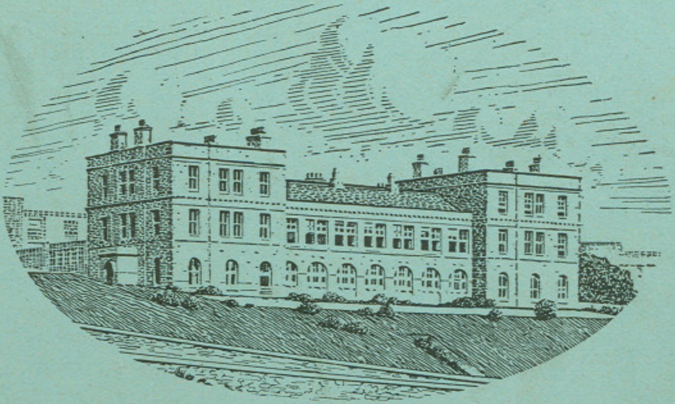
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME XXV, No. 4
(issued September 1943 and completing Vol. XXV)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1943

Price Fifteen Shillings net

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

PATRON

HIS MAJESTY THE KING

OFFICERS AND COUNCIL

President

G. P. Bidder, Sc.D.

Vice-Presidents

The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
Viscount Astor
Sir Nicholas Waterhouse, K.B.E.
The Earl of Iveagh, C.B., C.M.G.
The Lord Moyne, P.C., D.S.O.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. Peel, D.S.O., M.C.
Lord Mildmay of Flete, P.C.
The Right Hon. Sir Reginald Dorman Smith, M.P.
Sir Joseph Barcroft, Kt., C.B.E., F.R.S.
Prof. J. Stanley Gardiner, F.R.S.
Prof. Walter Garstang, D.Sc.

COUNCIL

Elected Members

Prof. H. Graham Cannon, Sc.D., F.R.S.
C. Forster-Cooper, M.A., Sc.D., F.R.S.
Prof. F. E. Fritsch, D.Sc., F.R.S.
Michael Graham
Prof. A. C. Hardy, D.Sc., F.R.S.
Prof. A. V. Hill, O.B.E., Sc.D.. Sec.R.S., M.P.
Miss Margery Knight, D.Sc.
Morley H. Neale
C. F. A. Pantin, Sc.D., F.R.S.
The Hon. Miriam Rothschild
J. E. Smith, Ph.D.
Prof. T. A. Stephenson, D.Sc.
Prof. W. M. Tattersall, D.Sc.
Prof. C. M. Yonge, D.Sc.
J. Z. Young

Governors

G. P. Bidder, Sc.D.
The Lord Moyne, P.C., D.S.O.
A. T. A. Dobson, C.B., C.V.O., C.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.
  Major E. G. Christie Miller
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
H. G. Maurice, C.B. (Zoological Society)
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S. (Royal Society)

Chairman of Council: Prof. J. Gray, M.C., Sc.D., F.R.S.

Hon. Treasurer: Major E. G. Christie Miller, 71 Park Street, London, W. 1

Secretary: Stanley Kemp, Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

SCIENTIFIC STAFF

Director: Stanley Kemp, Sc.D., F.R.S.

Assistant Director and Fishery Naturalist: E. Ford, A.R.C.Sc., D.I.C.

Head of Department of General Physiology:
W. R. G. Atkins, O.B.E., Sc.D., F.I.C., F.Inst.P., F.R.S.

Miss M. V. Lebour, D.Sc. (*Naturalist*)
H. W. Harvey, Sc.D., M.A. (*Hydrographer*)
F. S. Russell, D.S.C., D.F.C., B.A., F.R.S. (*Naturalist*)
A. Sand, Ph.D. (*Physiologist*)
D. P. Wilson, M.Sc., F.R.P.S. (*Naturalist*)
Mrs E. W. Sexton, F.L.S. (*Director's Research Assistant*)
G. A. Steven, B.Sc., F.R.S.E. (*Naturalist*)
G. M. Spooner, M.A. (*Naturalist*)
L. H. N. Cooper, D.Sc., F.I.C. (*Assistant Chemist*)

E. J. Allen.

EDGAR JOHNSON ALLEN

1866–1942

The late Dr E. J. Allen was the son of the Rev. Richard Allen, a Wesleyan minister and as such liable to change the sphere of his work every few years. For this reason E. J. Allen passed his childhood in Cornwall, went to school in Exeter, and lived during his late boyhood in the Worth Valley, going into Leeds to attend the Yorkshire College (now University of Leeds); his education was continued by the University of Berlin, an interval of teaching in Antigua, and University College, London, followed by a Royal Society research studentship at the Plymouth Laboratory. Excepting Antigua, every one of these epochs claimed in him its own loyalties: a few years ago he seriously considered going west to Cornwall to end his life where he first remembered it; he much admired Franz Eilhard Schulze, who taught him at Berlin, and W. F. R. Weldon, his Professor of Zoology at University College, yet kept a lively gratitude for what he had learned from Professor Miall at Leeds.

To this very varying environment during the first third of his life we may attribute through the next half-century much of his universal power of sympathy and contact with all sorts and conditions of men. Unselfish by nature, he had the example of a singularly wide-minded father; then bred as a boy in Cornwall, Devon, and West Riding, as a man among London University students and Berlin University students, with the West Indian interlude—there was no class or nation who could not feel an understanding with Allen.

I first heard of him from Weldon—probably in 1891. 'I say! I've got a new sort of student at U.C. now—name of Allen. I gave them the classification of the Crustacea, and at the next lecture he brought up to show me, in case anything interested me, a collection of Crustacea he had made in Antigua, showing some he found rather difficult to fit in!' Weldon had always a great regard and very high esteem for Allen: to this I should attribute Allen's whole connection with Plymouth, from his first visit for research in 1892 to his appointment as Director and Hon. Secretary in 1895.

We met in the Laboratory at the end of 1893. Bles (Director), Cunningham (Naturalist) and Garstang (Assistant Naturalist) were the Staff naturalists; Allen, Hickson, and myself, were the visiting naturalists. Our laboratory assistant was a young man of 22 named Joseph, who was monarch of all he surveyed on the laboratory floor, and was not quite conscious of his own limitations. Roach was our collector and fisherman, an admirable man at that time, who could do anything with the 18 ft. open boat, *Anton Dohrn*, which formed our fleet, always ably seconded by 'Bill', who, as W. Searle, now numbers 50 years of friendship among biologists working at Plymouth.

Outside his work on the nervous system of the embryonic lobster, Allen had started an experiment on filtering water from the circulation through Berkefeld porcelain filters. It was unsuccessful (he had not coped with the difficulties of keeping the filtrate sterile), but it was his first attempt in 1894 to deal with the problem, which he solved in 1910, of preparing sea water in which delicate larvae could be reared.

He lodged in Windsor Lane (ground floor on the right hand as you go down from the Hoe, I think the second door). We led quiet and studious lives, and he had a reserve or a shyness which I found difficult to penetrate at that time; looking back, I think a natural shyness was then accentuated as the result of eight years of uphill life in which he had not found the world gentle. Outside work, our greatest excitement was when J. T. Cunningham and his wife asked us to Sunday supper—hospitality most pleasantly given and most gratefully received by two bachelors in lodgings; Mrs Cunningham was a sweet-natured woman. Mrs Bles had a serious illness on her arrival at Plymouth, so that we did not visit the Director's house until later in the year. Hickson, in the laboratory compartment on my left, was the best of neighbours; Garstang was not only a mine of information on the fauna of the Sound but was a source of cheerfulness and good companionship to us all.

In the autumn of 1894 Bles gave up the contest, in which he had struggled valiantly and well, and Allen was appointed Director in his place; a place that had now been filled by four Directors in eight years. But Weldon had already confided in me that he thought the constitution of the Association was more to blame for these rapid changes than defective qualifications in the four Directors. The Hon. Secretary was in the habit of making criticisms to the Director and bringing before Council any matters in the conduct of the Laboratory which he considered desirable to be discussed with the Director. In other words it was the Secretary's duty to scratch the Director's back: and E. Ray Lankester scratched Heape's back good and hard, while G. H. Fowler did the same for Calderwood and Bles (G. C. Bourne could look after his own broad back). Remembering also that Allen was Weldon's pupil—and remembering all he did for me, who had also been his pupil—I attribute to Weldon salvation of the M.B.A. by the revolutionary change making Allen the first Director also appointed Honorary Secretary.

So, in January 1895, aged 28, Allen took up his duties, with behind him a discouraging Bluebeard's cupboard of ex-Directors, yet holding one immense essential advantage over them: that he had only to deal with the Council and the President, not with an official critic busy in preparing for them a synopsis of his three months' errors.

This was an immense advantage, but even so the prospect was enough to make even a bold man shrink. We had a fine well-designed marine laboratory, with comfortable 'tables' for eleven workers and two or three extra rooms. In December of 1893, when Garstang, Allen and Hickson had gone for Christmas holidays, for a week or two Cunningham worked on the north side of the Laboratory and I on the south side. The Director left his wife's sick bed to pay us each a diurnal visit, and Cunningham and I kept each other company for the rest of the day.

Financial stringency was dire. Income all in was £1950 (of which £1000 was granted annually by the government and £400 by the Company of Fishmongers). The salaries we paid were beggarly: £200 a year and a house to the Director, £250 to the Naturalist, £150 to the Assistant Naturalist, if there was one, and £350 in all to pay fishermen, laboratory attendant, engineer and clerk; yet Allen put the necessary minimum expenditure at £1800 without any assistant naturalist. There was the cavern of a Laboratory, weathertight and with pumps going, in which the Director, the Naturalist, and the Assistant Naturalist made their researches while a dozen naturalists visited them during the year, most of them for only a few weeks in the summer.

I came down to Plymouth in July 1895, when Allen had been six months in the saddle. July and December at the Laboratory were very different things and I found a most pleasant company: W. F. R. Weldon, W. Garstang, A. Bethe (Munich), J. D. Gilchrist, T. H. Riches and W. I. Beaumont, with T. V. Hodgson, newly appointed as Director's Assistant, and three undergraduates. Weldon's presence was a great pleasure to Allen and me. He was rearing 500 young crabs through a moult, to ascertain how far deviation from the normal was the same for the old and new carapaces of each crab; Allen had rigged him a perfect apparatus—a sloping rack of shelves under a corrugated iron pent house over the open-air tank at the back of the aquarium. On the shelves were 500 glass jars, each supplied with a jet of sea water and containing a live crab. (It looked so like a display at a grocer's shop that the irreverent referred to it as 'Gubbins & Co.') Every day each crab was fed with fresh fish, and the cutting of fillets of young soles the moment they were dead was hard manual labour. I think Weldon's visit lasted out August.

