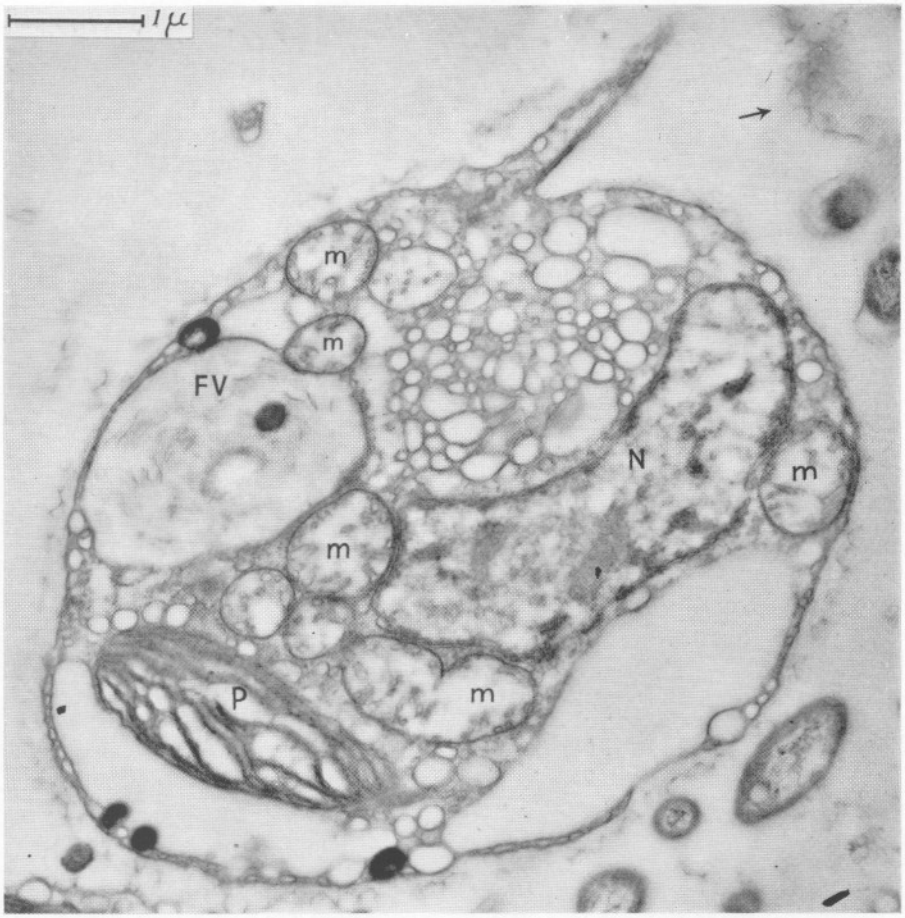
Fig. 40. Part of another section through the haptonema of Fig. 39 more highly magnified. Micrograph RS. 390, × 70,000.

Fig. 41. Part of the preceding more highly magnified and placed in a different attitude on the page; the six central fibres and three concentric membranes very clearly displayed with also (between the arrows) evidence that the outermost membrane is double. Micrograph RS. 390, × 100,000.

Fig. 42. Part of another specimen exhibiting 'blistering' but showing the three membranes and six central fibres very clearly when the inner membranes have split. Micrograph RS. 400, × 60,000.

Fig. 43. Part of another specimen to show a similar general anatomy in TS (lower arrow) and parts of an LS (upper arrow). Micrograph H. 1611, × 60,000.

Fig. 44. Section showing the two types of scale in position on a cell, the cup-shaped scales forming an outer layer and the plate-shaped scales below. Micrograph RS. 60, × *ca.* 60,000.



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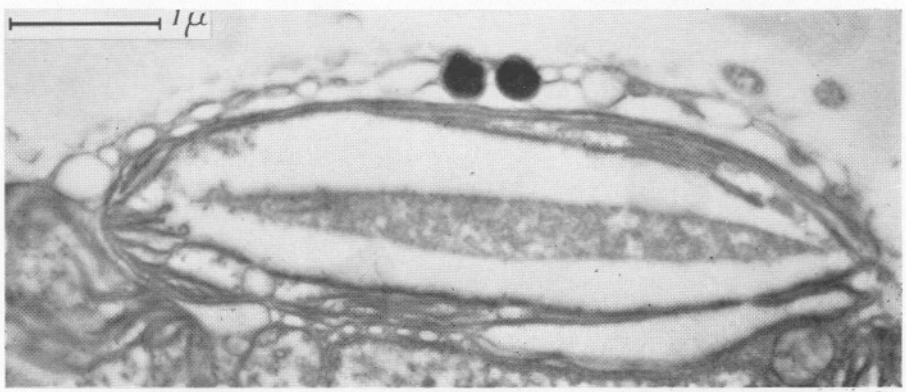

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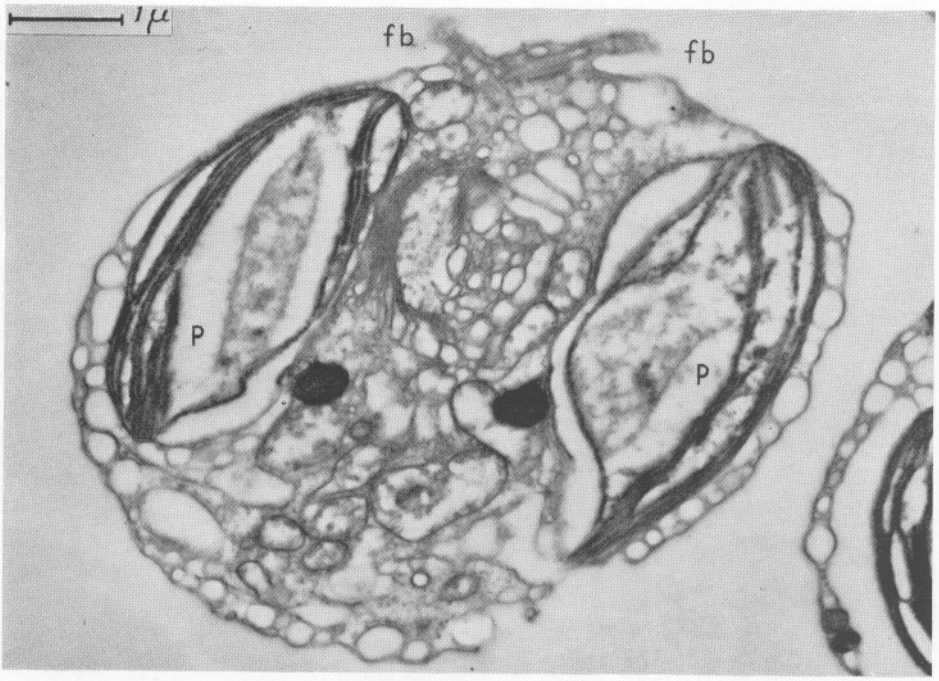

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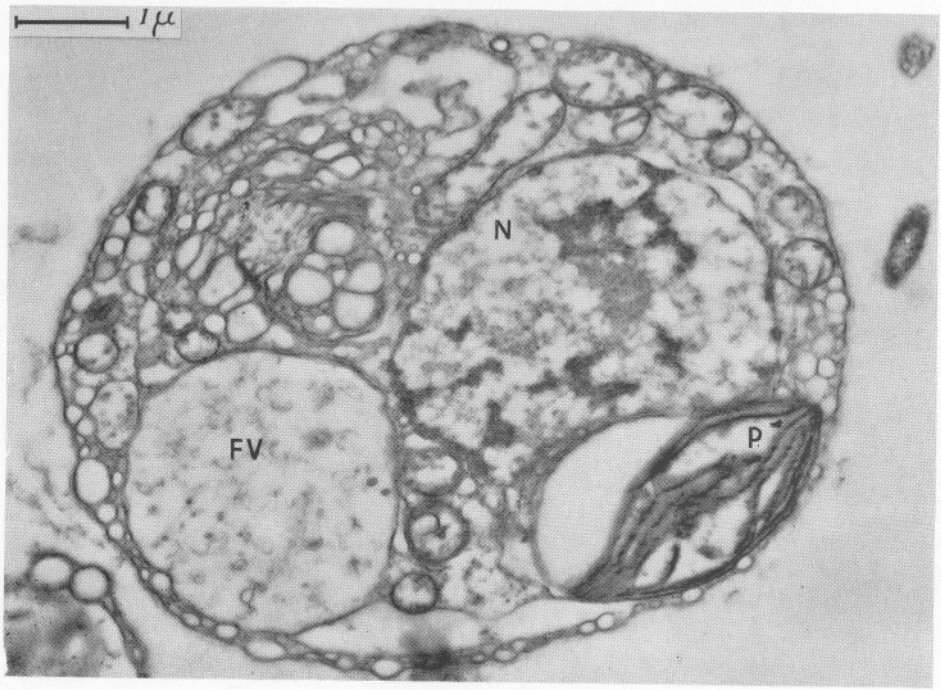

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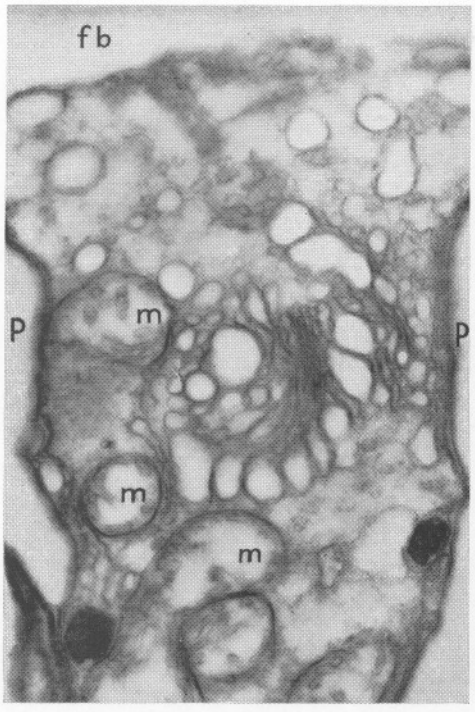

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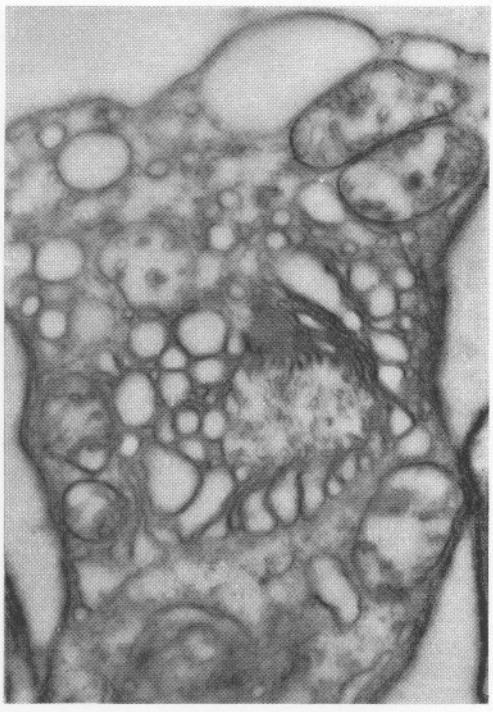

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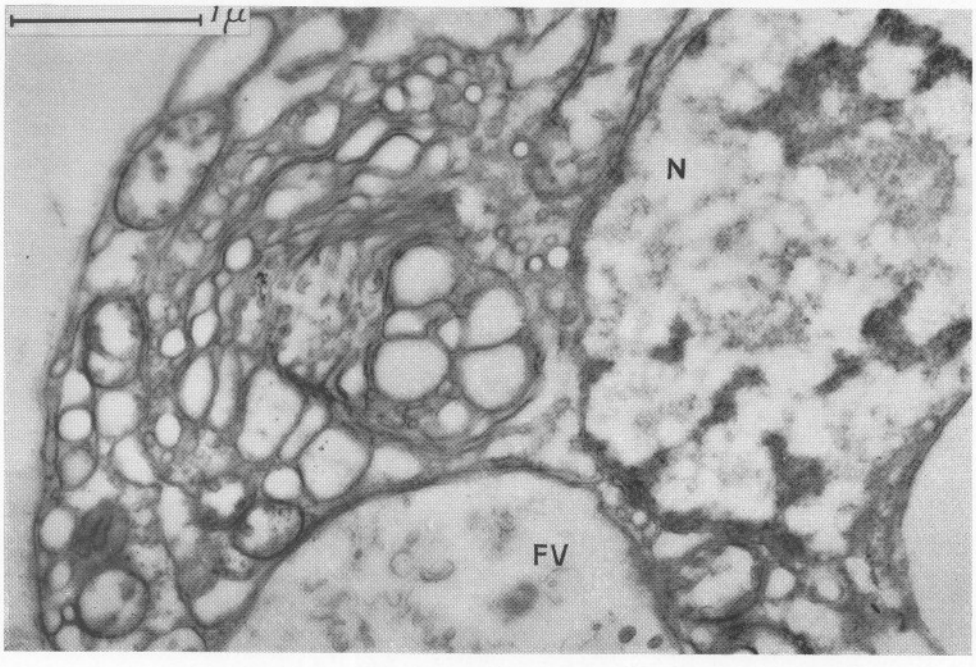

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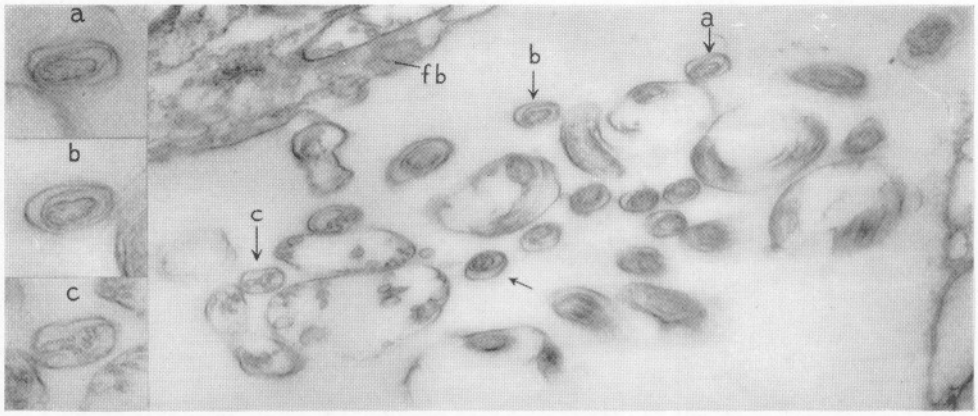

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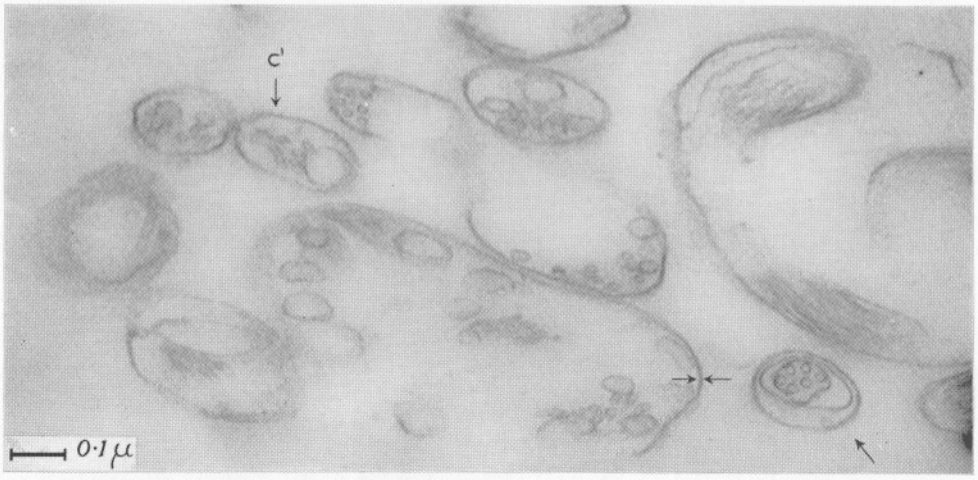

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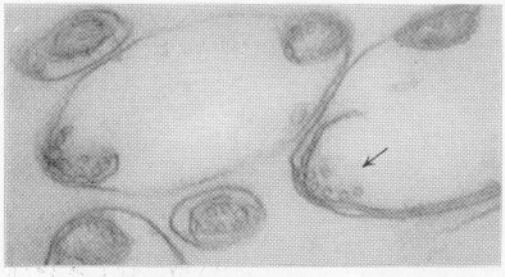

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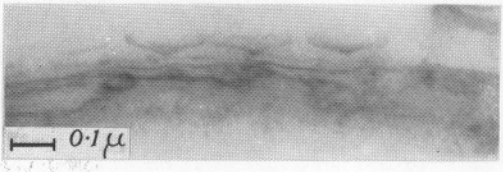

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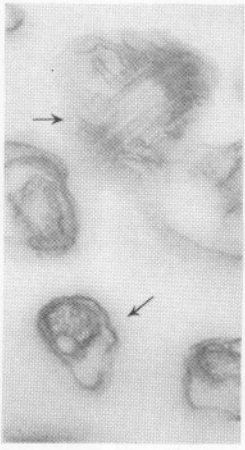

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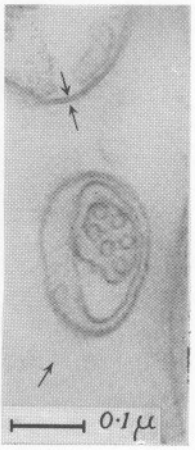

41

There is, however, no doubt that the observations recorded for the centre of the golgi area in our present species are unusual, and for this reason we have at once taken steps to ascertain whether or not we are here dealing with an idiosyncrasy confined to one species. Preliminary sections of two other of our previously described species, *C. ericina* and *C. ephippium* of Parke, Manton & Clarke, 1956, have, however, at once revealed exactly comparable details, and since at least one of these species seems to be a more favourable object for study than our present one we propose to defer further discussion of this organ until more evidence can be surveyed.