Garstang was no longer on the staff, but a Fellow and Lecturer of Lincoln College, Oxford. He was only down for five weeks, working at Tunicates, but also, as in a previous visit in March, was conducting a most important experiment: the first of 'Garstang's Classes'. This year there were only five pupils, two in March and three in July. 'This is, I am convinced, a useful extension of the work of the Laboratory', writes Allen in his Report to the Council; most zoologists of to-day would agree that the carrying on of these classes by Garstang, Orton, and their successors has been as important a piece of work as any that the Association has done. In the following year fifteen students came at Easter and three in the summer; now, for over 40 years, only war has interrupted the sequence of classes: not only have they been full to overflowing but so have been the similar classes which have followed them in other marine laboratories. Several thousand biologists must already have benefited from this new departure made by Garstang and Allen in Allen's first year.

Bethe, working at the crustacean nervous system, obviously came to Plymouth to be in the same laboratory as his fellow-worker, Allen, with whom he became great friends, as he did with me. I should like to record that with my own microscope, in my own well-examined preparation, when I requested him to recognize, looking down on a collar-cell, the stained cross-section of a flagellum $0{\cdot}5\mu$ in diameter, he said, 'Oh yes, stained on its surface, with a white lumen.' Which I could then see, but had not seen.

Late in August E. T. Browne came for a six weeks' visit, lodging over me at 7 Hoe Park Terrace. Browne's company was always very welcome to Allen; they had been at University College together, and I think, to the end, Browne was his most intimate friend and always his staunch ally. He was a learned, industrious and skilful zoologist, with a passion for his medusae. Like Riches, he suffered from the apparent infinity of time before him in which to publish a *magnum opus*, but he loved zoology, and the prosperity of the Laboratory became one of his greatest interests. He was gentle and much liked.

I had to spend month-ends in London, and on my return on August 31 Allen greeted me with startling news. There was to be a congress of journalists in Plymouth for the third week of September, they might be 400; the local Committee had approached Allen as to facilities for seeing the Aquarium and he had invited the congress to a soirée.

For a moment my breath stopped as I pictured our poverty-stricken, under-staffed Association throwing a party to four hundred strangers—then I saw Allen's genius! He invited them to the most imposing building of the neighbourhood outside the Citadel; in the Aquarium, the great laboratory and adjuncts, there was comfortable walking and standing room for two hundred people, there was that for them to look at which they could not see elsewhere in Britain and nothing in laboratory or aquarium to show our penury. It was a type of all that he did as Director—to see what advantages we had and to use them.

Then he fired his second barrel: 'The difficulty is that since Cunningham went to Grimsby in February, we have no fish expert here. Stead doesn't arrive until the 10th, and it wouldn't be fair to ask a man fresh from his tripos to take it on when he has only been a week in the laboratory. You will have to be our fish expert.' 'But I know next to nothing about fishes!' 'That doesn't matter, you've got nearly three weeks to learn them up in.' So, with microscope under its bell-jar, for the first half of September I read diligently in Couch and Day and the volumes of our *Journal*, or wandered round the Aquarium trying to memorize which fish was which.

The Soirée was a complete success—except for the fish expert! I don't think there were much short of two hundred guests, and it all went with a bang. There was a rocker-microtome on which someone cut sections. Browne had a beautiful show of hydroids and medusae, Riches had an appalling nemertine (was it 20 ft. long? or only 10?), there were half a dozen other shows, and the tanks lit up in the Aquarium and two or three printed leaflets to take away (I was put on to write one on making sections in paraffin), and every one was hard at it seeing things and all seemed to enjoy themselves. I gave lectures at the tanks to twenty or thirty young journalists, who listened eagerly to the carefully prepared stories. Unfortunately, they were joined by dear old Robert Bayly, one of our Governors and benefactors, who knew a good deal about fishes and was anxious to make the most of the opportunity of contact in the Aquarium with the Fish Expert of the Marine Biological Association. When his questions came—though I had not finished my stories—there was nothing for it but to look at my watch, say 'Excuse me, I'm wanted upstairs', and dash through the Director's House into the safety of the great laboratory.

The out-of-pocket expenses were about five pounds. Allen pleased many scores of people, he put the Laboratory on the map with at least a hundred journalists, he gave dignity to the M.B.A. before the face of Plymouth, and he added valuably to our self-respect.

Beaumont now became for many years the occupier of a table for the greater part of the year. He was a real naturalist, but led more to admire and enjoy than to investigate, and his greatest interest was yachting. At one period I laughed to Allen that I thought Beaumont only used his cubicle as a place in which to eat his lunch. But Allen was quite right to welcome him. He was very kindly and always ready to help anyone; he took his part in tedious identification of dredged samples and in considering problems concerning our boats. Principally, however, I think Allen saw the first urgency of building up a community to be a soul to the body of our buildings. Beaumont was an addition to that community, so was Hodgson. The Council allowed £100 for an 'Assistant to the Director', which in those days would have got him a good clerk. Instead he engaged, on a half-time basis, Hodgson, who had a job under the town council, as lecturer and later as Museum curator; having recently returned from the Antarctic expedition, on which he had been doing pycnogons and amphipods, he was naturally one of us.

The most important newcomer this year to the Laboratory, after the Director, has not yet been named. He was an old acquaintance of mine, A. J. Smith, who was assistant to Brockett in the Morphological Laboratory at Cambridge. Adam Sedgwick said in the winter: 'I don't know what to do about Smith. He is too good a man to go on in his present position and I can't offer him anything better. Do you think he would be of use at Plymouth?' I presume that Sedgwick put the same question to Allen, for Smith began in April that career of 45 years through which he incurred the gratitude of every biologist working at Plymouth, and was always the most loyal supporter of the Director. That invaluable addition to our strength we owe to Sedgwick and Allen.

On July 30 Allen made, off Prawle Point, the first four hauls of over a hundred, made with dredges, trawls, etc., during this and the next two years, to determine the relation between fauna and bottom deposits near the 30-fathom line from Eddystone Grounds to Start. He was enabled to do this by a Royal Society grant of £100 for boat-hire, and the Royal Society must have found his fine Report in 1899 (occupying No. 4 of Vol. v of our *Journal*) very ample justification for their assignment of this sum. Nearly everyone working in the

Laboratory assisted in the determination of the animals brought up, and Allen's friend R. H. Worth, the engineer and Devon archaeologist and geologist, gave essential help in analysis of the bottom deposits. It was a valuable effort in fundamental research, and the characteristic of the man was the skill with which our meagre resources were marshalled to undertake, and to carry through, such an important piece of team work.

Before I left at Christmas, Allen gave me another job, not involving false colours this time. The Colonial Secretary this year was the Right Hon. Joseph Chamberlain, who had been our champion in obtaining for us from the Government, first £500 a year and then £1000 a year. (He told me, when I showed him round the Stazione at Naples, that he would have liked to have got more for us, 'but you know those fellows Harcourt and the others take no interest in such things'.) It was quite natural, therefore, that he should instruct the Colonial Office to request from the Director of the M.B.A. a 'Report on Sponge Culture and Projects for the Improvement of Sponge Fisheries'. Allen asked me to look up the thing for him and show him the papers on which to found his Report. I did so, and wrote a note of my own (of which the Appendix may be the best part), and he made a business-like Report on the literature. I have just been re-reading some of his Reports in our *Journal* of these early years: 'Reproduction of the Lobster', 'Protection of Crabs and Lobsters', 'Fauna and Bottom-deposits'—and thinking what powerful writing there is in them. He does not deal in clichés, what he says he means; where there is a problem he puts to consider it the whole strength of a remarkable mind and writes his own opinion, clearly, logically, and briefly.

Early in this, his first year, the new Director made a revolution of far-reaching importance, with the object—to which he held tenaciously for 45 years—of enabling workers to rear delicate organisms in the Laboratory. The revolution was no other than a one-man revolt against the Crystal Palace tradition.

I can remember as a child the intense surprise and admiration elicited by the Crystal Palace Aquarium, where Londoners could see, living and moving, 'all' the denizens of the sea. The Crystal Palace was inland, 50 miles from the sea; Lloyd deserves the greatest credit for having designed a successful system whereby the tanks and reservoirs had only to be filled once, and then a few barrels to repair wastage sufficed to keep the exhibition brilliant. But when, shortly afterwards, he made the Brighton Aquarium, he used closely the same plan, which Westminster Aquarium of course followed. More remarkably, when Anton Dohrn founded his great Stazione Zoologica, he applied to Lloyd for advice, and Lloyd insisted that the closed circulation and the dark resting reservoir were essential to success. Lloyd had succeeded, so Dohrn followed his plan exactly, and nearly a quarter of a century after the opening of the Crystal Palace Aquarium, Lankester followed it at Plymouth.

But (*a*) the Crystal Palace had to have a closed circulation; Brighton, Naples, and Plymouth could take fresh sea water at negligible expense: (*b*) the closed circulation with the dark reservoir succeeded admirably for keeping in life the crabs, sea anemones, and so on, which I remember admiring at the Crystal Palace, or *Limulus*, a dozen of which they used to show us in the palmy days of the Brighton Aquarium; but you could not rear delicate larvae to be adults in that closed circulation. Allen threw overboard the Lloyd tradition, proclaimed that the less any tank is supplied with used water the better for its inhabitants, supplied the laboratory entirely with water which had never been under its roof before (passing it on to improve the aquarium circulation) and organisms lived in the laboratory which had hitherto been transitory visitors while soles spawned in the aquarium for the first time.

Already under the last directorship an occasional carboy of outside sea water was used in the laboratory, now those who requested it for delicate work had a wooden bucket of sea water brought to them from outside the breakwater, and in 1899 there was a pair of wooden 500 gallon reservoirs built at the top of the little stairs, from which by gravity 'outside water' was led through glass tubes to a few small jets in the laboratory; the cistern being replenished from a tank boat by force-pump.

As years pass the difference between the waters of Plymouth Sound and of the ocean becomes more and more noticeable, while the researches of the marine biologist become more and more delicate. Allen's plan of keeping the first reservoir supplied with high-tide water whenever it ran low had to be modified: it was found that often the Sound water was more poisonous than old Aquarium water, eventually new supplies were only taken rarely and the Aquarium acidity was corrected (I think Pantin devised this) with lime in the reservoir. Outside water in bell-jars took up the part it now plays, but never since Allen's revolution was the visiting naturalist advised to rear his larvae in many-year-old water drawn from Lloyd's resting reservoir.

Only by describing thus in detail the first year of Allen's directorship is it possible to give an idea of the character of the man and the reasons for his great success. One of his gifts it may not have brought out is his great business ability. With all his scientific abilities and knowledge and his passionate scientific interest he was a first-class business man.

He recognized at once that the first need to make the Laboratory live was to have it inhabited, and patiently, continuously, he warred against the desolation of barren tables. But his first year of work showed him another essential necessity: we must have a steamboat of our own. Hired boats, which the Royal Society had enabled him to employ, were too expensive to be used for ordinary collecting; also, even when most suitable, they had less than half the efficiency possible with our own boat, fitted with our own gadgets and our own special stores and a working cabin or deckhouse with tables, shelves, and appliances as experience proved necessary.

In January 1896 he reports to Council that 'the want at Plymouth which must be put before all others, is that of a suitable boat', 'the effective work of the Association could be increased by at least 50% if a suitable small steamer were in our possession'. On February, 13 1896 he adds, on the proof, a postscript to his Report: 'an opportunity of securing a small steam fishing yacht, upon advantageous terms, has presented itself...the Council decided it would be advisable to purchase without delay. The yacht, the *Busy Bee*, of Fowey, is now in our possession.'

She was 60 ft. long, 9 ft. 8 in. beam, gross tonnage 22·5—a giant compared with the gallant little *Firefly*, 38 ft. long, which we bought in 1889 and used hard for three years, or her successor *Pansy* of about the same size, given a bad name and sold again. That the prompt purchase of *Busy Bee* was wise is fairly proved by the fact that she served us well for five years, increasing our effective work nearer 100% than 50%. Allen paid £605 for her, spent about £85 in giving her a steam winch and other fittings for our work, and sold her in 1901 for £700.

In 1897 she replaced the hired sailing trawler with which sample periodic trawls had been made in the (nominally) closed bays since October 1895. She was a movable centre of work on such occasions, spending a fortnight each at Exmouth, Dartmouth and Falmouth. She worked hard, well and cheaply, but by 1901 Allen began to feel her too small. Our researches extended farther and farther into and up and down the Channel, for safety we needed something more powerful and for accommodation something larger; for each reason something beamier.

Keeping a watch on the lists of yachts for sale, Allen at length saw an offer which seemed very likely. The *Oithona* was a schooner steam yacht, 84 ft. long, 16 ft. beam, gross tonnage 69. Writing from memory, she had been built in 1876, but her engines were younger, she had been in the hands of a wealthy owner and—which attracted us most—her last cruise was all round Great Britain. A yacht 25 years old is not everyone's meat: she had been on the hard at Southampton all a year, and her price was now very moderate.

I think Allen and Beaumont went over to Southampton to look at her and that then Allen had her surveyed. Everything in her was of the very best quality, but her boiler was near its last legs. Allen bought her, with some small expenses, for £858. 8*s.* making £12. 10*s.* a ton as against £27 a ton for *Busy Bee* with a sound boiler.

There were of course alterations to be paid for, including the essential steam winch and deckhouse laboratory. When they were finished and she got to work, Allen was met by the verdict, 'That she is not a good sea boat and cannot be trusted to go far in doubtful weather.' For a vessel which has carried an expensive family all round Britain this seemed a strange conclusion. If it was final we had thrown away our chance—but the circumnavigation was a definite fact. We arranged to make our own judgement and took her out on a short trip when there was a good sailing breeze from the south-west.

There was no doubt, she was a wet ship! We met only little waves, but every one we went into came down on her deck. In a rough sea, clearly she would not only be uncomfortable, she would be alarming. We considered the matter carefully, there on board. Since her voyage from Lands End to John o' Groats and back we had added above deck level a heavy winch and a deck-house. These must be compensated, and to cure her dipping her nose we must lighten the bows.

Her chain cable was coiled absolutely in her eyes, resting on the inner surface of the cutwater. We ordered that to be coiled a few feet farther aft, behind a low bulkhead. There were two rather stouter chains as bowsprit shrouds, we condemned them. Then Allen became relentless—the bowsprit must go and be replaced by a light pole! It was a *beautiful* spar, and its great length finished her graceful proportions, but he was quite right: with that extreme leverage its great weight was a big load for her fine bows. So we condemned it, and one felt the trim rectified. There was still the question of buoyancy, and we now decided that her mainmast must be replaced by a pole (with the deck-house she could no longer ship a proper mainsail) and then Allen suddenly condemned the handsome teak panels which lined the bulwarks. It seemed a great pity—but teak is a heavy wood and 200 × 3 ft. of it a weighty deck ornament. I forget the weight that we estimated we were removing, but when we next went on the *Oithona* her deck remained dry, and she presently took on as her job a triangular voyage with its base over the Continental Shelf.

In her fourth year Allen replaced her long-suffering boiler and gave her a refit costing £847, so that with the winch, etc. she stood us in £1864. She was worth every penny of it. We worked her for some twenty years and sold her after the War to a Belgian biological station for £775. She was then due for extensive repairs—boiler-casing gone and boiler not too grand—and with the more extensive voyages we were undertaking (to trace the supplies of water to the Channel) we wanted something that was built to rough it: Allen did not like sending her to rough weather out of soundings. He felt very strongly his responsibility for the lives of those on our ships; he used to arrange for the *Huxley* to take the winter quarterly voyage when we were still doing the International Investigations.

We parted from the *Oithona* with great regret, she was a kindly ship.

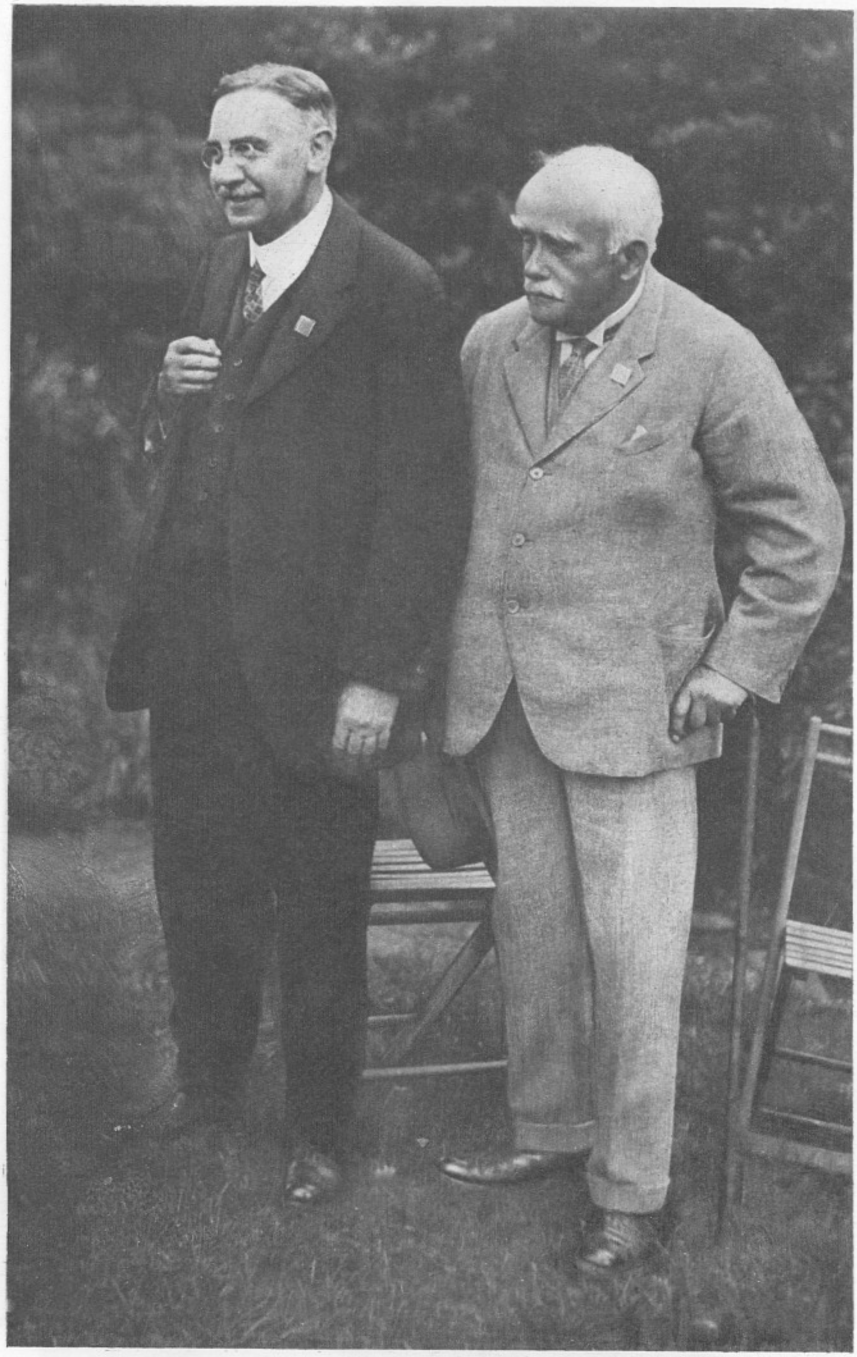
The *Huxley* was bought by Allen and me at Grimsby, but I made Allen speak the deciding word as to the price. When she was sold, the profits on the whole transaction founded the 'Ray Lankester Investigatorship'. *Salpa* was wished on us by the Government and her price fixed. The *Huxley*, *Oithona* and *Busy Bee* were each thoroughly profitable as monetary investments, their purchase having been settled by Dr Allen, the specialist on the nervous system of embryonic crustacea.

I lived at Plymouth for four years (1898–1902), so our friendship became very intimate, the more as I was elected to the Council in 1899, so that we collaborated at the Council table as well as in the Laboratory. In 1898 Browne's plungers were in use—the first had been set in motion on September 4

1897. At this time Allen and Browne were still experimenting on arranging an inverted funnel as a plunger so that it emits at its lowest position a continuous stream of air-bubbles (now known to be a work of superfluity). The plunger has made a revolution in all aquatic biological laboratory research and made easy what used to be impossible. But few who have not read Browne's paper (*J. Mar. Biol. Ass.* vol. V, p. 180) appreciate Allen's share in the invention: Browne says, 'It was his suggestions which led to the plunger being worked by such a simple method.' Browne's part was the discovery that the essential to healthy aquatic life is the movement of the water, Allen's part was the siphoned jar for a motor, which put the plunger at the disposal of the humblest laboratory that owns a tap.

Garstang returned in June 1897 as Naturalist, starting in that capacity a successful partnership of work with Allen as Director which lasted until, ten years later, Garstang was appointed Professor of Zoology in Leeds University. His lively and original mind helped to develop the fishery side of our investigations, particularly as to the passage of sea water into and up the Channel, to test which he instituted considerable bottle experiments and treated the results with great ingenuity. The following five years saw much good work done at the Laboratory with increasing efficiency and smoothness; but the bitter shortness of funds still continued. With Bles succeeding Calderwood as Director, the receipts for 1892–3, deducting donations and composition fees, were £1932. 16*s.* 6*d.* In 1897–8, the fourth year of Allen's directorship, the receipts after deducting donations and composition fees were £1973. 13*s.* 2*d.* and the donations and composition fees deducted were only £65. 9*s.* whereas in 1892–3 they were £226. 5*s.* 6*d.*: so that Allen had the spending of £160 less than Calderwood and Bles. Allen had done splendidly; there were twice the number of visiting naturalists, our capable little *Busy Bee* was working hard, our scanty salaries fund was stretched to cover a small staff, competent although disgracefully ill-paid, all kinds of people were working hard. The *Journal* shows a very fine output of valuable work, both from staff and visitors. Yet to keep up that great building, with engine, pumps, Laboratory and Aquarium, to keep our fishing yacht collecting, to pay all wages ashore and afloat, the salaries of the Director and Naturalist and anything that we could squeeze out from time to time for additional help in investigation, we received still under £2000; say, the family expenses of two average professional men in Kensington.