We are on firmer ground with regard to the pyrenoid and haptonema for which positive differences from *C. chiton* have been demonstrated. A pyrenoid of the type encountered here recalls very closely that recently described for *Hydrurus* by Hovasse & Joyon (1957). We can say further (Manton, unpublished) that similar pyrenoids, differing only in minor features of size and position, are present also in *C. ericina* and *C. ephippium*. It is therefore possible that in this character *C. strobilus* rather than *C. chiton* may represent the norm within the group.

With regard to the haptonema structure, external comparisons are not yet possible since knowledge is at present limited to the two species under discussion. Comparison between these species is, however, instructive in more than one way. The numerical difference in fibre number, 7 in *C. chiton* and 6 in *C. strobilus*, is not to be explained away as a sampling error since both numbers have been determined with equal certainty through a range of specimens. Each number seems to have the constancy of a specific character, but this only underlines the fundamental difference between the haptonema and a flagellum for which complete uniformity of internal structure prevails, not merely from species to species but right through the plant and animal kingdoms. The resemblances, on the other hand, are no less important since here we may believe that the two species are both contributing essential information towards a descriptive understanding of this complex and peculiar organ, which though still incomplete, is significantly enhanced by the new facts contributed by *C. strobilus*. The triple structure of the outermost membrane of the haptonema wall is most unlikely to be a specific peculiarity confined to *C. strobilus* since similar membranes are now known to be a normal covering to many external protoplasmic organs, e.g. cilia and flagella. This very fact, however, indicates fairly clearly that the special properties possessed by the haptonema are likely to be determined by the internal parts about which less is known.

With regard to the scales the presence of two distinct types arranged one beneath the other in separate layers seems to remove entirely the possibility of continuous production of scales from the body surface at all times. It seems necessary to conclude that scale production must in some way be a cyclic phenomenon, a conclusion which was also, though less definitely, formulated in connexion with the rather different scale arrangement in *C. chiton*.

SUMMARY

A new species of *Chrysochromulina*, *C. strobilus*, characterized by a very long haptonema capable of attaching at any point along its length and by very small scales of characteristic pattern has been described. The anatomy of the haptonema consists, as in a previous species, *C. chiton*, of three concentric membranes surrounding a ring of fibres and a central space. The outermost membrane is three-layered and there are traces of some intercalary material between this and the middle membrane. The number of fibres in the inner ring is 6 and not 7 as in *C. chiton*; each fibre is of the order of 200–250 A. in width. The organs internal to the cell show two major differences from those of our previous species, notably in the pyrenoid and golgi area. The pyrenoid is inside the chromatophore; its structure is described. The golgi area shows a central structure which is so unusual that a full description is reserved until more species have been examined.

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APPENDIX

Table 1. RECORDED DISTRIBUTION OF *CHRYSOCHROMULINA STROBILUS* SP.NOV.

Date	Position N.	Position W.	Depth (m.)
12. xi. 48	50° 19·5′	04° 10′*	10
1. ii. 49	50° 19·5	04° 10′	10
8. vi. 49	50° 19·5′	04° 10′	10
12. iv. 50	49° 25′	03° 47′†	0·5
13. iv. 50	50° 15′	04° 13′	0·5
4. v. 50	50° 15′	04° 13′	0·5
9. v. 50	49° 21′	04° 54′†‡	0·5
23. viii. 50	Tamar Estuary off Torpoint		—
20. ix. 52	Off the Azores§		0·5
17. i. 56	50° 02′	04° 22′	20
29. v. 56	50° 06′	04° 21′	5
29. xi. 56	50° 07′	04° 23·5′	0·5
2. i. 57	50° 03′	04° 04·5′	0·5
19. vi. 57	50° 09′	04° 15′	—
16. vii. 57	50° 02′	04° 22′	0·5
24. vii. 57	50° 11′	04° 14′	0·5
17. ix. 57	50° 02′	04° 22′	0·5, 5, 10, 20, 70
17. ix. 57	50° 06′	04° 21′	0·5
	50° 11′	04° 13′	0·5
	50° 15′	04° 13′	0·5
	50° 18′	04° 11′	0·5
	50° 20′	04° 10′	0·5
15. x. 57	50° 11′	04° 13′	0·5
	50° 15′	04° 13′	0·5
6. xi. 57	Tamar Estuary off Forder Mill		—
3. xii. 57	50° 02′	04° 22′	5, 10, 20, 70
3. xii. 57	50° 06′	04° 21′	0·5
3. xii. 57	50° 11′	04° 13′	0·5
	50° 15′	04° 13′	0·5
	50° 18′	04° 11′	0·5
	50° 20′	04° 10′	0·5
21. i. 58	50° 02′	04° 22′	20, 50
21. i. 58	50° 06′	04° 21′	0·5
	50° 15′	04° 13′	0·5
	50° 15′	04° 11′	0·5
	50° 20′	04° 10′	0·5
18. ii. 58	50° 02′	04° 22′	0·5
			5, 10, 20, 50, 70
18. ii. 58	50° 06′	04° 21′	0·5
	50° 15′	04° 13′	0·5
18. ii. 58	50° 18′	04° 11′	0·5
	50° 20′	04° 10′	0·5
16. iii. 58	47° 40′	07° 13′	10, 20
18. iii. 58	47° 46′	07° 05′	20
19. iii. 58	50° 02′	04° 22′	0·5, 5, 10, 20, 50, 70
19. iv. 58	46° 30′	08° 00′	10
20. iv. 58	47° 30′	07° 18′	10
	47° 38′	07° 10′	10, 225
21. iv. 58	47° 46′	07° 05′	10, 20, 163
22. iv. 58	50° 02′	04° 22′	0·5, 5, 10, 20, 50, 70
20. v. 58	50° 02′	04° 22′	5, 10, 20, 50, 70
20. v. 58	50° 06′	04° 21′	0·5
	50° 11′	04° 13′	0·5
	50° 15′	04° 13′	0·5
	50° 18′	04° 11′	0·5
	50° 20′	04° 10′	0·5
10. vi. 58	50° 02′	04° 22′	0·5, 5, 10, 15, 20, 50, 70
10. vi. 58	50° 06′	04° 21′	0·5
	50° 15′	04° 13′	0·5
	50° 18′	04° 11′	0·5
9. vii. 58	50° 02′	04° 22′	0·5, 5, 10, 70
9. vii. 58	50° 11′	04° 13′	0·5
	50° 15′	04° 13′	0·5
	50° 18′	04° 11′	0·5
26. viii. 58	50° 02′	04° 22′	0·5, 5, 20, 30, 50, 70
26. viii. 58	50° 06′	04° 21′	0·5
1. x. 58	50° 02′	04° 22′	0·5, 5, 10, 20, 50
22. x. 58	50° 02′	04′ 22′	0·5, 10, 20, 50, 70
	50° 20′	04′ 10′	0·5
18. xi. 58	50° 02′	04° 22′	0·5
	50° 06′	04° 21′	0·5
	50° 11′	04° 13′	0·5
	50° 15′	04° 13′	0·5
	50° 18′	04° 11′	0·5

* Strain of *Chrysochromulina strobilus* (Plymouth no. 4) isolated from this sample.

† Samples brought in by 'Sir Lancelot'.

‡ Type culture strain of *Chrysochromulina strobilus* (Plymouth no. 43) isolated from this sample.

§ Sample brought in by 'Discovery II'.

TABLE 2. SEASONAL DISTRIBUTION OF *CHRYSOCHROMULINA STROBILUS* SP.NOV.

	International Station E 1								Plymouth Laboratory Stations				
									L6	L5	L4	L3	L2
Depth (m) ...	0·5	5	10	15	20	30	50	70	0·5	0·5	0·5	0·5	0·5
Date													
17. ix. 57	3	3	3	—	3	—	0	1	2	3	2	2	3
15. x. 57	0	0	0	—	0	—	0	0	0	1	1	0	0
6. xi. 57	1	—	0	—	0	—	—	—	—	—	—	—	—
3. xii. 57	0	2	3	—	5	—	0	2	1	1	1	1	1
21. i. 58	0	0	0	—	2	—	1	0	1	0	2	1	2
18. ii. 58	2	3	3	—	4	—	1	3	2	0	3	2	3
20. iii. 58	3	3	4	—	4	—	5	5	—	—	—	—	—
22. iv. 58	6	6	6	—	4	—	3	3	—	—	—	—	—
20. v. 58	0	2	3	—	3	—	2	2	3	4	4	2	1
10. vi. 58	5	5	6	4	3	—	2	4	5	0	1	1	0
9. vii. 58	1	2	1	0	0	—	0	1	0	2	2	2	0
26. viii. 58	4	1	0	—	1	3	3	3	4	0	0	0	0
1. x. 58	2	2	3	—	1	—	1	0	—	—	—	—	—
22. x. 58	2	0	1	—	1	—	1	1	0	0	0	0	2
18. xi. 58	1	—	0	—	0	—	0	0	2	1	1	4	0

6, min. no. *C. strobilus* per l. 1000 — E 1 50° 02′ N., 04° 22′ W.
5, min. no. *C. strobilus* per l. 800 — L 6 50° 06′ N., 04° 21′ W.
4, min. no. *C. strobilus* per l. 600 — L 5 50° 11′ N., 04° 13′ W.
3, min. no. *C. strobilus* per l. 400 — L 4 50° 15′ N., 04° 13′ W.
2, min. no. *C. strobilus* per l. 200 — L 3 50° 18′ N., 04° 11′ W.
1, min. no. *C. strobilus* per l. 10 — L 2 50° 20′ N., 04° 10′ W.
0, Absent from sample

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ON THE BIOLOGY OF *PANDALUS BOREALIS* KRØYER, WITH REFERENCE TO A POPULATION OFF THE NORTHUMBERLAND COAST

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(Text-figs. 1–14)

The deep sea prawn, *Pandalus borealis* Krøyer, is fished extensively in Norwegian, Swedish and Greenland waters, some 4000 metric tons being caught annually, having a value of about £800,000. Its biology has been investigated by various workers in these countries. Comprehensive accounts have been given by Wollebaek (1903), Hjort & Ruud (1938), Rasmussen (1953) and Horsted & Smidt (1956). Despite this, relatively few populations have been sampled at regular intervals throughout a year. In high latitudes where much work has been carried out, ice, for varying lengths of time, prevents stocks from being sampled. Rasmussen (1942, 1949, 1953) has shown that the life history of *P. borealis* varies with locality in a range from southern Norway to Spitsbergen. When *P. borealis* was found in numbers in deep water off the Northumberland coast advantage was taken to investigate the biology of the species at the southern limit of its eastern Atlantic distribution and to compare the results with those of other workers. Knowledge of the biology of the prawn now covers the whole of its north-south distribution and some account of this is given. In addition, the study gives information on a population that has not been fished commercially and provides a more complete picture of sex reversal than has been obtained hitherto.

I am particularly indebted to Dr A. Ritchie of the Scottish Home Department Laboratory, Aberdeen, who has allowed me to use his data on the distribution, size and sex of *P. borealis* in British waters. I am also indebted to Dr H. O. Bull for many suggestions, for records of distribution and for temperature and salinity data. I wish to thank Mr R. Harrison, skipper of the R.V. 'Alexander Meek' for collecting in all weathers, and my wife for her criticism.

DISTRIBUTION

P. borealis occurs in both Pacific and Atlantic oceans (Fig. 1). Ekman (1953) refers to it as having a discontinuous north Atlanto-Pacific distribution and as a discontinuous circum-*boreal* species. Earlier records of its distribution are given by Rathbun (1904) and Hofsten (1916), the latter giving detailed

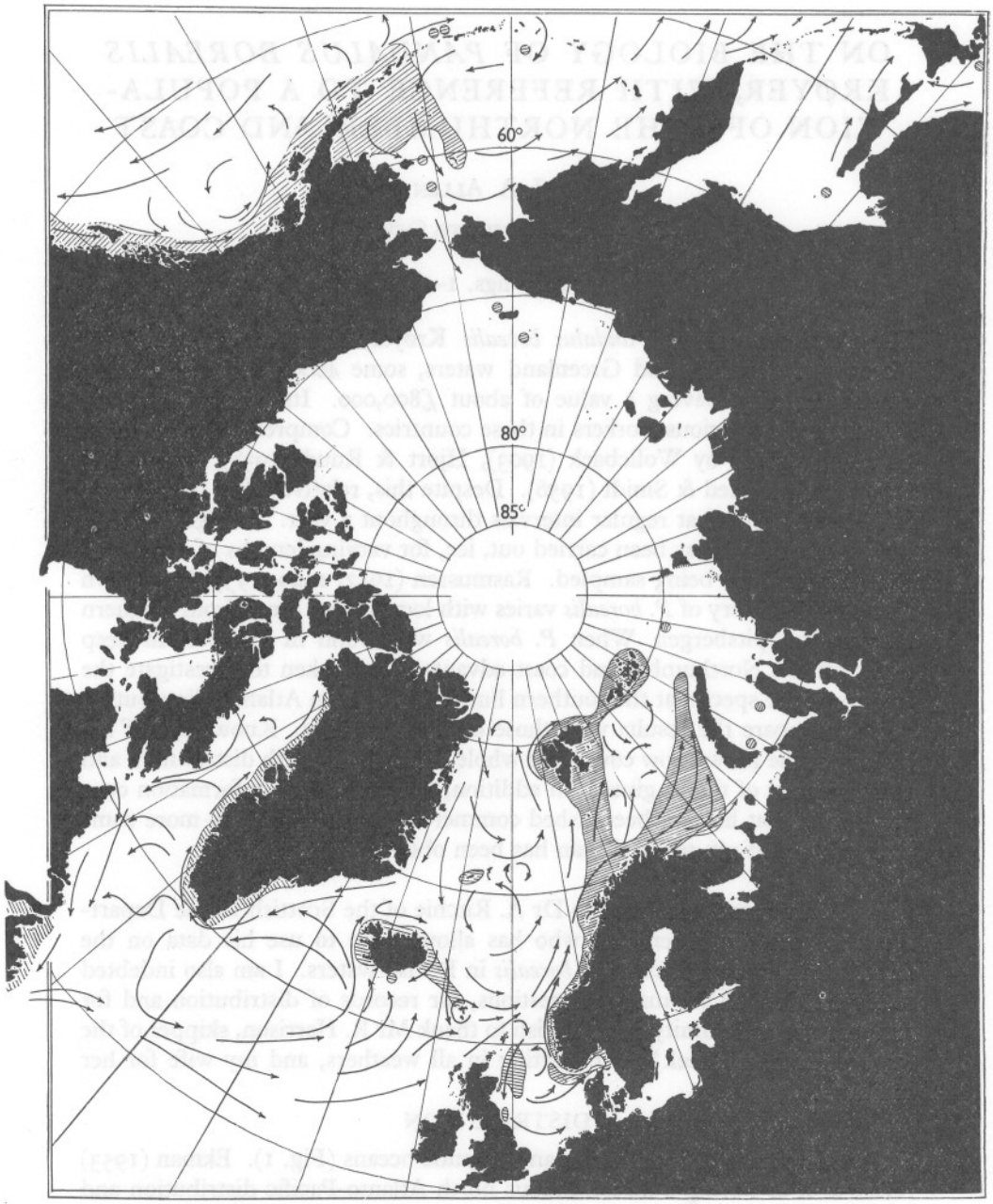

Fig. 1. Distribution of *Pandalus borealis* (shaded areas) Arrows indicate the general direction of flow of the surface currents. Records of Berkeley (1930), Blacker (1957), Bjørk (1935), Gorbunow (1934), Grieg (1925, 1926*a*, *b*, 1932), Heegaard (1941), Hjort & Ruud (1938), Hofsten (1916), Horsted & Smidt (1956), Hynes (1929), Johnson & Lindner (1934), Poulsen (1946), Pruter & Harry (1952), Rasmussen (1942, 1953), Rathbun (1904, 1929), Sivertsen (1932), Stephenson (1935) and the present work.

maps and references. The present maps (Figs. 1, 2) bring knowledge of its distribution up to date, the authorities being listed in the legends to the figures.