In 1899 Allen was getting very much discouraged. It was not only that he had to save candle-ends and starve his staff, it was the absence of prospect of anything better. And indeed five years later the Plymouth income was actually no more, though the gross receipts were £100 higher because of increased sale of specimens and of fishing gear, which involved fully the £100 in extra expenses. Allen talked to me seriously of throwing it up and earning his money in something that was not heart-breaking—perhaps business? The only post to which I could have helped him would have been a business one at about



Dr E. J. Allen and Prof. E. W. MacBride
British Association, Leeds, 1927

the salary he was earning but not taking a third of the amount of work, so that he would have had more time for researches. To my great relief—as a member of the M.B.A.—this did not tempt him, and he put his neck into the yoke again.

Then in 1902 came the dawn! The Government agreed to take part in the International Exploration of the North Sea, and invited the M.B.A. to undertake England's share in the work for three years, offering us £18,500 for the whole job. The one saving clause was that in the 6 months to March 31, 1903 we were to receive £7200, leaving £11,300 (really £5500 a year) to March 31, 1905. This enabled us to pay the rent for the *Huxley*, of £870 a year, with £2000 down and £305 a year in the second and third years, easing the latter years and knocking some 40% off the cash to be found for purchase of the *Huxley*; hence the result already recounted. The International Investigation money was of course for the staffing and maintenance of the research vessel and a shore laboratory at the harbour where she was based. Little money came Plymouth way; but Allen was able to give to some of his seamen, as well as to some of his naturalists, a lift up into the Lowestoft staff; a little of the work was done by Plymouth, and in any case we were all part and parcel of the great International Exploration, and no longer a voice crying in the wilderness.

Yet, when it was all over, and Lowestoft handed to the Board of Agriculture and Fisheries, and the *Huxley* sold, and Garstang teaching at Leeds—we were a little better off, but not much. The *Huxley* was sold in 1910 and the Development Commission gave us £500 a year in consideration of our doing some work for the International Investigation which could be better done by us than by the Agriculture and Fishery Board at Lowestoft. The Worshipful Company of Fishmongers now gave us £600 a year. Allen improved the tank room and receipts increased, more tables were rented, the prices of our specimen trade were increased and it more nearly paid its expenses. In 1914 our total income was close on £3500; the Director's salary was raised to the princely sum of £300, but what pleased him much more was that instead of only a Naturalist working under him he now had a Hydrographer, Senior Naturalist, Second Naturalist, Additional Naturalist and Assistant Naturalist. There was nothing grand about the scale of the Laboratory of the Marine Biological Association of the United Kingdom, nor fitting to the dignity of the United Kingdom; but the 70% addition to our gross income made it a place where one had not the piteous sense of wasted work and opportunity which was so oppressive before 1903: it was modest, and everyone was underpaid, but it was efficient.

Then, after the War, when the other biological stations sent S.O.S. appeals to the Government to save them from extinction, we started building.

Sir W. B. Hardy guided with genius the reorganization of biological effort in Britain to receive the benefits of the Development Fund through the

Ministry of Agriculture and Fisheries. It was for us the transformation scene of the pantomine. Allen's long labour was at length not in vain, the last third of his Directorship was passed at the head of the leading Marine Biological Station of the world, adequately maintained. The balance-sheet for 1926–7 shows as salaries: 'Director £1062. 10*s*., Physiologist £910, Naturalists £3211. 15*s*. 4*d*., Hydrographer £538. 6*s*. 8*d*.', making in themselves a total of three times the whole expenditure of 1895.

It was a great happiness to him to be the much loved head of this fine machine. The last time I went round with him as Director there were eighty biologists working in the Laboratory, yet we could both remember its echoing to our footsteps in 1894. To have wrought that change was a life's work of which a man might well feel proud.

I have not written of his research. It is not for me to appraise it; that has been done by every reading zoologist and especially by the Councils of the Royal Society and the Linnean Society. I think if he had been working as the Fellow of a College, instead of Director of the Laboratory, he would probably have kept on at the crustacean nerves and other histological work that suggested itself: he had the delight which only the histologist knows in looking with high magnification at the form and structure of cells. Exigencies of his organized survey turned him to polychaetes, and he then became extremely interested in the mysteries of regeneration. The water question—how to keep delicate organisms alive in a laboratory, he regarded as challenging every biologist with its urgency and its difficulty. He had taken up the glove and waged the battle for fifteen years. There again, in dutifully solving the problem obstructing our research, he discovered that no artificial sea water would grow more than a tiny tuft of diatoms, but that if 10 c.c. of real sea water were added to the litre and the whole sterilized—then the diatoms filled the jar. Hopkins had just published his 'vitamines' and the comparison interested them both extremely.

I think that in science, as in administration and in business, his leading talent was the rare one of discerning the essential.

But a picture of Allen's intellectual equipment is not given by describing alone the excellence of his research and the insight of his philosophical writing (Presidential Address, British Association, Section D, 1922; Hooker Lecture 1929, *Proc. Linn. Soc.*). Though it never made him dissipate his energies, he had the delightful gift of interest in everything. He said to me once in the 'nineties that people talked a great deal of rubbish about the oppressive mass of zoological literature, that it was perfectly possible to read it all as it came out, more or less carefully according to the paper, and that, so far as the available libraries went, he did it. Thirty years later he said, 'It is now completely impossible'; but the width of his biological reading was equalled by only a few men whom I have known. What you only found out by degrees was the extent to which he kept himself up to date in physiology, chemistry and physics; what you might never find out was the amount of his general reading and his keen love of poetry.

Given this mind and this learning, with the invention that devises new methods and new lines of research, adding to it his unlimited sympathy and great unselfishness, it is possible to understand how it was that few of those who worked at Plymouth ever failed to receive valuable help from the Director. His unswervingly honest mind and sensitive kindness made him the ideal critic. In the second and third decades of this century he became really important in the zoological world; I thought at one time that in him we were going to see again someone who could be called the leader of contemporary English zoology—but Lankester was the last who could be given that title and will remain the last. There was, however, no question of the widespread respect and affection shown to Allen wherever zoologists met together, and well-deserved distinctions began now to come fast. F.R.S. in 1914 was followed by the presidencies of the Devonshire Association in 1916 and of Section D of the British Association in 1922; a year later Denmark gave him the Hansen Memorial Medal and Prize, three years after that the Linnean Society awarded Allen their Gold Medal and in 1929 he gave their Hooker Lecture. Edinburgh conferred on him the Hon. LL.D.; he was made Foreign Member of the Royal Academy, Denmark; in 1935 he received his C.B.E. followed in 1936 by the Darwin Medal of the Royal Society and the Agassiz Medal for Oceanography from the National Academy of Sciences, Washington. University College, London, elected him a Fellow in 1939.

An end comes to everything, and in 1935 he told the Council that he wished to resign. He was sixty-nine and he felt the work too heavy for him. At the Council's request he agreed to stay on to September of the following year, but six weeks before the appointed terminus he was taken seriously ill and had to have an operation. While he was laid aside, his colleagues effected the transfer of his possessions to rooms already chosen in Reservoir House, Skardon Place, belonging to Mrs Sexton, his connexion by marriage as well as a valued colleague and collaborator; so when he left the nursing hostel he moved into his new home. It is a house of the Regency time, with the grace of proportion belonging to its period: the bow windows of his sitting-room looked over the garden to the reservoir; over the roofs beyond the water he saw Staddon Heights and the Sound. The attractive old garden, made pretty by Mrs Sexton's discerning care, is bounded by a low wall which forms the top of the reservoir retaining wall; the place offered a pleasant harbour for last moorings.

Here he set to work to cultivate wood-lice, and found them extremely interesting—as he would have found cockroaches or frogs or mustard and cress. But after two or three years he had to give up research because he found his memory had gone too much (the biographers tell the same of Faraday). When I was last at Plymouth, two years ago, he was hard at work reading modern physics, particularly the text-book just published in joint authorship by his brother and his sister's son, Roland Maxwell. 'I forget it all entirely in three months, but that does not spoil the interest.'

He was quietly happy, walking over to the Laboratory several times a week, and in contact with many old friends; but I think he found his rooms a little solitary after having lived a third of a century in the focus of a busy hive. He enjoyed his very occasional sallies up to London to stay with relations and friends and go to a meeting or two. He was up in April 1942 and spent 24th–29th at Cambridge, happy and making others happy. In November he had some bronchial trouble and was poorly the first days of December. By December 4th he seemed to have thrown it all off. He died suddenly and painlessly on the morning of December 7.

Allen was the best-loved of British zoologists, of whom most hailed him as a personal friend. With a shy manner, he was always unobtrusive and rather silent, always helpful, always transparently honest intellectually and morally, and always kind. He had a delicate reverence for women which they completely appreciated and he was delightful with children, who were all ready to adopt him as a new uncle or grandfather. With all his friendships, however, family affection held the central place with him. Very early in his directorship he brightened the Director's House with a long stay from his fifteen-year-old sister. I often heard of his brothers: it is unusual for two brothers each to be a Fellow of the Royal Society (Professor H. S. Allen, F.R.S., of St Andrews, is his younger brother), but he told me that their eldest brother Dr H. N. Allen (Principal of the Poonah College of Science), who died in 1932, was abler than either of them. When he received his own F.R.S. in 1914 and I congratulated him, he said bitterly, 'Why didn't it come when I should have valued it, it is too late now'—the value of such things being to show one's parents. That was temporary, his well-earned honours were not lost on him.

I knew Allen for half a century and I never knew him do a mean thing or a selfish thing. He was understandingly sympathetic and unfailingly helpful. Of all his gifts, his greatest excellency was as a friend.

G. P. B.

(*The plate facing page* 680 *is reproduced by courtesy of The Yorkshire Evening Post.*)

STUDIES IN THE FUNCTIONAL MORPHOLOGY AND EMBRYOLOGY OF *ONCHIDELLA CELTICA* (FORBES AND HANLEY) AND THEIR BEARING ON ITS RELATIONSHIPS

By Vera Fretter

Departments of Zoology, Birkbeck and Royal Holloway Colleges,
University of London

(Text-figs. 1–6)

CONTENTS

INTRODUCTION

Onchidella celtica, the only British representative of the family Onchidiidae, lives between tide marks in crevices of eroded rocks on the north and south Cornish coasts. Along the exposed southern coast between Rame Head and Looe many of the rocks rise to a steep escarpment on the north side, and here in the sloping crevices, sheltered from wave action and from strong sunlight, the animals are found in considerable numbers. They occur a few feet down from high-water mark, not above it as mentioned by Ellis (1926), and some are found in rocks uncovered only at low tide. They live in communities ranging from two or three individuals to over sixty, and in each community animals of varying ages are found. On warm days, and when uncovered by the ebbing tide, the molluscs emerge from their shelter in search of food, but during the colder months, between November and March, they remain in the rock crevices; then they are very inactive and pass through a period of hibernation. A similar annual period of limited activity is described by Arey & Crozier (1921) for *Onchidium verruculatum*.