Knowledge of the distribution of the prawn in the Pacific and off the eastern seaboard of America has been little extended since the work of Rathbun (1904). Rathbun (1929), Hynes (1929), Berkeley (1930), Johnson & Lindner (1934) and Hjort & Ruud (1938) all refer to its distribution but give few new localities. *P. borealis* is common off the coasts of Alaska and to the south as far as the Columbia River (lat. 46° N.). It is also common in the eastern part of the Bering Sea and off the Aleutian Islands. To the north of the Bering Straits it has been recorded in latitude 73° off Vrangelye Island. It is much less common off the western coasts of the Pacific but is reported from Japanese waters at least as far south as latitude 45° N. In the eastern Atlantic *P. borealis* occurs in large numbers in the Gulf of Maine and off Cape Cod. The most southerly record is in latitude 41° N. There is a curious lack of records between Cape Cod and the southern tip of Greenland (Fig. 1), although it has been presumed to occur (Johnson & Lindner, 1934; Hjort & Ruud, 1938). On the west coast of Greenland there are dense populations supporting a lucrative fishery (Horsted & Smidt, 1956), but there are no records of its occurrence on the west side of the Davis Strait (see p. 194). Miss V. Brawn of St Andrews Biological Station, N.B., Canada, in a personal communication, states that it is present in the Gulf of St Lawrence but has no record from farther north.

Large populations of *P. borealis* occur in eastern Atlantic waters off the Norwegian coast and as far north as Franz Josef Land (lat. 82° N.), but no farther east than longitude 79° E. They occur off the east coast of Greenland as far north as latitude 66° N., and off the coasts of Spitsbergen, Jan Mayen, Iceland and the Faroes. To the south of Norway the prawn is present in the Skagerak and Kattegat, but no farther south than latitude 56° N. It occurs in deep water (> 80 m) in the North Sea (Fig. 2). A single specimen has been recorded from south of the Dogger Bank in latitude 54° 24′ N. (Wedmeyer, 1912), but it is doubtful whether there is any permanent population south of latitude 55° N. *P. borealis* was first recorded off the Northumberland coast north-east of Coquet Island by Todd in 1907 (Norman & Brady, 1909). A specimen taken off the Scottish coast in 1904 by the 'Michael Sars' (Grieg, 1926*b*, see Appendix I) appears to be the first British record. Neither Bell (1853) nor Calman (1899) list *P. borealis*. Although Jorgensen (1923) records larvae as present in plankton samples from the Northumberland area this is probably incorrect (see p. 208). As yet there is no published record of larvae being taken from the North Sea by continuous plankton recorder surveys (Rees, 1952, 1955). Through the kindness of Dr I. Gordon, Dr A. Ritchie and Dr H. O. Bull unpublished records from British waters from 1930 to the present date are available (see Appendix I).

Information on *Pandalus borealis* is sufficiently complete to give a reliable picture of its ecology over the whole of its eastern Atlantic distribution. Temperature, salinity, substratum, and, possibly, depth are limiting factors in its distribution. Adult prawns have been taken from water with temperatures ranging from $-1{\cdot}68^{\circ}$ to $11{\cdot}13^{\circ}$ C (Fig. 3). Horsted & Smidt (1956) have

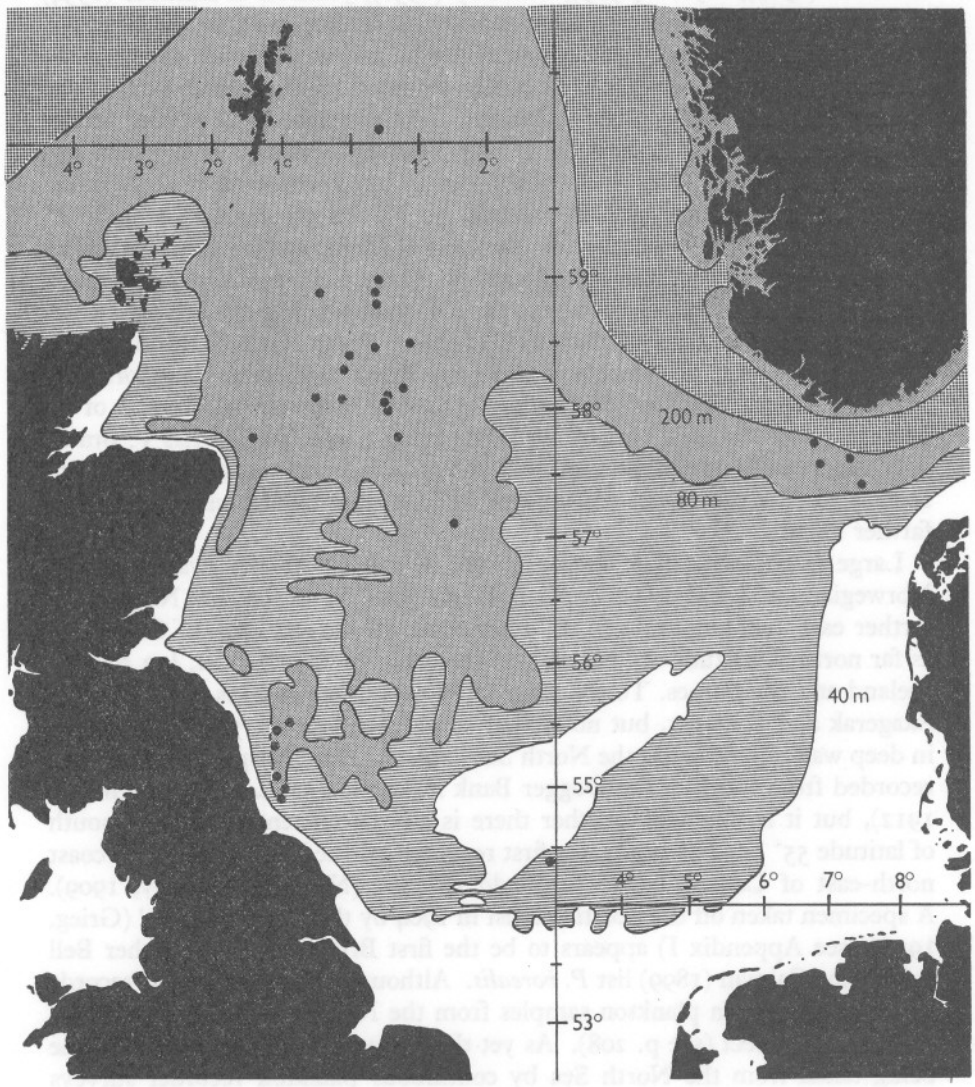

Fig. 2. The distribution of *Pandalus borealis* (black circles) in the North Sea relative to depth. Records of Allen (unpubl.), British Museum (unpubl.), Bull (unpubl.), Grieg (1926*b*), Poulsen (1946), Ritchie (unpubl.), Todd (Norman & Brady 1909) and Wedemeyer (1912).

shown that prolonged (2 months) temperatures of less than $-1°$ C are deleterious to prawns and caused mass mortality in the stocks at Holsteinborg during 1948–49 with the consequent failure of the fishery for the following 5 years. Ekman (1953) refers to *P. borealis* as a boreal species (as its name suggests) and presumes that it owes its existence in high arctic waters to transport from warmer regions, notably by means of the Gulf Stream and the North Atlantic Drift. He questions whether the species can propagate in high latitudes. While it undoubtedly owes its existence in high arctic waters to the north-east of Spitsbergen and the north of Novya Zemlya to the warm North Atlantic current, Rasmussen (1942) has shown that the Spitsbergen population reproduces. Similarly, populations off the West Greenland coast

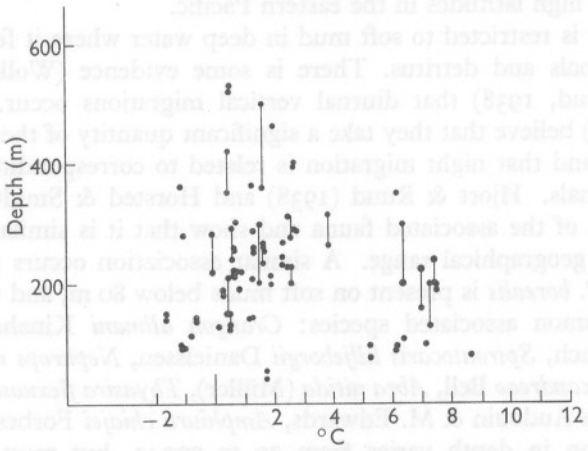

Fig. 3. Records of the depths of various populations of *Pandalus borealis* plotted against temperature of their environment. Authorities as listed in the legend to Fig. 1.

(lat. 75° N.) at temperatures close to limiting also reproduce (Horsted & Smidt, 1956). It is a true arctic-boreal species with little or no 'sterile expatriation area'. There is little doubt that the extremely cold water of the Labrador current is one factor that prevents the establishment of stocks on the west side of the Davis Strait. Temperature is probably the most important factor limiting distribution in high latitudes. It has been assumed that the upper limiting temperature is 8° C (Rasmussen, 1953, and others), although Poulsen (1946) showed that adults can live at 9·5° C and schizopod stages at 14° C in Danish waters. The present study shows that the adults can live and breed in temperatures as high as 11·1° C. The range in temperature of the water of the prawn grounds off the Northumberland coast during the present investigation was from 6° to 11·1° C and during the period July to December was 9° C or above. There are no records of temperatures at the southern limit of distribution off the Pacific and Atlantic coasts of America, but general charts, e.g. Schott (1942), indicate temperatures of approximately 8° C. It

appears likely that *P. borealis* off the Northumberland coast is living at the extreme upper limit of its temperature range. Apart from Poulsen (1946) who records larvae from water at 14° C in the Kattegat, there are no records of a high temperature sterile expatriation area.

Adult *P. borealis* are restricted to water of fairly high salinity. Although Poulsen (1946) found larval stages in salinities of 32‰, only in Oslo Fjord (33–33·6‰; Hjort & Ruud, 1938) has the prawn been recorded in salinities of less than 34‰. All other records range from 34·1 to 35·7‰ and only two records exceed 35‰. The salinity of the deep water off the Northumberland coast varies from 34·47 to 34·87‰. The species is stenohaline, therefore salinity, in addition to temperature, must limit its spread along the Labrador coast and in high latitudes in the eastern Pacific.

P. borealis is restricted to soft mud in deep water where it feeds on small bottom animals and detritus. There is some evidence (Wollebaek, 1903; Hjort & Ruud, 1938) that diurnal vertical migrations occur. Horsted & Smidt (1956) believe that they take a significant quantity of their food above the bottom and that night migration is related to corresponding migrations of food animals. Hjort & Ruud (1938) and Horsted & Smidt (1956) give detailed lists of the associated fauna and show that it is similar throughout the prawn's geographical range. A similar association occurs in the North Sea. Here *P. borealis* is present on soft muds below 80 m, and the following are the common associated species: *Crangon allmani* Kinahan, *Pandalus montagui* Leach, *Spirontocaris lilljeborgii* Danielssen, *Nephrops norvegicus* L., *Calocaris macandreae* Bell, *Abra nitida* (Müller), *Thyasira flexuosa* (Montagu), *Glycera rouxi* Audouin & M. Edwards, *Amphiura chiajei* Forbes.

Distribution in depth varies from 20 to 900 m, but most records fall between 80 and 650 m. Records taken from Rasmussen (1953) and Horsted & Smidt (1956) show that the higher the latitude the deeper is the densest population. Few prawns are found in the deepest water (>600 m) of the Skagerak, although conditions appear suitable (Poulsen, 1946). The most suitable substrata may not necessarily be in deeper water in the north. Salinity and temperature will be as significant as type of substratum in determining the depth of the population. Thus values of temperature and salinity are relatively high and constant in deep water (350–600 m) in high latitudes, while in shallower water limiting values may be exceeded.

There is a relationship between the distribution of *P. borealis* and the warm current systems (Fig. 1). Horsted & Smidt (1956) show that its distribution on the west coast of Greenland is closely related to the Irminger current. There is clear correlation between the eastern Atlantic populations and the ramifications of the Gulf Stream and also between the eastern Pacific populations and the warm northerly coastal currents off the west coast of America. The prawn does not occur west of the Orkney–Shetland channel in British waters, and it is possible that the North Sea stocks originate from Faroe or

Norwegian populations (Fig. 1). There appear to be suitable grounds for *P. borealis* off the west coasts but it is possible that the larvae are restricted to the northern fringe of the Gulf Stream and will not be carried to these waters.

METHODS

The prawns used in this study were all obtained from the same position—13 nautical miles east of Blyth harbour entrance. A 9 ft beam trawl fitted with a King's Lynn type prawn trawl was used. All hauls were of 20 min duration, the same trawl being used throughout the work. The position worked is also a hydrographical station, and Dr H. O. Bull has kindly allowed his records to be used. Many of the latter were taken at the same time as the prawn haul.

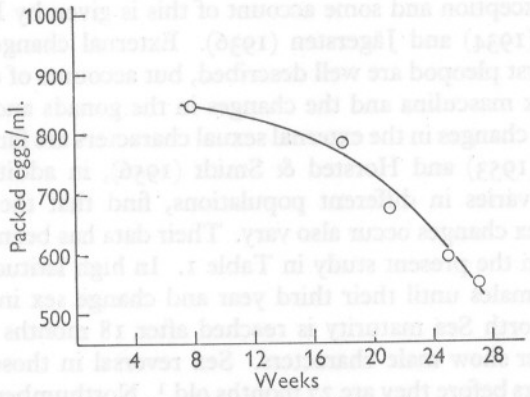

Fig. 4. Numbers of packed eggs/ml. (see text) plotted against age of the eggs.

The catch was examined alive and sorted. *P. borealis* was fixed in 4% neutral formalin in sea water and later transferred to 70% alcohol. All specimens were sexed and the carapace length from the posterior limit of the eye socket to the extreme posterior lateral edge of the carapace measured. Measurements were taken to the nearest millimetre. The correction factor for this population, that figure which when multiplied with carapace length gives total length, is 5·05 (extreme limits 4·8–5·2). This is a higher factor than that of Horsted & Smidt (1956). The latter using the same measurement of carapace obtained a factor of 4·6–4·7.

Eggs, when present, were counted, sized and examined for degree of development. The method used for counting was that of Rasmussen (1953). Eggs of a small number of specimens were counted and then hand-centrifuged in a calibrated tube and the packed egg volume noted. A conversion factor (packed eggs/ml.) is calculated and the egg numbers of the remaining specimens derived from packed egg volumes. As the egg volume increases with increasing age (Fig. 4), a new conversion factor has to be calculated for each sample.

Specimens, male, female and intersex, were selected from each size-group of each sample and the secondary sexual characters examined. The endopodite of the first pleopod, the appendix interna of the second pleopod and appendix masculina, if present, were drawn accurately with the aid of a squared eye-piece graticule. The same objective and eyepieces (magn. × 5 and × 10 respectively) were used throughout the work. Gonads from the selected specimens were removed for sectioning and the sections stained with Mallory's Triple Stain, and Eosin and Fast Green.

SEX REVERSAL AND GAMETOGENESIS

Most *Pandalus* species are protandrous hermaphrodites (Berkeley, 1930; Kubo, 1951; Pike, 1952; Pruter & Harry, 1952; Mistakidis, 1957). *P. borealis* is no exception and some account of this is given by Berkeley (1930), Leopoldseder (1934) and Jägersten (1936). External changes in the endopodite of the first pleopod are well described, but accounts of changes in form of the appendix masculina and the changes in the gonads and the relation of the latter to the changes in the external sexual characters are far from complete.

Rasmussen (1953) and Horsted & Smidt (1956), in addition to showing that life span varies in different populations, find that the ages at which maturity and sex changes occur also vary. Their data has been compared with that obtained in the present study in Table 1. In high latitudes prawns may not mature as males until their third year and change sex in the sixth year, while in the North Sea maturity is reached after 18 months and more than 30% may never show male characters. Sex reversal in those showing male characters occurs before they are 27 months old.[1] Northumberland prawns do not live for more than 38 months. Table 1 shows that intermediate populations (Eids, Ofoten and Mist Fjords) are also intermediate in respect of their age at maturity and at sex change. Thus the life history of the North Sea population most closely resembles that of the Oslo Fjord population. Hjort & Ruud (1938) found in the latter population that approximately 5% never function as males.

Hjort & Ruud (1938), discussing sex change in the southern Norway populations, suggest a 'labile equilibrium' between male and female potentialities where the age of female maturity depends on the age at which the male tendencies are repressed. Jägersten (1936) from work on *P. borealis* from Gullmar Fjord suggests that all individuals are hermaphroditic and have both male and female potentialities. Jägersten recognizes three categories: (1) primary females, in which potentiality is repressed so early that male characters never appear; (2) secondary females, in which male potentiality is repressed soon after male characters have appeared (these animals mature as females in their second year); and (3) hermaphroditic females, in which male potentialities are repressed after functioning as a male. Rasmussen (1953) shows a

[1] The age of the prawns is calculated from the date at which all the larvae are hatched, i.e. the end of the second week in April (see p 206).

definite relationship between size, maturity and sex (see Table 1); normally prawns less than 70 mm total length at the breeding season are immature, while those greater than 115 mm total length are females. Few prawns above 110 mm total length function as males and only a few mature females were recorded below 90 mm. Rasmussen (1953) was able to predict the percentage

TABLE 1. PERCENTAGE COMPOSITION OF POPULATIONS OF *PANDALUS BOREALIS*

The percentages of immature, mature male and mature female *P. borealis* at the breeding seasons of various populations. Total length measurements in mm are given in parentheses. Scandinavian data extracted from Rasmussen (1953) and Horsted & Smidt (1956).

Locality	Age yr.	% immature (length)	% mature ♂ (length)	% mature ♀ (length)
1. Northumberland	1½	—	63·5 (76–90)	36·5 (81–96)
2. S. Norway		—	82–99·5 (80–94)	0·5–18 (90–101)
3. Eids and Ofoten Fjords		0–0·2 (58)	99·8–100 (58–85)	—
4. Mist Fjord		100 (50)	—	—
5. W. Greenland and Jan Mayen		100(49)	—	—
6. Spitsbergen		100 (40)	—	—
1. Northumberland	2½	—	—	100 (100–126)
2. S. Norway		—	0–78·5 (96–111)	21·5–100 (120–130)
3. Eids and Ofoten Fjords		—	16–88·5 (92)	11·5–84 (100–103)
4. Mist Fjord		—	100 (77)	—
5. W. Greenland and Jan Mayen		100 (69)	—	—
6. Spitsbergen		86–99 (64)	1–14 (78)	—
2. S. Norway	3½	—	—	100 (130–140)
3. Eids and Ofoten Fjords		—	—	100 (122–143)
4. Mist Fjord		—	100 (96)	—
5. W. Greenland and Jan Mayen		—	100 (94)	—
6. Spitsbergen		—	100 (87)	—
2. S. Norway	4½	—	—	100 (150–159)*
3. Eids and Ofoten Fjord		—	—	?*
4. Mist Fjord		—	—	100 (113·5)
5. W. Greenland and Jan Mayen		—	71 (115)	29 (126)
6. Spitsbergen		—	100 (104)	—
4. Mist Fjord	5½	—	—	100 (120)
5. W. Greenland & Jan Mayen		—	—	100 (139)
6. Spitsbergen		—	—	100 (118)
6. Spitsbergen	6½	—	—	100 (121)
6. Spitsbergen	7½	—	—	100 (140)
6. Spitsbergen	8½	—	—	100 (> 140)*

* Very few specimens.

of immature, males and females from the size range of the age-group at the beginning of the breeding season. The size range of the North Sea prawn at the commencement of the first breeding period (1½ years) is 76–96 mm and approximately 35% are primary or secondary females (see p. 196), i.e. a much higher proportion than the 5–10% predicted from Rasmussen's data. As Rasmussen (1953) points out, variations in relationship can be found in different localities, although it seems likely that this particular variation is significant. In the Northumberland population the slight increase in the

number of females during the first 18 months of the life of the year group (Fig. 5) corresponds with sex reversal to secondary females. Although it is the largest of the immature male prawns of each sample that show reversal, there does not appear to be a minimum size below which reversal does not take place. Increased growth rate, rather than the attainment of a certain size, appears to be related to sex reversal. Observations support a theory of hormonal control (see pp. 205 and 214).

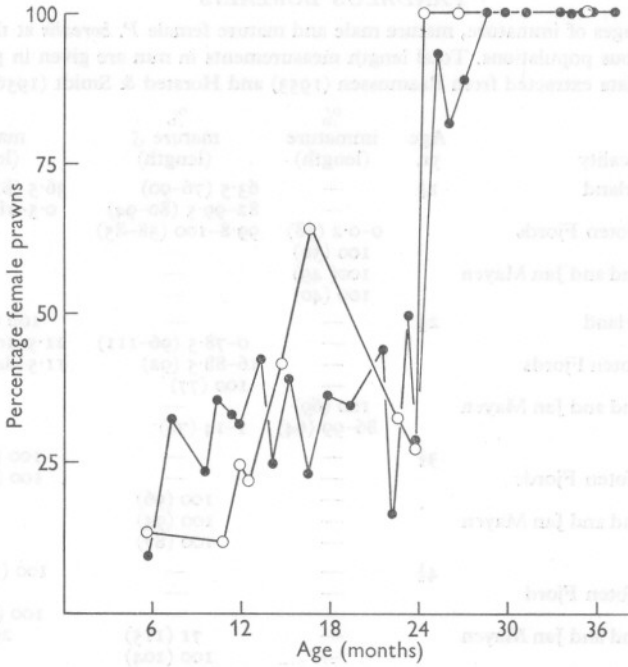

Fig. 5. The variation in the percentage of female *Pandalus borealis* during the life of a year group. Calculated from Northumberland (dots) and Scottish data (rings).

It might be expected that where late reversal of sex takes place both eggs and sperm may be produced by the same animal at 18 months. No prawn was taken that carried eggs and also possessed male external sexual characters, but sections of one prawn, 14 months old, male, with the terminal setae of the appendix masculina slightly shorter than normal, showed proliferating oocytes as well as primary spermatocytes (see p. 204). Similarly, reversal might be so retracted in the case of a male that the prawn acts as a male for a second time at $2\frac{1}{2}$ years. Hjort & Ruud (1938) report four such animals from southern Norway, all very large specimens 116–126 mm. Two specimens showing unmodified external male sexual characters 4 months after egg-laying were taken, but sections of the gonads showed that oocytes only were present. It is unlikely that specimens of the Northumberland population act twice as males.

Secondary sexual characters

The change in form of the endopodite of the first pleopod and the appendix interna and appendix masculina of the second pleopod that occurs with sex reversal in the Northumberland population is shown in Fig. 6. The endopodite and appendix interna of the primary females (outlined, but not hatched) gradually increase in size throughout the life of the prawn. There is little change in shape, only the tip of the endopodite becoming more attenuated with age. The form and arrangement of the setae are not shown. 'Breeding dress' is assumed at the moult preceding egg-laying. In this condition the setae are numerous, long, feathery and adapted for the attachment of eggs. Høglund (1943) gives an excellent description of the change. In Fig. 6 those pleopods shown stippled are drawn from prawns in breeding dress.

The male endopodites (black in Fig. 6) bear the copulatory organ which projects just below the apex. A number of small hooks or cincinnuli are present on the tip of the organ, 4–6 in young prawns and more than 10 in older specimens. Below the copulatory organ are 3 or 4 small spine-setae and the remainder of the setae on the endopodite are typically long and pinnate. The above details are very similar to those described by Mistakidis (1957) for *P. montagui*. In young prawns the copulatory organ is relatively long and slender and extends beyond the apex. In older males the organ is considerably broader in relation to its length and barely extends beyond the more defined apex. The male endopodite is somewhat larger than that from a female of the same age, the change in shape with age being shown in Fig. 6. The appendix masculina, situated between the side of the endopodite of the second pleopod and the appendix interna, was present in all male prawns and no difficulty was experienced in sexing the youngest specimens. The appendix masculina of 6-month prawns is a small rounded projection bearing two or three small apical setae. The projection grows rapidly in length and by 12 months is almost as long as the appendix interna, the number of setae increasing to five terminal and three lateral. The setae are almost as long as the appendix masculina itself. Maximum size is reached at about 16 months. Atrophy occurs after the sperms have been released.

The form of the external characters of the males after spawning may change at 22 months or as late as 28 months (Fig. 6 hatched appendages). The copulatory organ becomes progressively thinner and the apex of the endopodite more pointed. There appear to be three transitional stages before the copulatory organ is finally lost. In many specimens the tip of the organ is lost at the third stage, the base remaining. The appendix masculina is slower to disappear than the copulatory organ and at least one extra moult is necessary before it too is lost, i.e. at least five moults are required for the complete reversal of the external male characters. The first indication of change in the appendix masculina is reduction in size and number of the setae, followed by the

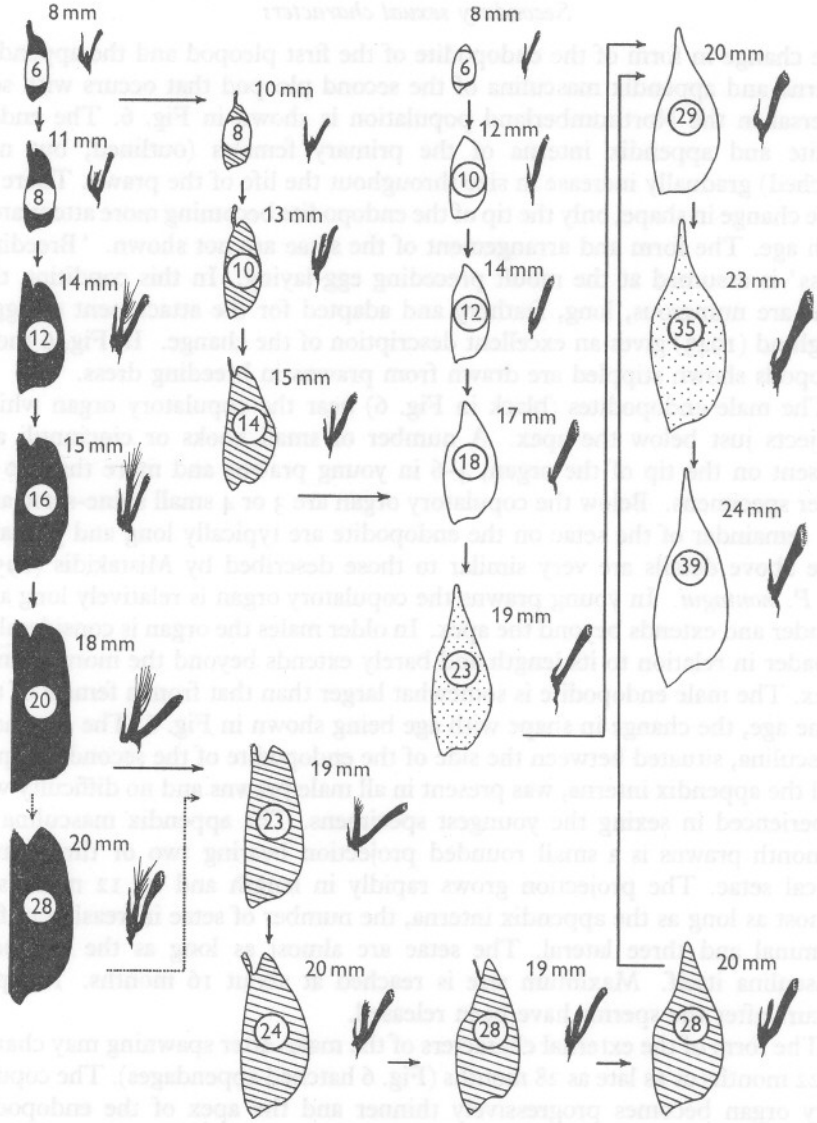

Fig. 6. To show the changes in form with increasing age of the endopodite of the first pleopod and the corresponding appendix interna and appendix musculina of the second pleopod of *Pandalus borealis* from the Northumberland population. Age in months is given in the ring in each endopodite and the carapace length (mm) above each figure. Male endopodite, black; transitional, cross-hatched; female, outlined; those in breeding dress, stippled. Arrows indicate sequence.

gradual reduction in size of the appendix. Transition stages in immature prawns were found on re-examination of Northumberland samples. The youngest was 8 months old. A similar series of stages were found to those described above, although the appendix masculina never becomes fully setose (Fig. 6).