When wandering over the rocks *Onchidella celtica* avoids long exposure to strong sunlight and the wind-swept surfaces; in stormy weather it does not appear. Not every animal emerges at an appropriate tide, though the majority are active on still summer days when the sky is overcast, or there is a heavy sea mist, and then they may browse on the southern slopes of the rocks which are not visited in sunny weather. Their food consists of young algae and encrusting diatoms, and in search of these they travel with considerable rapidity: the sensory lobes of the head always in contact with the substrate, the tentacles protruding from under the anterior margin of the mantle, and the posterior edge of the mantle upturned to expose the pulmonary aperture, which is then widely open. They may wander a yard or so from the rock crevice from which they emerged, selecting food at intervals and eating it ravenously, or their journey may only be a few inches; they frequently visit the beds of young mussels or barnacles to rasp the organisms which settle on the shells. At the rising tide the molluscs retreat to their shelter and this they reach before the water covers them. Although some exceptions have been observed, on the whole each animal returns to its own particular crevice, or one near by; the exact path of the outward journey is not retraced. This homing habit has been previously observed in *Onchidium floridanum* (Arey & Crozier, 1921), which lives on the shore rocks at Bermuda. The crevice which is chosen may have an extremely small opening to the exterior, is always sandy, and mingled with the sand are diatoms washed in by the waves; these the animals often eat. Forbes & Hanley (1853), in citing observations made by Mr Couch, state that *Onchidella celtica* occurs between Polperro and Fowey about a foot or two from the sea, and migrates up and down the shore as the tide rises and falls to maintain its distance from the water. No such migration has ever been seen and the animals appear to live at the same level throughout the year. During the summer months the egg capsules are laid in the rock crevices inhabited by the adults, and within the capsules the embryos develop to a creeping stage which superficially resembles the parent.

The anatomy and development of *O. celtica* have been described by Joyeux-Laffuie (1882). This is the only member of the Onchidiidae in which the development has been studied. No sections were made of the embryos and this probably accounts for his misinterpretation of some points in their structure, and his failure to elucidate from the development certain features in the anatomy of the adult. A little histology of the alimentary and reproductive systems of the adult is given, but the correlation between the structure and function of the various organs is only slight. Although Joyeux-Laffuie mistook the lung of *O. celtica* for a kidney which had acquired some respiratory function, yet he recognized the mollusc as a pulmonate which in some features approached the nudibranchs; with this Brock (1883) agreed. Since Cuvier (1804) described the anatomy of *Onchidium Peronii* and pointed out its close resemblance to the slugs, most investigators have accepted the Onchidiidae as pulmonates, though their exact affinities within this subclass have been subject to controversy; in a number of characters they stand isolated from the air-breathing molluscs. Bergh (1885) states that they are derived from land snails, and represent a terminal twig in the evolution of the Stylommatophora. On the contrary, Plate (1893), who studied the anatomy of several members of the family, concluded that their origin must be sought in the tectibranch opisthobranchs, and hence he considers that they are more closely allied to the Basommatophora. Von Wissel (1898) maintains that they approach this order more closely, though he is unable to decide whether they are primitive or degenerate. In a comparatively recent paper Labbé (1934) describes the occurrence of siliceous spicules in the tissues of several members of the Onchidiidae, and he claims strong opisthobranch affinities for the group, consequently he renames it the Silicodermatae and places it under the opisthobranchs. The pulmonates he groups with the prosobranchs and gives the following classification of the gastropods:

Prosobranchs: Prosobranchs *sensu stricto*;
Pulmonates.

Opisthobranchs: Opisthobranchs *sensu stricto*;
Silicodermatae.

The work here recorded was done at the Marine Laboratory, Plymouth, and at Birkbeck and Royal Holloway Colleges. I wish to express my indebtedness to the University of London for the use of their table at the Plymouth Laboratory, and to Birkbeck College for a grant towards the cost of publication.

The Alimentary Canal

The head lies between the anterior edge of the mantle (Fig. 1 A, *am*), which covers it dorsally, and the foot (*f*), and is separated from the latter by a deep groove which leads to the opening of the pedal mucous gland (*o*). The mouth (*m*) is ventral, and when the animal is not feeding it appears as a longitudinal slit, bordered on each side by a muscular and sensory lobe (*sl*) which has a broad, flat, ventral surface. Dorsal to each lobe is a tentacle (*t*), black in colour as the rest of the head and bearing an eye (*e*) at its apex. When the animal is resting in the rock, or if it is disturbed during its perambulations, the tentacles are invaginated and completely withdrawn, and the whole head region may be protected by the anterior border of the foot covering it ventrally. The mouth leads into a short oral tube which is a ventral prolongation of the buccal cavity and can be closed by a sphincter. The sensory lobes and the oral tube are covered by a cuticularized, columnar epithelium, through which penetrate the ducts of subepithelial glands. Some of these are mucous cells producing secretion for the lubrication of the surfaces; others are plentiful on the sensory lobes and contain small colourless spherules—not dissolved in any fixative, staining black with iron haematoxylin and probably secreting a cement. On the anterior wall of the oral tube, below the point at which it opens into the buccal cavity, the cuticle is thickened to form a transverse ridge with a sharp and slightly irregular summit. The ridge acts as a jaw against which the radula can work, and assists in biting the food which is drawn in by the radula. A mid-dorsal ciliated channel runs down the length of the buccal cavity to the oesophagus, and is separated from the more ventral part of the cavity by a longitudinal fold of connective tissue on each side. The ventral part is covered by cuticularized columnar cells, and its floor is hidden by the odontophore which projects forwards to the oral tube. A large number of mucous cells lie in the connective tissue beneath the epithelium and open between the columnar cells. Ventral to the anterior tip of each longitudinal fold is the opening of a salivary duct which passes back and penetrates the buccal musculature; when free from this it swells into a small vesicle which is surrounded by a thick coat of circular muscles, and then runs down the side of the buccal mass for a short distance to be encircled by the white flocculent lobes of the gland. This spreads ventrally to the nerve ring, to which it is attached by connective tissue. The gland is made up of mucous cells, and scattered rather infrequently among these are secreting cells of a different type: their protoplasm is vacuolated and the vacuoles contain small spherules which stain deeply with iron haematoxylin and orange or red with azan. The cells, all with large nuclei and well-marked nucleoli, are grouped in clusters, and from each of these a short duct opens into the main salivary duct, which is also

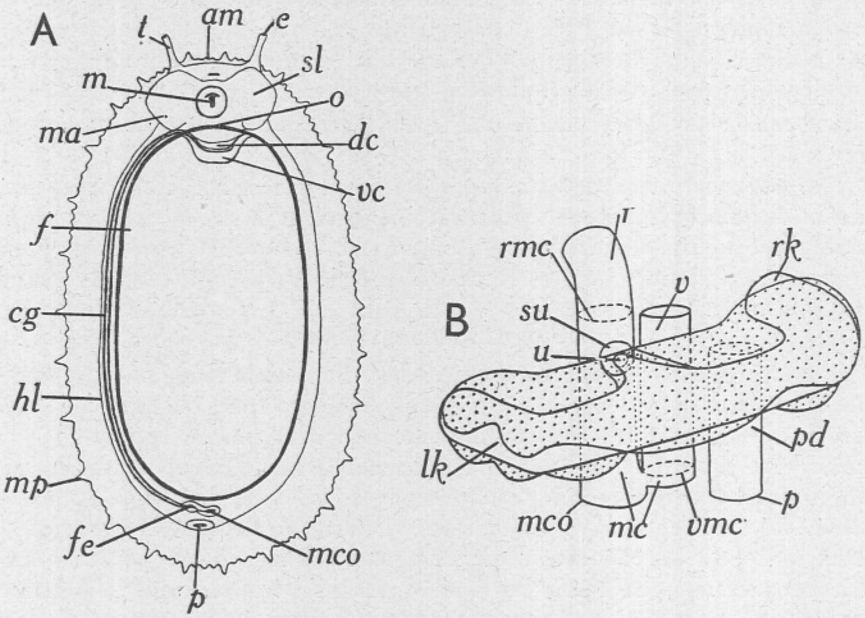


Fig. 1. A. Diagrammatic ventral view of *Onchidella celtica* showing the position of the external apertures and the course of the ciliated groove: ×4. B. Diagram showing the opening of the rectum, secondary ureter and vagina into the mantle cavity, and the position of the pulmonary duct. The stippled area represents the lung wrapped around the kidney: × about 8. *am*, anterior edge of mantle; *cg*, ciliated groove; *dc*, dorsal chamber of pedal mucous gland; *e*, eye; *f*, foot; *fe*, female aperture; *hl*, hyponotal line; *lk*, left limb of kidney; *m*, mouth; *ma*, male opening situated beneath sensory lobe; *mc*, mantle cavity; *mco*, opening of mantle cavity previously called anus; *mp*, marginal papilla; *o*, opening of pedal mucous gland; *p*, pneumostome; *pd*, pulmonary duct; *r*, rectum; *rk*, right limb of kidney; *rmc*, opening of rectum into mantle cavity; *sl*, sensory lobe; *su*, opening of secondary ureter; *t*, tentacle; *u*, opening of primary ureter; *v*, vagina; *vc*, ventral chamber of pedal mucous gland; *vmc*, opening of vagina into mantle cavity.

surrounded throughout this part of its course by gland cells. The ducts are ciliated and between the epithelial cells open the surrounding gland cells. Their secretion is passed along the ducts by the cilia, and pumped into the buccal cavity by the muscular vesicle. In the connective tissue which binds the gland cells together are a few muscle fibres.

The two dorso-lateral longitudinal folds of the buccal cavity extend towards the middle line and fuse with one another at their free edges at the beginning of the oesophagus, so that the ciliated dorsal channel runs imperceptibly into the oesophagus. This is directed back over the buccal mass and curves ventrally to pass through the nerve ring. Behind the nerve ring it forms a capacious crop which describes a curve to the left before leading back to the stomach. The whole oesophagus is characterized by a well-developed musculature. The lining is thrown into pliable longitudinal folds (Fig. 2, *lf*) by the variation in thickness of the underlying connective tissue; when the crop is full the folds are completely obliterated. Joyeux-Laffuie (1882) states that they increase the absorbing area, but no absorption takes place in this part of the gut. The epithelium is composed of columnar cells, which are ciliated in the anterior oesophagus as far as a region just behind the nerve ring and in the posterior part of the tube which opens into the stomach; between these two areas the epithelium is cuticularized. The nuclei lie towards the base of the cells, and above them the cytoplasm contains small yellow pigment granules. A large number of mucous cells are distributed in and below the epithelium, most numerous in the anterior oesophagus. Circular and longitudinal muscles run through the connective tissue and radial muscles penetrate the folds; the circular muscles form a sphincter around the entrance to the buccal cavity and the stomach.