Histology of gonads

The general morphology of the gonads has been described by Wollebaek (1903), Berkeley (1930), Leopoldseder (1934) and Jägersten (1936). They are elongate, paired, tubular structures joined by a bridge about a third the distance from the anterior end. The vas deferens and oviduct join the gonad

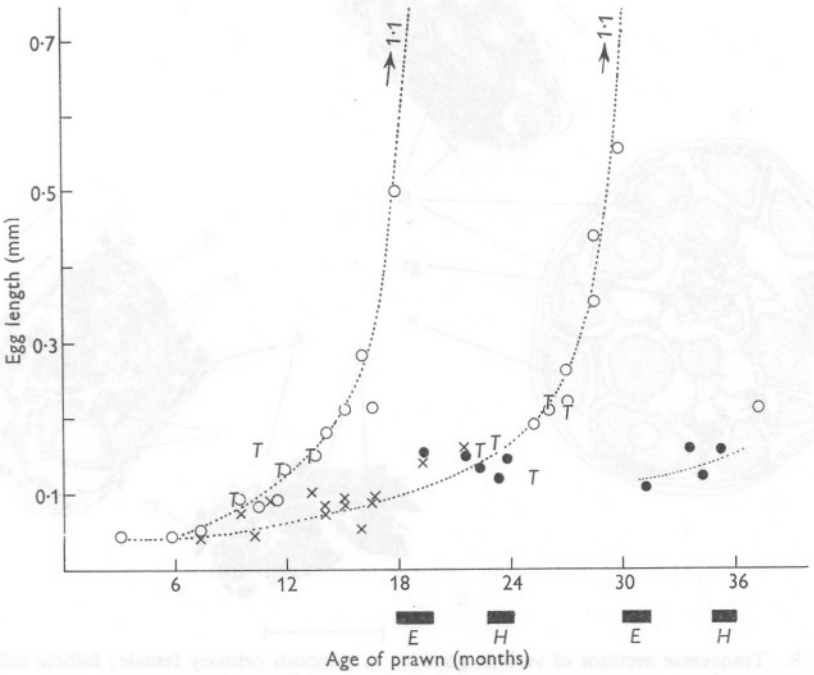

Fig. 7. Graph to show the increase in length of the oocytes (dotted line) with the age of the prawn. The plotted lines may be continued upwards linearly, and at a size of about 1·1 mm the oocytes have developed into eggs. The symbols indicate the sex of the prawns; ●, female carrying eggs on the pleopods; ○, female not carrying eggs; × male; *T*, transitional; *E*, egg-laying; *H*, hatching of larvae.

mid-laterally, the oviduct being anterior to the vas deferens (Berkeley, 1930, p. 130). Sections, mainly transverse, were cut from some 70 gonads representative of all ages and external sexual characters. The maximum oocyte diameter was recorded for each gonad to give information on oocyte growth (Fig. 7).

Primary females. The maximum oocyte diameter of the youngest female prawn taken (3 months) was 0·04 mm. The oocytes occupy approximately half the ovary. The remainder of the ovary is filled with small cells which are probably early follicle or interstitial cells. Aoto (1952) describes a similar condition in *Pandalus kessleri*. The proliferating strand of oocytes is not central but on the inner, ventral side of the gonad. During the next 3 months there is little increase in oocyte size but proliferation continues until much of the ovary is filled. There appear to be fewer interstitial cells, but this may possibly be due to the attenuation of their cytoplasm and new arrangement.

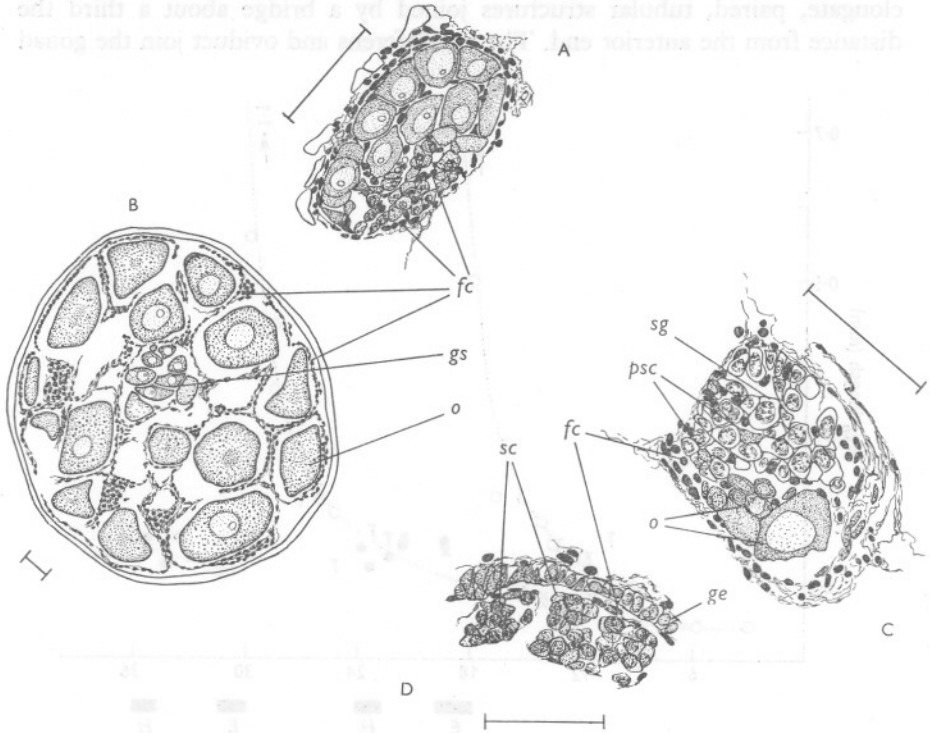

Fig. 8. Transverse sections of various gonads. A, 7-month primary female; follicle cells at oocyte interstices. B, 27-month female; a single layer of follicle cells surrounding each oocyte. C, 7-month hermaphrodite female; oocytes occupy $\frac{1}{3}$ of gonad, the spermatogonia are not grouped. D, 15-month hermaphrodite female; a small part of the periphery of the gonad showing two groups of spermatocytes close to the gonadial epithelium with follicle cells beginning to surround each group. *fc*, follicle cell; *ge*, gonadial epithelium; *gs*, germinal strand; *o*, oocyte; *psc*, 'primary sex cell'; *sc*, grouped spermatocytes; *sg*, spermatogonia. Each scale represent 0·1 mm.

In prawns 7 months old the walls of the gonad are lined with a layer of follicle cells while others surround the developing oocytes (Fig. 8). The nuclei of the follicle cells stain heavily, while the 'attenuation' of the cytoplasm makes it impossible to distinguish any cell walls. Oocytes are still being proliferated,

the largest are peripheral and 0·05 mm long. The oocytes are angular with the follicle cell nuclei in the interstices. In 9-month primary females growth rate of the oocytes increases, although the general appearance of the ovary remains the same. The rate of proliferation of oocytes is maintained, the gonad increasing in diameter until the prawn is 11½ months old when the rate begins to drop. By this time the largest eggs are 0·15 mm long and small vacuoles appear in the cytoplasm. The interstitial cells show no change in appearance, but the germinal strand, while still asymmetrical, is more centrally placed. The oviduct is still a narrow tube. Acceleration of the growth rate of the oocytes continues, reaching a maximum rate in the 16-month prawn and this rate is maintained until the eggs are laid. At 16 months yolk granules appear and the oocytes are more rounded. The largest recorded oocyte diameter was 0·5 mm. This was recorded from a prawn in a sample in which most females had laid their eggs. During the last few days before laying or perhaps immediately after laying the oocyte must more than double its diameter as the smallest newly hatched eggs measure 1·1 mm (maximum diameter). The cytoplasm of the follicle cells of 16-month old females is better defined and the number of cells increases. The germinal strand remains after the eggs are laid and a number of small oocytes remain close to it. The largest remaining oocytes (0·15 mm) quickly take up a peripheral position where they are surrounded by the now very well-developed follicle cells. The latter, both round the oocytes and lining the ovary epithelium, are two or three layers thick. From the release of the mature eggs (about 18 months) until the 24th month little change occurs in the ovary. The follicle cells if anything increase slightly but the number of oocytes appears to remain constant. The remaining oocytes do not grow and show no sign of disintegration. Prior to the larvae hatching, the follicle cells decrease in size and number. The central cells are the first to return to the 'resting state', those at the periphery remain prominent until after the larvae are hatched, i.e. 25 months. At this time the remaining oocytes start to grow again and proliferation of new oocytes recommences. In 27-month-old prawns yolk is appearing in the large peripheral oocytes (0·22 mm max. diam.) and a similar cycle of events to that described follows. Maximum growth of the oocytes is reached when the prawn is 28 months old and by this time there is little proliferation of new cells, although the germinal cord surrounded by small cells remains. The maximum recorded oocyte size was 0·53 mm in a 30-month-old prawn. Egg laying commences at 30½ months. As before, only those eggs more than 0·15 mm are released, and the follicle cells again are greatly developed. The largest remaining oocytes take up a peripheral position surrounded by follicle cell layers. There is no further proliferation of oocytes and at 33 months the first sign of disintegration is seen. The prominent nucleolus is lost and the nuclear membrane is no longer clearly defined. By the 35th month the cell walls of the oocytes have broken down and the follicle cells are reduced.

As before, the latter are well developed while the eggs are carried on the pleopods.

Hermaphrodite females. All prawns showing external male characters have an ovarian germinal strand, together with a few oocytes which occupy between a quarter and a third of the area of the gonad in cross-section. The oocytes are in the 'mature' condition (Berkeley, 1930) having a clear nucleus, well-developed nucleolus and an enlarged heavily staining cytoplasm. The ovarian portion is acentric occupying a dorso-lateral position. The maximum oocyte size in the smallest prawns ($5\frac{1}{2}$–7 months old) was 0·04 mm. In these specimens, spermatogonia filled the rest of the gonad and although the cells are tightly packed there is no definite tubule structure (Fig. 8). The nuclei show the typical 'bouquet' stage of actively dividing primary and secondary spermatogonia described by Runnström (1925) with clumps of chromatin material at the periphery. Follicle cells line the gonadial walls, and typically, the oocytes, and there are a few scattered between the spermatogonia. A few cells among the latter stain heavily with the acid fuchsin of Mallory's Triple Stain and these probably correspond with the 'primary sex cells' described by Berkeley (1930). Sections show little change until after the prawns are 11 months old. By the 13th month spermatocytes are present. The gonad is larger and the oocytes still occupy about a third of the gonad. There has been some proliferation of oocytes to maintain the relative proportions and there is slight growth of the outer oocytes (0·08 mm max. diam.). Spermatogonia are still present close to the oocytes as a tight packed mass, but peripherally the cells are no longer in the 'bouquet' stage and are lighter staining than the latter. There is no obvious tubular arrangement and follicle cells are scattered between the spermatocytes. In a 14-month-old prawn the peripheral spermatocytes appear to be divided into groups. Although a few follicle nuclei are present between the groups the latter do not appear to be surrounded by the follicle cells (Fig. 8). The tenuous nature of the follicle cell's cytoplasm makes it difficult to determine this with any surety. Berkeley (1930) refers to this cytoplasm as a 'plasma without cell walls'. By 16 months the peripheral groups are clearly surrounded by follicle cells. While there are still many densely packed spermatocytes close to the oocytes, much of the testis is filled with the groups of larger spermatocytes. During the next month sperms are produced. These are of the typical four-rayed type. At the same time there is a great increase in the number of follicle cells. As yet there are no sperms in the vas deferens, but by 18 months most of the sperms have been transferred and the follicle cells surrounding the remaining spermatocytes increase further. The remaining spermatocytes are the remnants of those that were close to the oocytes. The oocytes, also surrounded by follicle cells, proliferate rapidly and the peripheral oocytes have grown to 0·15 mm (max. diam.). By $21\frac{1}{2}$ months fertilization has occurred and the immature oocytes nearly fill the gonadial cavity. The walls of the gonad are very thick and this is due

in part to follicle cells and in part to the remains of what appear to be spermatocytes. A similar condition is reported by Aoto (1952) for *P. kessleri* and by Fasten (1926) in the crab *Lophopanopeus bellus*. Both these authors consider that the 'spermatocytes' have (or had) a nutritive function. As yet there is no correlated change in the external sexual characters. This does not occur until the prawn is at least 22 months old (see p. 199). During the transition of the external characters the follicle cells return to the interbreeding state, but as much as an eighth of the gonadial space may be occupied with the remaining spermatocytes. The latter gradually disappear and few prawns older than 25 months have any trace of male cells in the gonad. The oocytes completely fill the gonad, the largest having a maximum diameter of 0·18 mm. By the 27th month the growth rate of oocytes is maximum and their future development is similar to that of primary females of the same age. It was not appreciated until sections had been examined that there was a considerable lag in the change of male external characters. Thus typical male external characters may be present in a prawn 27 months old yet the ovary may show no remains of spermatocytes, no hypertrophy of the follicle cells and oocytes proliferating rapidly. There is no change in the male external characters and no proliferation of oocytes until the follicle cells (and perhaps the remaining spermatocytes) regress. It also appears (p. 203) that there is a similar correlation between the regression of the follicle cells and the development of the second batch of oocytes in the primary females. Inhibition by the follicle cells can be postulated. In case of the hermaphrodite female this may modify the effect of a sex reversal hormone of the X organ-sinus gland.

Secondary females. Gonadial evidence of sex change in immature prawns with male external characters were found. Earliest sections were of a $9\frac{1}{2}$-month-old prawn with typical male external characters. In this case the oocytes were greatly developed and occupied two-thirds of the gonad. The peripheral oocytes were twice normal size for that age (0·09 mm max. diam.). Male cells were restricted to the inner lateral side and were atypical, the spermatocytes stained very densely and the nuclei were difficult to distinguish. Follicle cells were typical and were scattered among the spermatocytes as well as among the oocytes. A second prawn of the same age showing transitional external characters had no trace of male cells in the gonad. A third prawn, 11 months, showing transition characters, had male cells restricted to an eighth of the gonad. Others examined showed a similar picture. This clear lag between change in the gonad and change in the external characters will be further discussed (p. 215).

BREEDING

One brood is produced each year, and Rasmussen (1953) has shown that temperature affects the time of egg-laying and hatching. Thus, prawns from southern Norway (average temperature approximately 7° C) start to lay eggs

about the second week in October and finish laying between early November and mid-December. Hatching occurs from the first week in March to the end of April (Fig. 9). There is an over-all period of 7 months when some females can be found with eggs attached to the pleopods. (The ovigerous period—completion of egg-laying to completion of hatching—is 5 months.)

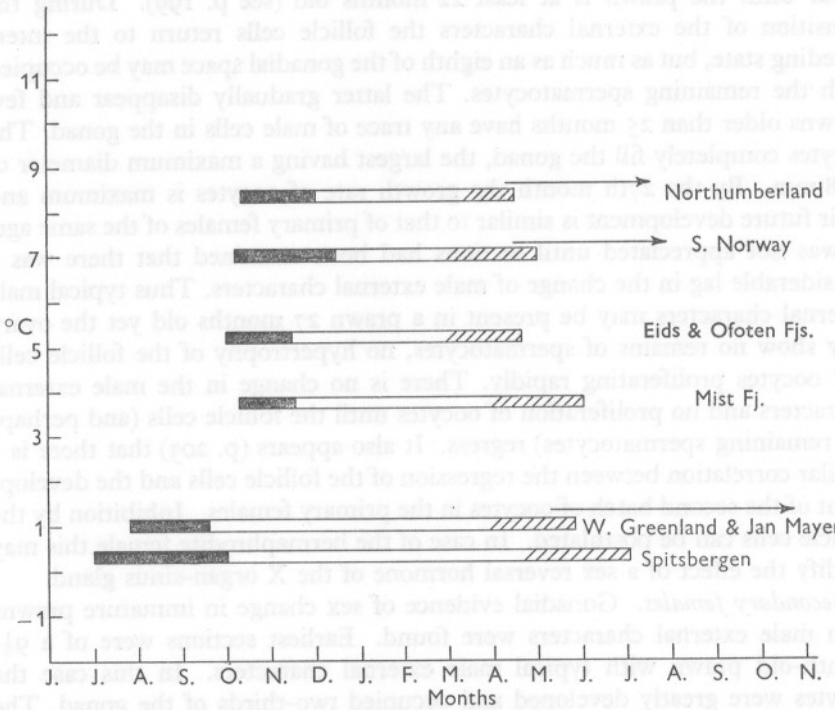

Fig. 9. Comparison of the breeding seasons of various prawn populations. Blacked section, egg-laying period; hatched section, period when larvae hatch. Arrows indicate duration of larval stages. Vertical arrangement corresponds to the mean temperature of the environment. Data extracted from Rasmussen (1953), Horsted & Smidt (1956) and the present work.