The structure of the stomach may best be studied when it is filled with food (Fig. 2), for when empty the thin-walled regions are contracted and their full extent is not realized. The most conspicuous feature is the large globular triturating sac or gizzard with its massive dorsal (*d*) and ventral (*v*) plates, which are hinged to one another laterally. The oesophagus (*oe*) does not open directly into this sac, but communicates with its anterior end through the thin-walled initial chamber (*ic*) of the stomach. This receives anteriorly and dorsally the right (*rd*) and left (*ld*) ducts from the corresponding anterior lobes of the digestive gland. The intestine likewise is separated from the gizzard by a distensible pouch, the terminal chamber of the stomach (*tc*), and this overlies the initial chamber. The terminal chamber opens ventrally into the initial chamber and posteriorly into the gizzard. From each of the two anterior digestive gland ducts emerges a fold, the two folds running back parallel with one another along the dorsal wall of the initial chamber and then curving dorsally into the terminal chamber, along the ventral wall of which they pass forwards. These longitudinal folds, separated only by a deep gulley, terminate in a small caecum (*c*) which occupies a mid-ventral position at the origin of the intestine (*i*). The left one is larger than the right and curves around the left and posterior margins of the opening of the caecum before entering it; the right fold runs straight into the pouch. The excretory matter from the anterior ducts of the digestive gland is directed along the folds and so by-passes the triturating stomach. Similar longitudinal folds are described and figured by Plate (1893) for *Onchidium verruculatum*, and their occurrence in such diverse groups of the gastropods as chitons (Fretter, 1937), *Patella* (Graham, 1932) and tectibranchs (Fretter, 1939) suggests that they constitute one of the characteristic features of the gastropod stomach. There is a third liver duct in *Onchidella* (*pd*) which arises from the distensible posterior wall (*pw*) of the gizzard, and passes ventrally to the smallest of the three lobes. The excretory matter from this less important duct has no directed course to the intestine. When the stomach is empty it can be seen that the longitudinal folds of the oesophagus (*lf*) continue down the ventral and lateral walls of the initial chamber. This is ciliated and rich in mucous cells; in histological detail and in musculature it resembles the posterior oesophagus. The histology and musculature of the terminal chamber is also similar, but the epithelium is more deeply folded. The folds (*ft*) arise at the opening into the triturating stomach and pass to the region of the caecum, where they end abruptly. Epithelial mucous cells are frequent, increasing in number towards the caecum, in which they are sufficiently numerous to alternate with the ciliated columnar cells. Their cytoplasm, which is vacuolated and contains small colourless secretion spherules, stains with iron haematoxylin; it is little affected by mucicarmine, though the discharged secretion, which usually fills the pouch, is susceptible to this stain. The nuclei of the secreting cells are round, basal and nucleolated. The caecum is muscular and the muscle fibres are mainly circular in direction. The dorsal gizzard plate (*d*) lies anterior to the ventral one (*v*). Their crushing surfaces are covered by a smooth cuticle, and the

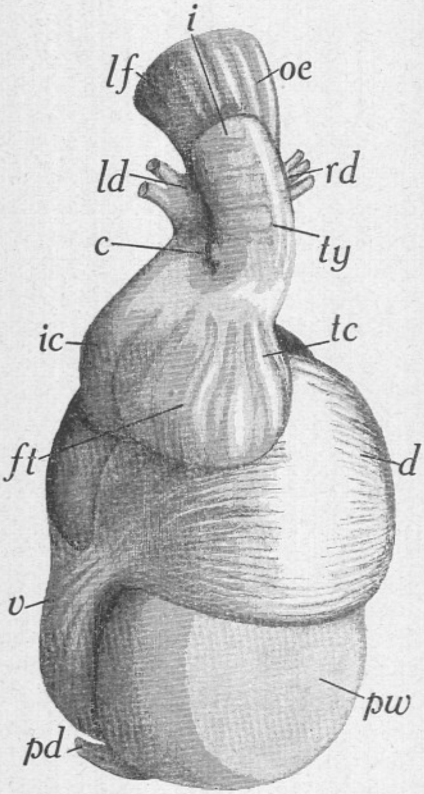


Fig. 2. Distended stomach seen from above and slightly to the left: × 17. *c*, caecum; *d*, dorsal plate; *ft*, longitudinal fold of terminal chamber; *i*, intestine; *ic*, initial chamber; *ld*, left duct of digestive gland; *lf*, longitudinal fold of oesophagus; *oe*, oesophagus; *pd*, posterior duct of digestive gland; *pw*, distensible posterior wall; *rd*, right duct of digestive gland; *tc*, terminal chamber; *ty*, typhlosole; *v*, ventral plate.

subepithelial tissue comprises alternating bands of circular and longitudinal muscles. Laterally the muscle layers are thin and are covered externally by compact connective tissue which binds the two plates together. Elsewhere the walls of the gizzard are lined by columnar ciliated cells, and are thrown into deep longitudinal folds when the stomach is empty; a thick layer of circular and longitudinal muscles surrounds the epithelium and assists the triturating action. In the epithelium which secretes the thick cuticle of the plates the cytoplasm is vacuolated, and immediately above the basal nuclei it contains, in each cell, a small clump of darkly staining spherules; distally a few pigment granules may be seen—these are most distinct in young animals in which the cuticle is thin. Fibrillae run through the cytoplasm and merge into the most recently secreted cuticle, which stains lightly with iron haematoxylin and blue with azan. The older part has a different staining reaction and is black after iron haematoxylin and red with azan.

The digestive gland lies dorsal to the reproductive organs and for the most part anterior to them. Of the three lobes the posterior one is by far the smallest; it embraces the posterior wall of the triturating stomach and spreads beneath it. The right and left anterior lobes extend anteriorly as far as the buccal mass, covering on their respective sides the oesophagus and stomach, and the right mass forms a packing for the coils of the intestine. Blood vessels, opaque white in colour since they are coated in tissue rich in crystals of some calcium salt, branch over the surface of the gland. The epithelium is composed of three types of cells arranged according to a definite plan. The most frequent type is the digestive cell, which lines the tubules except in the crypts at the angles of the wall, and here the two other types, the excretory and lime cells, occur exclusively. The digestive cell arises from a narrow base to a height which exceeds that of the other cells. The distal border is regular and slightly rounded in starved animals, but in animals which have recently fed it has an irregular outline. The cytoplasm is vacuolated throughout and the oval nucleus, with a very definite nucleolus, lies towards the base. The vacuoles are smallest at the free ends of the cells, where the cytoplasm is more dense, and they increase in size proximally. The tiny vacuoles contain colourless secretory spherules, and the deeper ones are filled with brown or green particles which, immediately above and below the nucleus, may be aggregated into large clumps. Fat droplets are also found in vacuoles in the more distal cytoplasm. In the crypts, which are constricted off from the rest of the tubule so as to project into the haemocoel, the excretory cells are frequently clustered around the lime cells. They are club-shaped with a rounded free end and are taller than the lime cells which are triangular in longitudinal section with a broad base. The cytoplasm of the excretory cells is vacuolated and the vacuoles contain brown homogeneous spherules of excretory matter which are not dissolved in any fixative. They vary in size: there may be a large number of tiny brown spherules in one cell, or fewer spherules of a larger dimension, or all may be fused into one dark brown clump. The nucleus lies beneath the excretory masses, and is readily distinguished from the nucleus of the lime cell which is larger and has a more prominent nucleolus. In the lime cells the cytoplasm is dense and very vacuolated, and the vacuoles are filled with lime spherules.

From the terminal chamber of the stomach the intestine passes over the surface of the digestive gland, and just beneath the buccal mass, to the right side of the body cavity. It dips ventrally under the anterior aorta and then curves dorsally again to describe an anterior U-shaped loop. From this it leads back, above the digestive gland and the reproductive organs, to a mid-ventral opening behind the posterior edge of the foot. The intestine possesses throughout its length a dorsal typhlosole (Fig. 2, *ty*) which arises opposite the ventral caecum of the stomach. The epithelium is thrown into folds which, together with the typhlosole, are formed by variations in the thickness of the underlying connective tissue. In the anterior part of the intestine, and up to the point at which it passes beneath the aorta, folds arise on either side of the typhlosole, and each runs obliquely backwards around the lateral wall to terminate mid-ventrally. In the posterior part of the tube the folds are directed longitudinally and, except in the rectum, are less pronounced. The columnar ciliated epithelium is taller over the typhlosole than elsewhere and is rich in gland cells. These are of two kinds—mucous cells and club-shaped cells which are filled with small spherules and have a more limited distribution: few are found at the anterior end of the intestine, they increase in number towards the dorsal loop, in which they are numerous, and beyond this are entirely lacking. The spherules stain black with iron haematoxylin and red with azan: when secreted they swell to form a white viscid fluid which binds together the faecal matter. Such cells are not found in the epithelium of the typhlosole. Mucous cells occur in all parts of the epithelium; they are most abundant in the anterior intestine and some lie in the connective tissue beneath the typhlosole. The cytoplasm of the ciliated cells contains small pigment granules which impart to the wall its yellowish brown colour. A double muscular coat consisting of inner circular and outer longitudinal layers surrounds the epithelium, and radial muscles run through the connective tissue of the folds.

When the animal starts off on its feeding foray the crop and stomach are empty of food, containing only a brownish fluid, with a few sand grains in the triturating stomach; when it returns both are fully distended and the contents consist mainly of pieces of algae—filaments up to a centimetre or more in length—and innumerable diatoms. Mixed with these there may be scraps of sponges, foraminiferans such as *Polystomella* and *Gromia*, and a mass of sand and detritus. The food is rasped from the rock surface and drawn into the dorsal part of the buccal cavity by the radula, while the sensory lobes take a firm grip of the feeding ground to anchor the head in position. The radula works against the chitinous jaw and is lubricated by a copious secretion of saliva. The viscid salivary fluid also binds together the food particles. The cilia on the dorsal channel and the anterior oesophagus help to direct the food into the crop, although here, as in other parts of the gut, its passage is mainly effected by muscular action. It is passed into the stomach as more food is taken in, and both regions of the gut act as a storage place; the contents are digested at leisure during the full tide.

The lumina of the tubules of the digestive gland rarely contain any particulate matter: a few diatom cases may be found there, but these are not taken up by the cells of the gland—in fact no particulate matter appears to be ingested. In animals which have fed on a mixture of diatoms, algal filaments and insoluble iron saccharate the iron has never been traced into the digestive cells, though large quantities are present in the gut and a few particles in the liver tubules. If soluble iron is eaten, it is absorbed by the digestive cells and appears in a very weak solution in the terminal vacuoles. Later it passes to the deeper parts of the cytoplasm and is adsorbed to the green and brown masses which fill the vacuoles—these are apparently accumulations of excretory matter, and at intervals they are expelled from the cells and passed to the intestine. Such observations suggest that only the soluble products of the food are ingested by the digestive gland, and that particulate matter is only carried into the ducts accidentally. Throughout the gut there is no other site of absorption. The ingesting cells have also a secretory function and the free tips of the cells, which contain small spherules, are cut off from the epithelium and pass into the stomach and crop.

An examination of the faeces shows that a large part of the food which is eaten is indigestible since no cellulase appears to be present, and some is undigested. Except for mechanical action the cell walls of the algal filaments are unaffected by their passage through the gut; it is only the contents of cells which have been opened that are utilized. The diatoms constitute a large proportion of the animal's diet and the majority of these are digested, though a number appear in the faeces still with their protoplasmic contents.

The food is crushed by the mechanical action of the stomach; when this is full all the chambers exert pressure on the contents forcing them towards the triturating sac. In this way they are compressed by the dorsal and ventral plates. At the same time the food is mixed with the enzymatic fluid secreted by the digestive gland, so that the available digestible parts are broken down. The soluble products of digestion are wrung from the food and forced into the liver ducts—the two anterior ones receiving the greatest quantity. The fluid is prevented from being regurgitated into the oesophagus by closure of the oesophageal sphincter. Whilst active the gizzard tends to rotate on its longitudinal axis, the dorsal and ventral plates swinging through less than 90° in a clockwise direction and then back to their original position. Their thick chitinous covering protects the walls against the large number of sand grains which are taken in with the food, and which also help in grinding it. The gizzard is rarely free from sand grains, and Joyeux-Laffuie (1882) considers them to be of such consequence that he likens them to the stones in the gizzard of a bird. Heidermanns (1924), in his study of freshwater pulmonates, suggests that the muscular stomach is developed in proportion to the quantity of sand eaten, and attributes to it the function of forcing the indigestible matter along the intestine. This it certainly does in *Onchidella*: when matter is to be passed from the stomach the gizzard drives its own contents forward, and since at the same time the initial chamber of the stomach contracts, the only available outlet is dorsal, into the terminal chamber, and thence to the intestine. If an animal be collected on its return from a meal and dissected about four hours later, food remains are massed in the intestine, although the crop and stomach are still amply distended. Frequently the animal takes in more food than the digestive system can cope with, and the quantity of undigested material in faeces which are discharged within a few hours after a meal is greater than that contained in later faecal masses. The pellets are rod-shaped and may be a centimetre or more in length. The sand grains, detritus, algal filaments and diatom cases, of which each is composed, are compacted and covered by a cementing fluid. Firmly attached to each pellet is a longitudinal beaded strand of excretory matter from the digestive gland, and directly opposite this is a shallow longitudinal groove—the impression of the typhlosole. The excreta from the digestive gland are moulded into characteristic form by the caecum, in which the longitudinal folds from the anterior liver ducts terminate. The flow of waste matter passing along the folds feeds the caecum, and when this is full its contents are moulded by its muscles, and cemented, by the viscid fluid from its walls, into a compact oval mass which is then expelled. A succession of pellets is thus formed connected end to end, and plastered against the flow of faecal matter from the stomach, to which it firmly adheres. This function of consolidating and moulding the faecal matter from the digestive gland is also attributed to the caecum of *Aplysia* (Howells, 1942). The small quantity of waste from the posterior liver duct is voided with the food remains from the stomach. The excretory phase of the digestive gland, which follows one of absorption, involves the digestive and excretory cells. If animals are injected with soluble iron saccharate, the iron is taken up by the three different types of cells in the gland, though most active absorption occurs in the crypts, where it either forms small spherules in the young excretory cells or is added to the brown spherules already present in the older ones. In the lime cells it appears as minute masses in the dense cytoplasm between the calcium spherules. Its ultimate fate has not been traced. Small quantities of iron are taken up by the digestive cells and accumulate with the food remains in the basal vacuoles; with these they are expelled from the distal ends of the cells and passed from the gland in the faecal stream. At the same time the oldest excretory cells, which are filled with brown spherules or in which the spherules have fused into one large clump, leave the epithelium. It would appear that the function of these cells is to take up waste matter from the blood and build it up into concentrated masses which accumulate until the cell becomes effete. A similar function has been suggested for cells in the digestive gland epithelium of tectibranchs (Fretter, 1939).

The passage through the intestine is lubricated by mucous secretion from the epithelium. The muscles of the tube compress the faecal matter and fashion it into a smooth rod, and the fluid from the club-shaped gland cells binds the particles together. Since the excretory matter from the digestive gland is directly opposite the impression made by the typhlosole, it is attractive to imagine that this structure exerts a pressure which helps the excretory matter to adhere to the faecal rod. During defaecation variable lengths of the rod are voided; the greater length of the intestine may be emptied at one time.

RESPIRATION

One of the most interesting features of the Onchidiidae is the presence of a lung which opens by a small pneumostome (Fig. 1 A, *p*) at the posterior end of the body, slightly to the right of the mid-line and behind the openings of the anus and vagina (*fe*). Owing to an inadequate knowledge of its anatomy and histology the lung has been the subject of much controversy in times past: Joyeux-Laffuie (1882) and von Jhering (1877) maintain that it is a kidney which has to some extent taken over a respiratory function, whilst Semper (1876–7) and Bergh (1885), on the contrary, state that it is primarily a respiratory organ and quite distinct from the kidney, although they maintain that the two open into one another. According to Plate (1893) it is a reduced mantle cavity which has no connexion whatsoever with the kidney, since the latter discharges through the ureter into the rectum. Von Wissel (1898) accepts this interpretation, though Haller (1894) opposes it.

When an *Onchidella* moves actively over the rocks which are uncovered by the tide, the posterior tip of the mantle is raised to expose the pulmonary aperture. This is widely open and may remain so for some minutes. The opening leads through a short duct to a spacious cavity which, in sections, can be traced forwards on either side of the median body cavity as branching diverticula; these extend to the level of the posterior end of the heart. The lung is thus U-shaped and it follows the course of the kidney with which it is closely associated. The kidney, however, extends farther forwards than the lung: its right limb spreads around the median wall of the pericardium, and under the ventral wall, as far as the anterior tip of the heart. The renopericardial duct opens into the posterior end of the pericardial cavity. The left limb is less developed than this, but passes forward to about the same level. The U-shaped part of the haemocoel, in which lie the kidney and (on the right side) the heart, is separated from the general body cavity by a muscular diaphragm. This is incomplete anteriorly on the right side, so that the lateral and median haemocoelic spaces communicate by a wide opening, and through this passes the anterior aorta. Branching diverticula of the lung penetrate between the lobes of the kidney and push into the tissues of the mantle, so that they come into intimate contact with the blood spaces.

The lips of the pneumostome are lined by a columnar ciliated epithelium which is surrounded by subepithelial mucous cells; the cilia beat out of the lung cavity and guard against the entry of small particles. A section through the delicate respiratory tissue of the lung is shown in Fig. 3A. A thin outer sheet of squamous cells (*os*) lines the cavity, and a corresponding inner layer (*is*), which rests upon the tissues of the mantle (*tm*) or the muscles surrounding the kidney tubules (*m*), runs parallel with it, the two being separated in most places by a series of channels formed by cells of similar histological character running at right angles to the two layers (*sc*). Blood from the surrounding haemocoelic spaces (*h*) runs through the network of channels, and is thus separated from the lung cavity only by the rather structureless and lightly staining outer sheet of squamous epithelium. Here and there a mucous cell pours its secretion on to the respiratory surface. Should the mollusc be immersed in water the pulmonary opening closes immediately, and, since the cavity decreases in size with the contraction of the muscles of the mantle, air escapes through it. The diaphragm and muscles

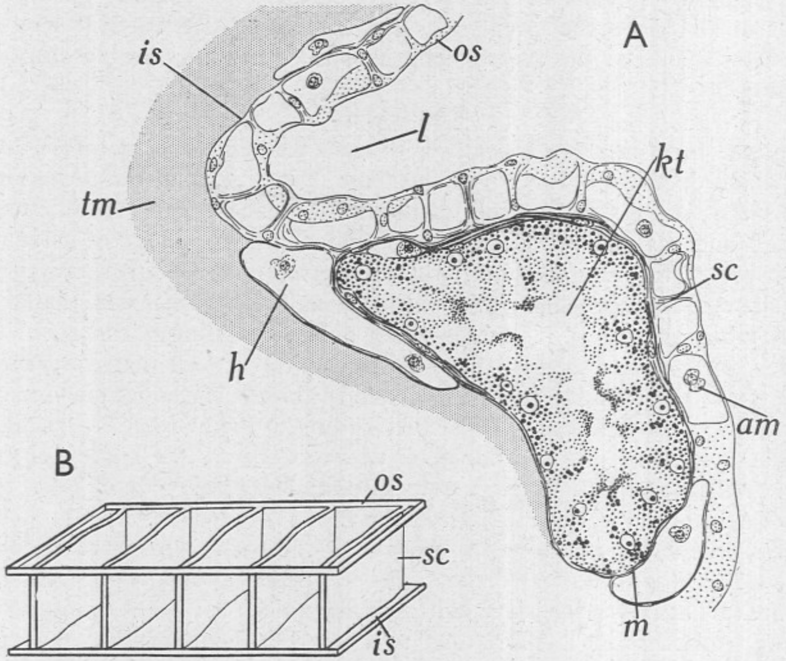


Fig. 3. A. Transverse section through wall of lung, underlying kidney tubule, mantle and associated blood spaces: ×400. B. Diagram to show arrangement of blood channels in wall of lung: ×about 580. *am*, amoebocyte in blood channel; *h*, haemocoelic space; *is*, inner sheet of squamous epithelium; *kt*, lumen of kidney tubule; *l*, lumen of lung; *m*, muscles surrounding kidney tubule; *os*, outer sheet of squamous epithelium; *sc*, squamous cells subdividing space between *is* and *os*; *tm*, tissues of mantle.

surrounding the kidney tubules may also be concerned with the ordinary respiratory movements. Normally the animal has settled in its crevice by the time of the rising tide, and the aperture has closed and remains so until the next period of activity. In the sluggish interlude pallial respiration is adequate.

The surface of the mantle is papillated and when exposed to the air is moistened by the secretion of pallial glands: these are unicellular and are grouped in clusters between the cuticularized epithelial cells. If the mollusc be removed from water and the dorsal surface thoroughly dried, it is covered, within a few minutes, by fluid from the glands. Along each side of the mantle project a number of marginal papillae (Fig. 1A, *mp*) which are larger than the rest and equidistantly placed. Each bears at its apex a small pore through which, when the animal is irritated, a spirally coiled stream of white secretion is discharged. The secretion is produced by a large flask-shaped multicellular gland, which is embedded in the thickness of the mantle at the base of the papilla (Fig. 6C, *mg*); it is squeezed from the various types of cells sharing in its composition, and forced through the long straight duct, by a surrounding muscle layer of considerable thickness. The histology of the glands appears to be similar to that of *Oncidiella* (= *Onchidella*) *marginata* and *O. juan-fernandeziana* (von Wissel, 1898). The marginal or peripheral glands in *Onchidium* are referred to by Arey & Crozier (1921) as repugnatorial glands, and it is stated that sea anemones and crabs refuse to eat food tainted with the secretion.