As temperature decreases so spawning starts earlier and hatching later. A maximum ovigerous period of 9 months is recorded for prawns of the Jan Mayen and Spitsbergen populations. It was expected that the Northumberland population with a high average temperature (8·5° C) would have a shorter ovigerous period. This was confirmed (Fig. 9 and Appendix II). Egg-laying commences about 10 October and all mature females are carrying eggs by 1 December. The larvae hatch between 10 March and 16 April. This represents an ovigerous period of about $4\frac{1}{2}$ months (2–4 weeks less than the southern Norwegian stocks). Hatching is completed about 2 weeks earlier and the larval stages may be expected to metamorphose at least this much earlier than the Norwegian stocks.

The number of eggs varies with the size of the prawn (Fig. 10). The Northumberland population shows significant differences from the southern Norwegian stocks. The minimum total length of an ovigerous Northumberland prawn is 80 mm compared with 85 mm of the Norwegian prawns. The

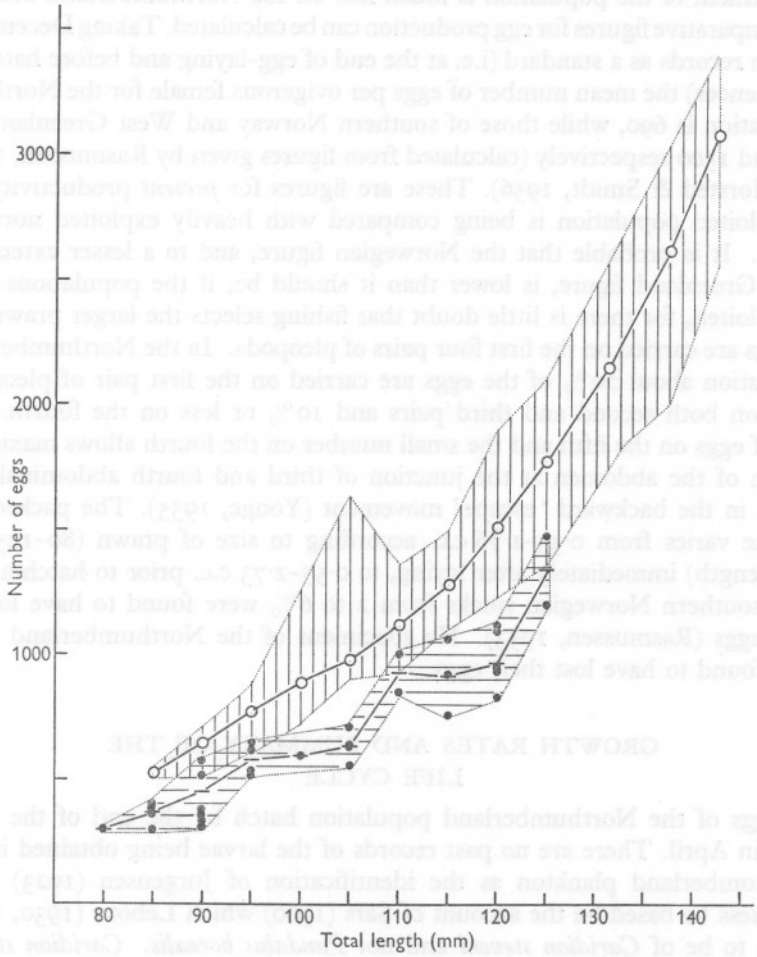

Fig. 10. Comparison of the numbers of eggs carried by *Pandalus borealis* of various lengths from Northumberland and Norwegian waters. Norwegian data (vertical hatching) extracted from Rasmussen (1953). Northumberland data (horizontal hatching). Mean numbers are indicated by the continuous line.

maximum number of eggs carried by the Northumberland prawns rarely exceeds the minimum number of eggs carried by a Norwegian prawn of the same size (Fig. 10). Thus a Northumberland prawn 85 mm total length will carry an average of 160 eggs less than a Norwegian prawn of the same length,

while the largest prawn (125 mm length) carries an average of 500 eggs less. The total number of eggs carried by the Northumberland prawn varies from 300 to 1500. Female prawns from Oslo Fjord may grow 20 mm longer than the largest Northumberland prawn and carry over 3000 eggs, i.e. the potential recruitment of the population is much less off the Northumberland coast.

Comparative figures for egg production can be calculated. Taking December–March records as a standard (i.e. at the end of egg-laying and before hatching commences) the mean number of eggs per ovigerous female for the North Sea population is 690, while those of southern Norway and West Greenland are 760 and 1300 respectively (calculated from figures given by Rasmussen, 1953; and Horsted & Smidt, 1956). These are figures for *present* productivity; an unexploited population is being compared with heavily exploited northern stocks. It is probable that the Norwegian figure, and to a lesser extent the West Greenland figure, is lower than it should be, if the populations were unexploited, for there is little doubt that fishing selects the larger prawn.

Eggs are carried on the first four pairs of pleopods. In the Northumberland population about 20% of the eggs are carried on the first pair of pleopods, 35% on both second and third pairs and 10% or less on the fourth. The lack of eggs on the fifth and the small number on the fourth allows maximum flexion of the abdomen at the junction of third and fourth abdominal segments in the backward 'escape' movement (Yonge, 1955). The packed egg volume varies from 0·35–1·76 c.c. according to size of prawn (80–125 mm total length) immediately after laying, to 0·55–2·73 c.c. prior to hatching.

In southern Norwegian stocks from 2 to 6% were found to have lost all their eggs (Rasmussen, 1953). No specimens of the Northumberland stock were found to have lost their eggs.

GROWTH RATES AND SUMMARY OF THE LIFE CYCLE

All eggs of the Northumberland population hatch by the end of the third week in April. There are no past records of the larvae being obtained in the Northumberland plankton as the identification of Jorgensen (1923) must doubtless be based on the account of Sars (1900) which Lebour (1930, 1940) shows to be of *Caridion steveni* and not *Pandalus borealis*. *Caridion steveni* occurs in Northumberland waters. Excellent descriptions of the larvae are given by Berkeley (1930). There are six stages during which time the larvae grow from 6 to 17 mm. Hjort & Ruud (1938) confirm this work from their plankton records from Oslo Fjord where metamorphosis occurs 3 months from hatching. First-stage larvae were collected from the Northumberland prawn grounds on 16 April 1957, but no other stages have been taken so far. Except for stages 1 and 2 both Berkeley and Hjort & Ruud found very few larvae in the plankton. Berkeley considers that they disappear from water

close to the adult population at stage 3. Figures given by Hjort & Ruud (1938, p. 66) support this view.

The smallest post-larval prawn recorded by Hjort & Ruud (1938) was 21 mm total length (15 July 1933); but the average length of this brood on that date was 31 mm. This compares with 35 mm (2 August 1957) from Northumberland and 45 mm (October 1938) from Scottish waters (Ritchie) (Fig. 11, Appendix II). It has been established that the newly metamorphosed prawns tend to be in shallower water than the adults (Berkeley, 1930; Tåning, 1937; Hjort & Ruud, 1938; Horsted & Smidt, 1956) and these join the adult population some 9 or 10 months after hatching. In Oslo Fjord this joining of the two populations is marked by a heavy increase in the number of small prawns in catches during February–May representing between 88 and 97% of the total. Ritchie's records from Scottish waters (Appendix II) show a similar picture. There is a massive increase of young prawns in the Northumberland catches 7 months from hatching (Fig. 12). This early appearance of the new brood may be due to the small mesh size of the net, although a high growth rate and natant movement of the larvae under hydrographical conditions that tend to move them offshore may be of significance. An extensive programme of small-mesh trawling over the last 4 years in inshore waters (5–35 fathoms) has failed to catch any *P. borealis*. However, the present samples indicate that there is little mixing of the year groups, and perhaps even of sexes, for there are wide differences in the percentage composition of the various hauls (Figs. 11, 12). The young prawns of the new year-group may comprise from 20 to 80% of any sample. The average figure is 60% and this is maintained until the onset of egg-laying (Fig. 12).

Growth rate of the Northumberland population is given in Figs. 11 and 13. For the first 13 months the increased growth of the primary females over the males is slight and the average differences in total length at the end of the first year is approximately 2 mm. The average increase in length is high, 15–16 mm per month over this period. A slight drop in the rate from 7 to $8\frac{1}{2}$ months coincides with low temperatures of the water during December and January before the spring increase of plankton but this may not be significant. After 13 months there is a considerable drop in the growth rate of the males which is probably related to increased testicular activity (p. 204). Between 13 and 23 months the average increase in length of the males is fairly constant at about 1·5 mm per month. There is no change at maturity. After 14 months the primary females also show a gradual falling off in their rate of growth until maturity is reached and the eggs are laid. At their first maturity the primary and secondary females are about 10 mm longer than the males. During the period when the eggs are carried (19–24 months) there is no growth, i.e. no moulting takes place while egg-bearing. From 23 to 28 months male external characters change to the female state. During this period growth rate is fairly rapid, approximately 4 mm/month. After the

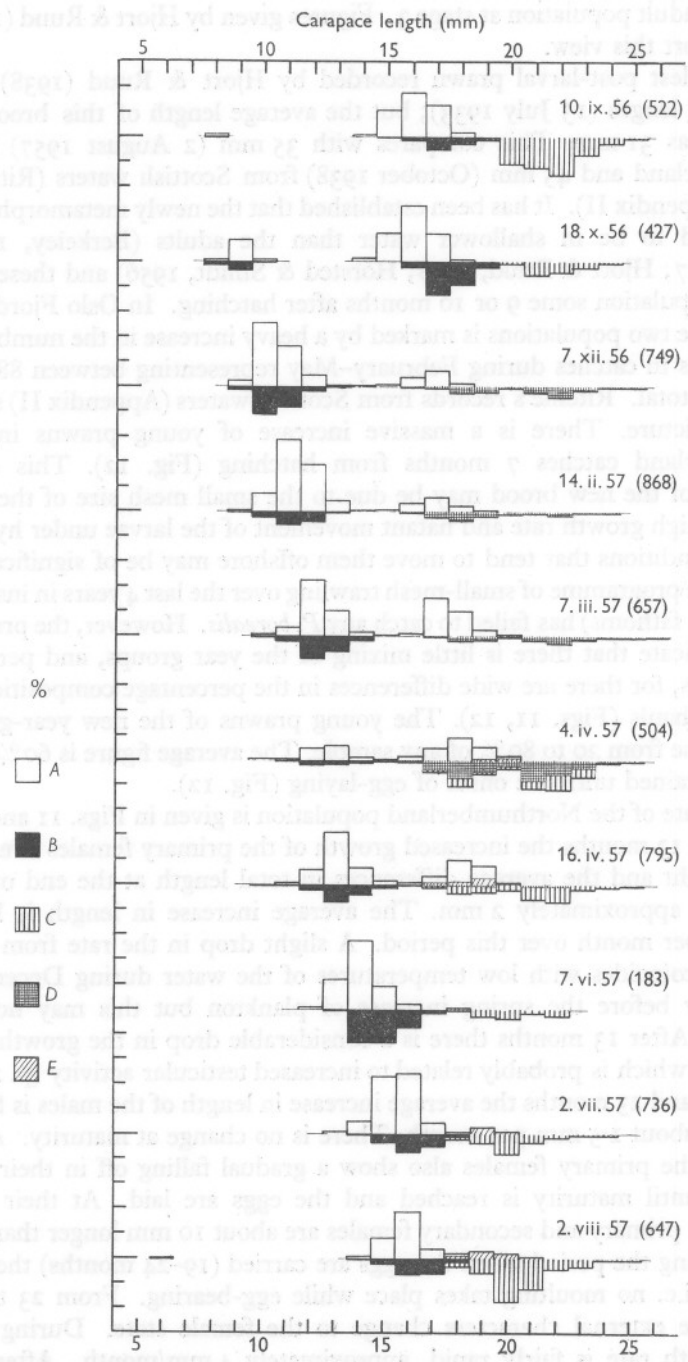

Fig. 11. Percentage size-composition of ten samples of *P. borealis* from Northumberland waters. *A*, males; *B*, immature females; *C*, females + eggs; *D*, females − eggs; *E*, transitional. The total number of prawns in each catch is given.

larvae have hatched the growth rate of the primary females is similar to the transitional males until 29 months, 2 months before the eggs are due to be laid. By this time the external characters have completely changed and the average length of a 29-month-old prawn is 108 mm. Further growth is slow and little more than 2 mm is added to the length before eggs are laid. After egg-laying no further growth occurs and the prawns die soon after the larvae hatch 4 or 5-months later. Ritchie's figures, which are a compilation of several years samples (Appendix II), show a similar picture.

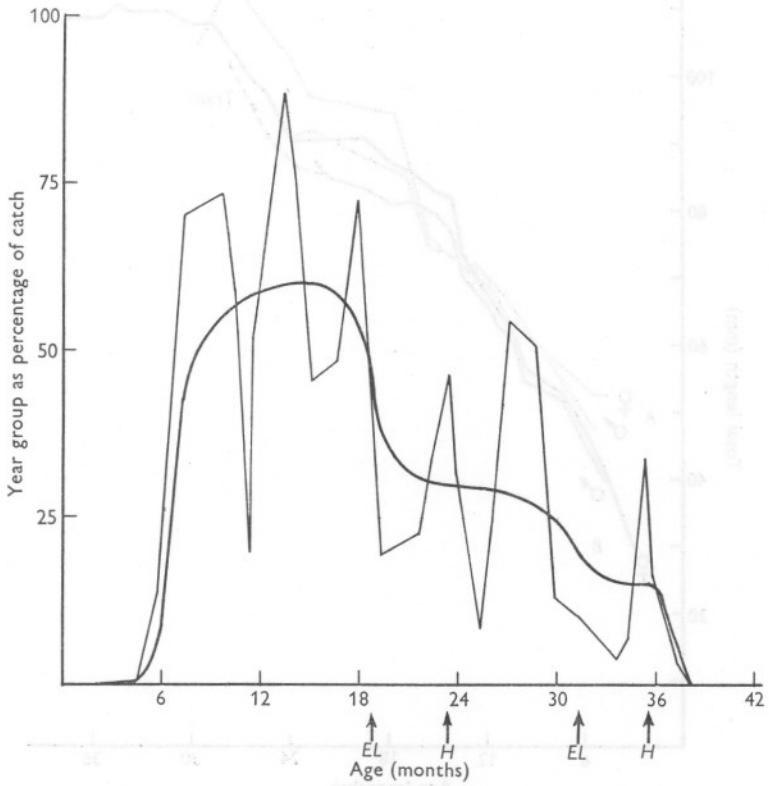

Fig. 12. Graph to show the variation in the percentage representation of one year group within the Northumberland population during the group's life. Estimated from the percentage composition of various samples. Thick line is the calculated mean. *EL*, egg-laying; *H*, hatching of larvae.

As might be expected, there is a very high mortality rate at the spawning period (Fig. 12). 50% of 18-month-old prawns die. This mortality takes place at egg-laying rather than egg-hatching and there is evidence of a second increase in the mortality rate at 31 months. Obviously this is of considerable significance for prawn fisheries, particularly as there is evidence that there is a tendency towards overfishing in Norwegian waters.

The growth rate of the Northumberland population (Fig. 14) is similar to that of southern Norway (Rasmussen, 1953). The higher temperature does not give rise to a marked increase in the growth rate. However, the maximum length attained by the Northumberland prawns (110 mm) is significantly less than that of other populations (> 120 mm). Although difficult to postulate a

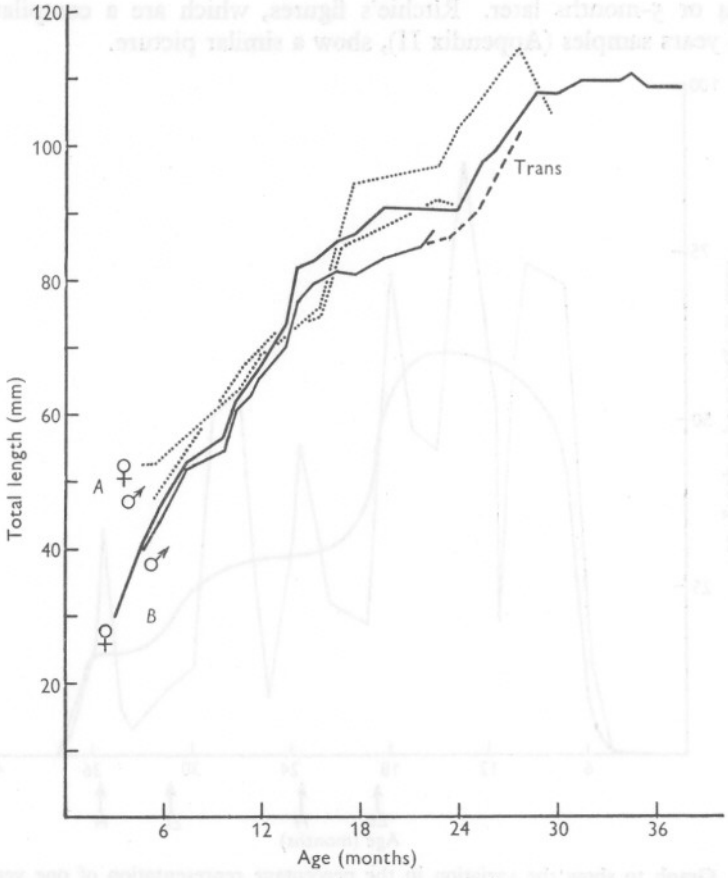

Fig. 13. Average growth-rate curves of male and female prawns from *A*, Scottish and *B*, Northumberland waters. *TRANS*, transitional Northumberland prawns.

reason in the case of *P. borealis* this may well be a temperature effect. As a generalization, animals living at low temperatures are likely to be larger than related warm water species. It is of interest that the maximum prawn lengths of populations off the Scottish coast (Appendix II) are intermediate between Northumberland and southern Norway.

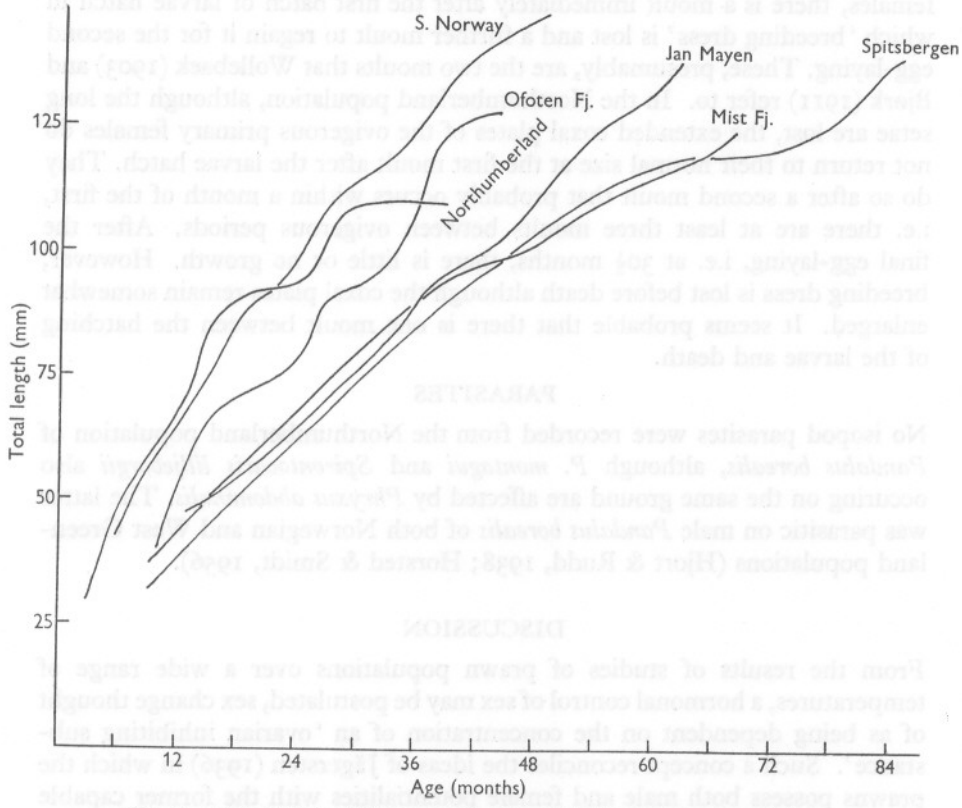

Fig. 14. Comparison of the growth rates of various prawn populations. Data from Rasmussen (1953) and present work.

MOULTS

Knowledge of the frequency of moults is incomplete. Berkeley (1930) shows that there are six larval stages. The seventh moult involves metamorphosis. Hjort & Ruud (1938) conclude that there are many moults during the first year of life until maturity, as many as fourteen in growing from 21 to 93 mm body length. Following maturity fewer moults take place. Wollebaek (1903) and Bjørk (1911) believe that large females have two moults only between each ovigerous period, although they note that 'soft' prawns are always present in their samples.

The present work gives additional information. There are at least three transitional first pleopod stages between full male and female structure. It is probable that four moults transform the male characters of the first pleopod and at least one more is required for final hypertrophy of appendix masculina. The assumption of 'breeding dress' involves a further moult. In the primary

females, there is a moult immediately after the first batch of larvae hatch in which 'breeding dress' is lost and a further moult to regain it for the second egg-laying. These, presumably, are the two moults that Wollebaek (1903) and Bjørk (1911) refer to. In the Northumberland population, although the long setae are lost, the extended coxal plates of the ovigerous primary females do not return to their normal size at the first moult after the larvae hatch. They do so after a second moult that probably occurs within a month of the first, i.e. there are at least three moults between ovigerous periods. After the final egg-laying, i.e. at $30\frac{1}{2}$ months, there is little or no growth. However, breeding dress is lost before death although the coxal plates remain somewhat enlarged. It seems probable that there is one moult between the hatching of the larvae and death.

PARASITES

No isopod parasites were recorded from the Northumberland population of *Pandalus borealis*, although *P. montagui* and *Spirontocaris lilljeborgii* also occuring on the same ground are affected by *Phryxus abdominalis*. The latter was parasitic on male *Pandalus borealis* of both Norwegian and West Greenland populations (Hjort & Rudd, 1938; Horsted & Smidt, 1956).

DISCUSSION

From the results of studies of prawn populations over a wide range of temperatures, a hormonal control of sex may be postulated, sex change thought of as being dependent on the concentration of an 'ovarian inhibiting substance'. Such a concept reconciles the ideas of Jägersten (1936) in which the prawns possess both male and female potentialities with the former capable of repression early in life, and of Hjort & Ruud (1938) who postulate a 'labile equilibrium' between male and female potentialities, with that of Rasmussen (1953) who links sex with size. Recently Carlisle is reported to have found that sex reversal in *P. borealis* is essentially similar to that in *Lysmata seticaudata* (*Rep. of Council of M.B.A.* 1956–7, p. 17)—'reversal is controlled primarily by action of the X organ-sinus gland complex in secreting the ovarian inhibiting substance, which appears to be the only hormone concerned. This hormone, or rather the cessation of its secretion, is responsible for the control of the onset of sex reversal. *The actual assumption of female form seems to take place at the moult following the attainment of minimum ovarian size. The degeneration of the testis which follows sex reversal* is probably to be attributed to the blocking of the opening of the vasa deferentia which *takes place when the animal develops a female shell*'.[1] While this report may fit the observed details of the biology of the Swedish prawns on which this work was based, it does not entirely fit with the present work on the Northumberland population. Although there seems little doubt that the control of the

[1] Author's italics.

attainment of the female phase is due to lack of hormonal secretion of the X organ-sinus gland complex, it is clear that 'minimum ovarian size' is not critical, at least in southern Norway and North Sea populations. Presumably temperature must play a considerable role in sex reversal. In addition, the present study shows that testis degeneration begins before the animal develops a female shell. External changes may lag considerably behind gonadal changes and specimens found with no trace of spermatocytes may still show male external characters. Sections suggest that the state of the follicular tissue may be of importance in the change of external characters. Until the follicular tissue degenerates there is no external change. Follicular tissue is not proliferated in immature specimens so that there is no bar to the rapid change of external form. Sections also suggest that proliferated follicular tissue has an important role during the incubation of the eggs perhaps as a growth inhibitor to the prawn and the onset of the increase in the rate of proliferation of oocytes also appears to coincide with degeneration of follicular tissue.

While the X organ-sinus gland is probably all important, modification of its action may come through hormones produced within the gonad. If growth rate and gonadal development are controlled directly or indirectly by hormones, it is likely that maturity will be reached within narrow size limits, and temperature, by its general effect on metabolism (including hormone action) will influence the age of maturity and also the onset of the breeding season.

Gonadal development and histology is similar to other *Pandalus* species described by Berkeley (1930), Aoto (1952) and Mistakidis (1957).

Present data show that there can be little prospect of a fishery for this prawn in the North Sea. Ritchie's samples from Scottish waters (mostly from the Fladen area) show that the population is patchy and that numbers are not very large. The *maximum* catch off the Northumberland coast was 3 l./h using a 9 ft. beam trawl. Presumably this can be increased by using a larger trawl but cannot compare with the catches, considered very good, of 60–100 l./h from the Gulf of Maine and Norwegian waters. Even higher catches are recorded from West Greenland (Horsted & Smidt, 1957). It is difficult to extract figures from the papers referred to, but the average daily yield per boat in Norwegian waters, approximately 10 kg ≡ 18 l., could perhaps be equalled off Northumberland only under the most favourable conditions. This is likely to be the exception rather than the rule.

The ground is not extensive and is some distance from the coast. By using the commercial pink shrimp trawl, large numbers of small prawns were caught during this work and if normal British shrimp trawls were used to fish the stock it would soon be depleted. Stocks will survive if only the largest prawns (>95 mm) are removed, fishing being limited to the period May to September when recently hatched prawns have yet to join the adult stocks.

Weather largely limits the use of small inshore boats to this period anyway, but it must be concluded that this population can only support an occasional fishery.

SUMMARY

Data on the distribution of *Pandalus borealis* have been brought up to date, and the factors controlling its distribution (temperature, salinity, substratum and depth) are discussed.

An account of the biology of the population off the Northumberland coast is given and compared with accounts of work on other populations. Knowledge of the biology of this species now extends over the entire north-south range in the eastern Atlantic.

Details of the histology and development of the gonads are given, particularly with respect to the development of the ova and to sex reversal. Sex changes in the gonad are considered in relation to changes in external form.

The growth rate of the North Sea prawn is described and compared with that of other populations.

It is unlikely that the North Sea populations can provide an additional fishery.

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APPENDIX I

Records of Pandalus borealis *from British Waters*

	Date	Position	Depth (m)	No. of specimens
J. A. Grieg	1904	57° 9′ N.–1° 30′ W.	96	?
R. A. Todd	26. viii. 07	55° 31½′ N–0° 33′ W.	90	30
H. Wedemeyer	1912	54° 24′ N–2° 59′ E	40	1
H. O. Bull	8. ii. 33	12 miles E. of Coquet	?	6
	28. viii. 33	Off Coquet	?	Hundreds
	27. i. 34	' N.E. Bank'	?	1
	30. i. 34	Off Coquet	?	3
	10. iii. 34	Off Coquet	?	1
	20. ix. 34	17 miles E. of Tyne	?	Hundreds
	29. i. 35	Off Newbiggin	?	3
	10. ii. 35	Off Newbiggin	?	3
	24. ix. 35	14 miles E.S.E. Tyne	?	Many
A. Ritchie	7. iv. 36	58° 05′ N.–0° 31′ E.	150–152	81
	8. iv. 46	58° 27′ N.–0° 01′ W.	145–147	59
	26. iv. 36	58° 30′ N.–0° 24′ W.	140	1
	7. iv. 36	58° 05′ N.–0° 05′ W.	128–133	1
	13. viii. 36	58° 07′ N.–0° 52′ E.	150	114
	13. viii. 36	58° 32′ N.–0° 56′ E.	140	32
	19. ix. 36	58° 21′ N.–0° 04′ W.	134	6
	9. iii. 37	58° 05′ N.–0° 31′ E.	149	170
	24. iii. 37	58° 05′ N.–0° 25′ W.	135	16
	17. viii. 37	58° 02′ N.–0° 30′ E.	145	51
	24. iii. 38	58° 05′ N.–0° 05′ W.	140	26
	2. v. 38	57° 47′ N.–0° 40′ E.	127	48
	14. v. 38	60° 06′ N.–0° 10′ E.	121	8
	9. v. 38	58° 50′ N.–0° 26′ E.	145	6
	9. x. 38	55° 32′ N.–0° 55′ W.	98	196
	16. iii. 39	58° 01′ N.–0° 31′ E.	145	104
	18. ii. 39	59° 01′ N.–0° 25′ E.	140	12
	26. iv. 39	58° 05′ N.–0° 05′ W.	147	156
	13. iv. 39	57° 47′ N.–0° 40′ E.	130	2
	23. viii. 39	58° 55′ N.–0° 25′ W.	132	18
J. A. Allen	1955–58	13 miles E. of Blyth	90	Hundreds
British Museum (Nat. Hist.)	6. xi. 07	55° 31½′ N.–0° 53′ W.	100	12
	16. x. 35	14 miles E.S.E. Tyne	80	10

APPENDIX II

Scottish samples 1936–39

Collected by Dr A. Ritchie, Scottish Home Department Laboratory, Aberdeen.

(Young prawns, classed as 'immature' by Dr Ritchie, have been assumed to be immature females on the grounds that (i) males of a similar size range are recorded from the same samples, and (2) the present work shows that young prawns of the same size from Northumberland can be sexed.)

Total length (mm)	March 1937 '38 '39						April 1936 '39						May 1939				August 1936 '37 '39						September 1936				October 1938			
	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total
45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	2
50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	4	—	1	—	—	5
55	13	—	—	—	—	13	—	3	1	—	—	4	1	—	—	—	—	1	1	—	—	—	—	1	7	—	—	—	—	7
60	20	—	2	—	—	22	14	4	5	—	—	23	8	—	—	—	—	8	—	—	—	—	—	—	1	—	—	—	—	1
65	36	—	4	—	—	40	26	4	13	—	—	43	16	—	1	—	—	17	1	—	—	—	—	1	—	—	—	—	—	—
70	16	—	5	—	—	21	20	3	8	—	—	31	13	—	5	—	—	18	2	—	1	—	—	3	—	—	—	—	—	—
75	3	1	1	1	—	6	8	3	1	—	—	12	6	—	1	—	—	7	14	—	3	—	—	17	2	—	—	—	—	—
80	2	—	—	3	—	5	1	—	—	—	—	1	2	—	—	—	—	2	8	—	—	—	—	35	9	—	—	—	—	—
85	8	7	—	10	—	25	3	2	—	—	1	6	—	—	—	—	—	—	27	35	1	13	—	49	35	1	—	—	6	41
90	19	19	—	14	1	53	13	8	—	—	3	24	—	—	—	—	—	—	15	1	2	11	—	26	15	—	—	—	25	40
95	19	35	—	4	—	58	7	22	—	—	5	34	—	—	—	—	1	1	5	2	4	—	—	15	2	—	1	—	29	31
100	4	14	—	11	1	30	—	48	—	—	20	68	—	—	—	—	—	—	1	4	—	—	—	20	1	—	1	1	26	27
105	2	13	—	13	1	29	—	17	—	—	11	27	—	—	—	—	1	1	5	—	—	—	—	22	1	—	1	—	13	15
110	—	9	—	8	2	19	—	17	—	1	4	22	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—	—	11	11
115	—	2	—	2	1	5	—	—	—	—	4	4	—	—	—	—	1	1	—	—	—	—	—	11	—	—	—	—	4	4
120	—	—	—	—	1	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—	—	1	1
125	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
130	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
135	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
140	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T	142	100	12	66	8	328	92	131	28	1	49	301	46	—	13	—	3	62	105	7	40	—	63	215	3	—	—	—	3	6	78	—	2	1	118	196

Total length (mm)	Total
45	2
50	5
55	7
60	1
65	—
70	2
75	9
80	41
85	40
90	31
95	27
100	15
105	11
110	4
115	1
120	—
125	—
130	—
135	—
140	—
T	196

Date: March 1937 '38 '39 | April 1936 '39 | May 1939 | August 1936 '37 '39 | September 1936 | October 1938

APPENDIX II

Northumberland samples, 1956–57

Carapace length (mm)	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total
6						
7						
8	1		2			3
9						
10						
11						
12						
13	2					2
14						
15	29		2			31
16	92		9			101
17	63		28			91
18	7		16			23
19			4		5	9
20	1				61	62
21					65	65
22					81	81
23					39	39
24					13	13
25					3	3
26						
T	195	—	61	—	266	522
Date	10 September 1956					
6						
7						
8	6		2			8
9	35		12			47
10	3		2			5
11						
12	6					6
13	47					47
14	93		12			105
15	50		58			108
16	4		30			34
17			10			10
18			1		2	3
19					24	24
20					20	20
21					9	9
22					1	1
23						
24						
25						
26						
T	244	—	127	—	56	427
Date	18 October 1956					
6						
7						
8	21		32			32
9	178		257			257
10	121		184			184
11	33		48			48
12	2		3			3
13	1		1			1
14	5		5			5
15	29		31			31
16	51		57			57
17	10		32			32
18			18			18
19			6			6
20			21			21
21			34			34
22			13			13
23			5			5
24			2			2
25						
26						
T	541	—	169	129	—	749
Date	7 December 1956					
6						
7						
8	3		4			7
9	61		26			87
10	228		72			300
11	160		39			199
12	36		5			41
13	2		1			3
14	4					4
15	29			3		32
16	53			15		68
17	24			37		61
18	1			18		19
19				14		14
20				11		11
21				16		16
22				3		3
23				3		3
24						
25						
26						
T	601	—	147	120	—	868
Date	14 February 1957					
6						
7						
8	5		1			6
9	148		22			170
10	65		15			80
11	10		66			76
12	1		42			43
13	7		14			21
14	92		1	10		103
15	66			15		81
16	18			10		28
17	2			3		5
18				13		13
19				19		19
20				8		8
21				2		2
22				2		2
23				1		1
24						
25						
26						
T	436	—	138	83	—	657
Date	7 March 1957					
6						
7						
8						
9						
10						
11						
12						
13						
14						
15						
16						
17						
18						
19						
20						
21						
22						
23						
24						
25						
26						
T	179	5	33	187	100	504
Date	4 April 1957					
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12	25		11			36
13	30		10			41
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16	9			1	1	11
17	25			17	8	50
18	46			37	17	100
19	27	1		26	3	57
20	5	4		13	5	27
21				41	17	58
22				30	30	60
23				18	17	35
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T	179	5	33	187	100	504
Date	4 April 1957					
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10	2					2
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12	49					49
13	165					165
14	52					52
15	12					12
16	7			1		8
17	23			3		26
18	73			7		80
19	40		19	4		63
20	7		4			11
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T	430	33	130	13	189	795
Date	16 April 1957					
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12			20			69
13			58			223
14			33			85
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16			1	1	3	12
17				1	11	38
18				2	24	106
19				1	24	84
20					12	23
21				4	42	46
22				4	50	54
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T	94	1	68	—	20	183
Date	7 June 1957					
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13	50		25			75
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17					1	2
18		1			5	6
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T	94	1	68	—	20	183
Date	7 June 1957					
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13	3					3
14	36		5			41
15	169		29			198
16	176		58			234
17	30		39			69
18	3		8			11
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T	417	39	139	—	141	736
Date	2 July 1957					
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14	4		1			5
15	53		16			69
16	90		44			134
17	25		42			67
18	7	6	11			35
19		20				59
20		13				132
21		2				85
22						30
23						23
24						4
25						4
26						
T	179	41	114	—	313	647
Date	2 August 1957					

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

ALLEN, J. A., 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Phil. Trans.* B, Vol. 241, pp. 421–84.

The functional morphology of the Lucinacea is described. In particular, comparative accounts of the feeding, respiratory and cleansing currents are given. All species construct an anterior inhalant tube from particles of the substratum cemented together by the secretion of the glands in the tip of the modified vermiform foot. Particles entering by this tube are sorted by the ciliated epithelium covering the elongate anterior adductor muscle. An evolutionary sequence can be demonstrated showing that as the size and efficiency of the anterior adductor increases there is a related decrease in the size and efficiency of the gills and palps and the sorting mechanisms on them. Progressive reduction in sorting mechanisms of the stomach and in numbers of apertures to the digestive diverticula is demonstrated. This simplification emphasizes the essential mechanisms involved in the functioning of the eulamellibranch stomach. J.A.A.

ATKINS, W. R. G., 1957. The direct estimation of ammonia in sea water, with notes on nitrate, copper, zinc, and sugars. *J. Cons. int. Explor. Mer*, Vol. 22, pp. 271–7.

A method for estimating ammonia not involving distillation appears to be provided by the use of chloramine T and a pyridine pyrazolone reagent devised by J. Kruse and M. G. Mellon in 1952. A purple colour is produced and can be extracted with carbon tetrachloride and matched or measured in a spectrophotometer at 450 mμ. Even with a 1 cm cell as little as 0·025 parts per million can be determined. Other constituents of sea water do not interfere. The advantages of the diphenyl benzidine reagent for nitrates are stressed, as are also those of carbon tetrachloride for extracting copper diethyl-dithiocarbamate. For zinc the dithiocarbamate is preferable to ferrocyanide but *p*-dimethyl-aminostyryl-β-naphthiazole methiodide is better. Sugars, as arabinose, may be estimated in sea water and unialgal cultures by the use of *n*-ethyl carbazole recommended by Collier, Ray and Magnitzky. W.R.G.A.

ATKINS, W. R. G. & POOLE, H. H., 1958. Cube photometer measurements of the angular distribution of submarine daylight and the total submarine illumination. *J. Cons. int. Explor. Mer*, Vol. 23, pp. 327–36.

The average obliquity of submarine daylight in the English Channel was again found to be between 30° and 40°. It varied little, if at all, with depth below surface, or with surface or daylight conditions, hence the ratio of the total to the vertical illumination in water never differed much from 1·25. In air it is unlikely to be less than 1·5, and may run up to 5 or 6 with low sun.

Accordingly, the ratio (total illumination in water)/(total illumination in air) is equal to the corresponding ratio for the vertical illuminations multiplied by a factor which may vary from about 1·25/1·5 for high sunlight to about 1·25/6 for low sunlight, approximately a fourfold variation.

The upward light in clear water is about 2% of the downward, but may rise to

3·5 % or more nearer shore. As before green light penetrated best; for though in pure water extinction is a minimum for blue, the effects of scattering and more especially of the absorption of plankton chlorophyll and of yellow pigments cuts down the transmission relatively heavily in the blue. W.R.G.A.

BIDDER, A. M., 1957. Evidence for an absorptive function in the 'Liver' of *Octopus vulgaris* Lam. *Pubbl. Staz. zool. Napoli*, Vol. 29, pp. 139–50.

A number of specimens of *Octopus vulgaris* were fed with crabs, previously injected with a dense suspension of carmine. The carmine was traced into the caecum, and thence, chiefly in solution, into the 'liver'. After entering the liver cells, the carmine becomes invisible, and can remain thus in the body for at least 3 days, being eliminated periodically with excretory granules contained in excretory vacuoles formed in the liver cells. The liver is shown to have three functions which each cell performs in turn: enzyme-secretion, absorption, excretion. Carmine also penetrates the liver of *Sepia officinalis*. The results are compared with those previously described for *Loligo vulgaris*, in which the liver has no absorptive function. A.M.B.

BODEN, B. P. & KAMPA, E. M., 1958. Lumière, bioluminescence et migrations de la couche diffusante profonde en Méditerranée occidentale. *Vie et Milieu*, Tome IX, 10 pp.

The presence of a migratory sonic-scattering layer in the Golfe du Lion was established. This layer was found to be established with the 5×10^{-3} μwatt/cm^2 isolume during its twilight migration toward the surface.

As the layer approached the surface, during its period of most rapid migration it appeared to overtake this isolume. Numerous bright flashes of bioluminescence were recorded at this time, and these may have obscured the true relationship between the depth of the scattering layer and the amount of transmitted light. The possibility that scattering-layer organisms possess discriminatory mechanisms which enable them to distinguish components of ambient light is discussed.

The layer did not rise above a depth of about 48 m. A sharp thermocline was present at this depth and it is suggested that this may have been a barrier to further migration. B.P.B.

CALDWELL, P. C., 1958. Studies on the internal pH of large muscle and nerve fibres. *J. Physiol.*, Vol. 142, pp. 22–62.

An investigation of the internal pH of the muscle fibres of *Carcinus maenas* and *Maia squinado* and of the giant axons of *Loligo forbesi* is described. The internal pH was measured with micro-glass pH electrodes. Normally it is near 7. When the muscle fibres and the axons were immersed in saline or sea water saturated with CO_2 it fell to values in the region of 6, but in the other bathing solutions used it changed more slowly, usually by a smaller amount. During contractures of *Maia squinado* muscle fibres induced with 0·6M-KCl no changes in pH greater than the limits of sensitivity of the method of measurement (about 0·1 of a pH unit) could be detected. The changes in squid axons after depolarization with 0·6M-KCl were also less than the limits of sensitivity of the method.

The results indicate that the internal pH is regulated mainly by the external CO_2 tension and possibly also by some process which brings about the active extrusion of H ions. It does not appear to be regulated by the Donnan equilibrium. P.C.C.

CAMBRIDGE, G. W., 1958. Responses of the anterior retractor muscle of the byssus of *Mytilus edulis*. *Nature, Lond.*, Vol. 182, p. 35.

A preliminary investigation of some agents which render the anterior retractor muscle of the byssus (ARMB) of *Mytilus edulis* insensitive to electrical stimulation and to acetylcholine (ACh) is reported.

Contrary to the findings of Schild using vertebrate smooth muscle, after treatment with 0·56M-KCl the ARMB does not respond to either electrical stimulation or to ACh. The contraction produced by KCl is abolished by previous treatment with propylene glycol monophenyl ether. Both this and the KCl effect are reversible on washing with sea water. The toxin of *Gymnodinium veneficum* does not prevent the response of the muscle to d.c. stimulation.

G.W.C.

CARLISLE, D. B., 1958. A crustacean chromactivator. *Nature, Lond.*, Vol. 182, pp. 33–4.

Chromactivating substance A which is the stored form of one of the main colour change hormones of Crustacea is not present as such in extracts of the ganglionic X organ whose neurones appear to be the centre of production. If these extracts, however, are treated with any reagent which breaks hydrogen bonds substance A appears in large amounts. It is probably present in the form of an inactive precursor in the untreated extracts.

D.B.C.

COOPER, L. H. N., 1958. Consumption of nutrient salts in the English Channel as a means of measuring production. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. 144, pp. 35–7.

Evidence is produced that this powerful method of estimating minimum productivity of the English Channel has served its turn and other methods are needed for further advance. A cruise in January 1947, designed to test the uniformity of distribution of phosphate in the Western English Channel, revealed areas with phosphate contents varying by as much as 1·7:1. Moreover, the waters poorest in nutrients had been most productive of animals. The apparent winter maximum of phosphate in 1950 occurred a month late—in February. There is evidence for the view that this apparent maximum occurred in a narrow belt of coastal water created by a storm. The figure to represent the winter maximum for a wide area needs to be a lower one observed in January and March. A process of partition of nutrients consequent upon the prevailing winds is described.

L.H.N.C.

GREEN, J., 1958. *Dactylopusioides macrolabris* (Claus) (Copepoda; Harpacticoida) and its frond-mining nauplius. *Proc. zool. Soc. Lond.*, Vol. 131, pp. 49–54.

Nauplii and an associated adult female of *Dactylopusioides macrolabris* were found in mines between the two epidermal layers of the brown alga *Dictyota dichotoma* at Torquay, Devon. This is the first British record of this copepod, and the first record of a copepod mining the fronds of a member of the Phaeophyceae.

The second antenna of the nauplius is modified to form a biting appendage, while the mandibles are not capable of biting.

J.G.

HEDLEY, R. H., 1958. A contribution to the biology and cytology of *Haliphysema* (Foraminifera). *Proc. zool. Soc. Lond.*, Vol. 130, pp. 569–76.

The grey-white, arenaceous and monothalamous foraminifer *Haliphysema tumanowiczii* is very common near Penlee Point in the Plymouth area where it can be found firmly attached, by means of a basal disc, to the fronds of the red weed *Delesseria sanguinea*.

The test, usually 1–2 mm long and exceptionally 5 mm, is composed mainly of sponge spicules, detritus and quartz grains cemented together by a mucopolysaccharide. Not many attached arenaceous foraminifera grow away from the substratum to the same extent as does *H. tumanowiczii* and this may be correlated with the presence of an organic sheath secreted by the animal on the inside of the test wall in the basal disc and first quarter of the pedicle. This is a flexible and fibrous component, composed of a mucoprotein, with the longitudinal axes of the fibres parallel to the major axis of the test. Because of the mechanical buffer action of the organic sheath the animal is able to withstand the relatively rough conditions of the littoral zone. At times an unattached spheroidal individual is released from the attached animal. These individuals were seen to move over the substratum, settle, form basal discs and eventually to grow, becoming typical attached individuals. In the opinion of the author the following forms are probably synonyms of *H. tumonawiczii* Bowerbank: *H. primordiale* Haeckel, *H. echinoides* Haeckle, *H. globigerina* Haeckel and *H. advena* Cushman.

R. H. H.

JONES, W. CLIFFORD, 1958. The effect of reversing the internal water-current on the spicule orientation in *Leucosolenia variabilis* and *L. complicata*. *Quart. J. micr. Sci.*, Vol. 99, pp. 263–78.

Oscular tubes of *Leucosolenia* were excised and tied on the ends of fine glass tubes through which a current of sea water was allowed to siphon. The tubes were mounted either at the basal or at the oscular end, with or without the original oscular rim. Spicules subsequently developing in the wall tended to be oriented towards the distal end in the distal part of the tube and towards the mounted end in the proximal part, a confused zone lying in between. The orientation was but little affected by the removal of the original oscular rim, and only coincided with the direction of the internal water-current over part of the tube. The orientation cannot, furthermore, depend on static structural features in the wall. A mechanical hypothesis explaining the orientation is briefly described.

W. C. J.

SOUTHWARD, A. J. & SOUTHWARD, E. C., 1958. Pogonophora from the Atlantic. *Nature, Lond.*, Vol. 181, p. 1607.

SOUTHWARD, A. J., 1958. Abundance of Pogonophora. *Nature, Lond.*, Vol. 182, p. 272.

Several species of *Siboglinum*, including some new species, have been dredged up from the continental slope between lat. 47° 56′ N., long. 7° 56′ W. and lat. 48° 32′ N., long. 10° 11′ W., at depths of 300 to 710 fm. Specimens of the same genus have also been found in bottom samples taken by Mr N. A. Holme in 80–90 fm. off Dingle Bay, Ireland. The Pogonophora now appear to be among the commonest animals from muddy bottoms, and not only in deep water. Previous recognition may have been hindered by the resemblance of the tubes to fibres used in dredge and trawl netting.

A. J. S.

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, 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, and, since that date, a new library and further laboratory accommodation have been added.

The Association is maintained by subscriptions and donations from private members, universities, scientific societies and other public bodies; 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. Accounts of the laboratory and aquarium and the scope of the researches will be found in Vol. 27 (p. 761) and Vol. 31 (p. 193) of this *Journal*.

The laboratory is open throughout the year and its work is carried out by a fully qualified research staff under the supervision of the Director. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology, physiology and other branches of science. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat, and these also collect the specimens required in the laboratory.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officer and Council; they receive the Journal of the Association free by post; they are admitted to view the laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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