In *O. verruculatum* (Hirasaka, 1922) the dorsal papillae of the anterior two-thirds of the mantle bear eyes, and those of the posterior third are produced into tree-like gills. Neither of these are developed in *Onchidella*, though the respiratory importance of the mantle is very considerable owing to the interlacing network of blood capillaries below the epithelium. The mollusc can live under water for long periods, relying entirely on pallial respiration; its activities, however, are then reduced. It can also rely on this alone when it is inactive at low tide. Pulmonary respiration supplements pallial respiration when the respiratory requirements of the animal are increased during activity out of water, but experiments show that either is sufficient by itself to keep the animal alive for at least a week. If the dorsal surface be vaselined and the animal placed in a humid atmosphere, the pulmonary aperture is opened and the lung is used continuously; frequently the edges of the mantle are upturned as if in an attempt to increase the respiratory area. The behaviour appears to be more normal when the pneumostome is blocked with vaseline, and specimens thus treated may occasionally wander about, though only over a limited distance. Should both mantle and lung be thrown out of action death follows in a few hours.

Although *Onchidella* is on the whole restricted to damp situations in which the humidity conditions approach those of saturation, the fact that in mid-August it can be seen to leave the shady rock and travel over sunny surfaces, shows that it can survive, at least for a short time, in lower humidities. In order to investigate the degree of desiccation which the animal can resist specimens were subjected to relative humidities of less than 100%. The required humidities were obtained by placing dishes with sulphuric acid-water mixtures of known specific gravity in the bottom of large jam jars, and placing above the open dishes a platform of perforated zinc. Eight animals were introduced into each jar and a glass plate was sealed to the opening with vaseline. The animals appeared to show a distinct negative geotaxy: they invariably attached themselves to the glass plate or to the sides of the jar, and rarely descended as far as the zinc platform. Edney paper hygrometers were used for measuring the humidity. The results are contained in the following table:

Temperature 12–13° C.

75% R.H.	Little activity, lung rarely used. All dead or moribund after 2 days.
80% R.H.	After 2 days all appeared shrivelled and inert. 7 dead within 3½ days.
90% R.H.	No apparent effect of dryness for 3 days.
95% R.H.	Lived for 7 days before showing signs of desiccation Quite active, pulmonary aperture frequently open.
100% R.H.	All appeared normal and active.

When introduced into a humidity gradient ranging from 75 to 95% R.H. the animals made no attempt to aggregate in regions of optimum humidity—they are completely akinetic.

THE REPRODUCTIVE SYSTEM

The account of the reproductive system given by Joyeux-Laffuie (1882) includes little histology, and important points in the anatomy are overlooked. Plate's (1893) and von Wissel's (1898) descriptions of other members of the Onchidiidae indicate that throughout the family the gross structure of the reproductive organs is remarkably uniform, though in no case is the detailed course of the male and female ducts elucidated, and such essential structures as the fertilization chamber, with its associated receptaculum seminis, and the large prostate gland on the male duct have not previously been described.

In *Onchidella celtica* the yellowish brown hermaphrodite gland, which lies in the posterior part of the body cavity, is divided into two main lobes, each acinous in structure. Young individuals are protandrous, but later both types of sex cells are found in all acini of the gland, with the spermatozoa always far more numerous than the ova. The ducts through which the genital products pass to the hermaphrodite duct are ciliated. The proximal part of the hermaphrodite duct acts as a vesicula seminalis; it is coiled in a close spiral which passes forwards for a short distance on the left side of the haemocoel. The epithelium is columnar and ciliated, save for a longitudinal strip of gland cells, which, in animals dissected during late summer and autumn, appears as a deep brown streak; in spring there is little or no external indication of the glandular area. The pigmentation is due to brown refringent granules in the highly vacuolated protoplasm of the gland cells. The free ends of the cells may be irregular in outline and here the protoplasm is more dense than elsewhere. Sperm are entrapped by the dense protoplasm and engulfed; they have never been seen in the deeper layers of the cells, so the granules which accumulate there are probably products of sperm digestion. A similar activity on the part of the corresponding region of the male duct has been described by Linke (1933) in three species of *Littorina*, and also in *Ocenebra erinacea*, *Nucella lapillus*, *Nassarius reticulatus* and *Buccinum undatum* (Fretter, 1941). The distal part of the hermaphrodite duct is closed off from the vesicula seminalis by a sphincter, and turns abruptly to the right to lead straight back towards the hermaphrodite gland. At the end of this part of its course it winds into a knotted mass of fine coils, which are not visible superficially, since all are bound together by connective tissue and covered externally by a connective tissue sheet supplied with circular muscles (Fig. 4, *chd*). The fine coils lead anteriorly and open into a wider region of the duct (*hd*) which runs forwards and ventrally, through the flocculent mass of the albumen gland, to a small fertilization chamber (*fc*). The opening into this wider region lies at the base of a shallow longitudinal groove which leads posteriorly to the opening of a small caecum (*c*), and continues along the duct anteriorly for a short distance. The caecum has a narrow neck and broadens at its blind end; the epithelium, which is covered by extremely long cilia, is thrown into a few deep folds, and these subdivide the lumen. It is referred to as the vesicula seminalis by Joyeux-Laffuie (1882), though he failed to realize that the proximal part of the male duct acted as such, and actually only on one occasion have a few sperm been found in the pouch. Its size appears to vary throughout the Onchidiidae: in the genus *Onchidella* it would appear to be generally small since von Wissel (1898) describes it as a small diverticulum, about 0·5 mm. in length, in *Oncidiella* (= *Onchidella*) *marginata* and *O. juan-fernandeziana* and alleges that it is absent in *O. coquimbensis*. In the genus *Onchidium*, however, it is considerably larger and is figured by Plate (1893) in *O. verruculatum* and *O. nigrum* of such a size that the name vesicula seminalis is well merited. Hence it would appear that in the genus *Onchidella* it is an incipient or vestigial structure. The distal part of the hermaphrodite duct is lined throughout by a ciliated epithelium, with circular muscles beneath the basement membrane and longitudinal fibres outside. The cilia are long in the coiled region (*chd*), but in the caecum they may exceed five times the height of the cells; here, also, the muscle coat is very thick.

The ducts of subepithelial glands open between the ciliated cells which line the fertilization chamber (*fc*). The glands are embedded in a layer of connective tissue, and their cytoplasm contains small secretion spherules which stain deeply with iron haematoxylin. A few may lie in the epithelium. The chamber receives paired ducts, one from the left and the other from the

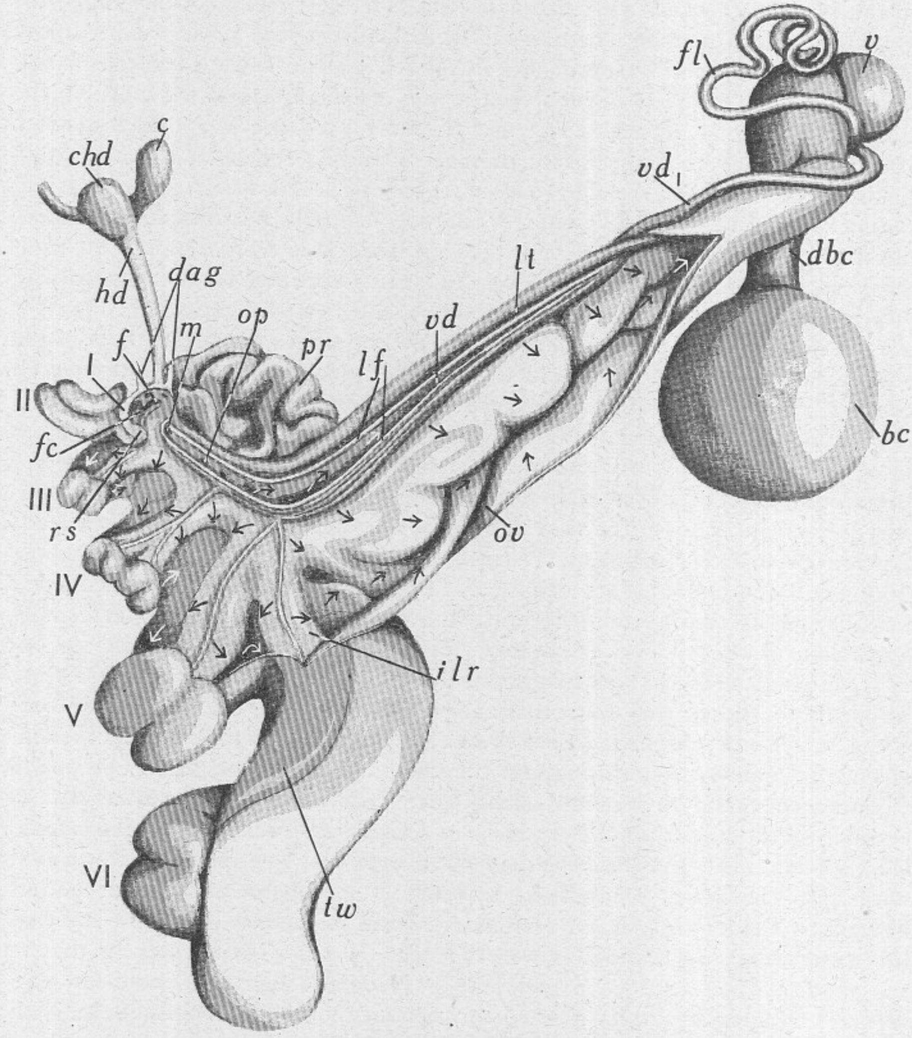


Fig. 4. The reproductive ducts: ×20. The middle glandular section of the hermaphrodite duct has been slit open longitudinally and the duct uncoiled. The albumen gland has been removed. *bc*, bursa copulatrix; *c*, caecum; *chd*, fine coils of hermaphrodite duct covered by connective tissue; *dag*, duct of albumen gland; *dbc*, duct of bursa copulatrix; *f*, opening of hermaphrodite duct into oviduct; *fc*, fertilization chamber; *fl*, flagellum; *hd*, hermaphrodite duct; *ilr*, internal longitudinal ridge of oviducal pouch; *lf*, longitudinal flange; *lt*, longitudinal tract leading from receptaculum seminis to duct of bursa; *m*, opening of hermaphrodite duct into vas deferens; *ov*, oviduct; *op*, opening of prostate; *pr*, prostate; *rs*, receptaculum seminis; *tw*, thin wall of spiral caecum; *v*, vagina; *vd*, vas deferens; vd_1, non-glandular part of vas deferens; I–VI, oviducal pouches.

right lobe of the albumen gland (*dag*). This is orange in colour and the two lobes are bound together by connective tissue and lie dorsally over the oviduct and vas deferens. Their ducts are short and ciliated, and each is formed by the union of smaller collecting ducts. The secreting cells, all of a single type, are grouped in small clusters which are bound to one another by a thin layer of connective tissue. The cytoplasm is filled with yellow, granular spherules and these stain an intense blue with azan, are not affected by mucicarmine, and stain rather deeply with iron haematoxylin.

The lumen of the hermaphrodite duct, on approaching the fertilization chamber, appears as a longitudinal slit, which becomes divided into left and right channels by a slight constriction. The duct runs beneath the chamber for a short distance and the left channel, which is the larger of the two, opens laterally into it (*f*); the opening is opposite those of the albumen ducts. Through this passage the eggs are conducted to the oviduct (*ov*). The right channel, on the other hand, is the beginning of the vas deferens (*m*), but, although here the male and female passages are separated from one another, during the next part of their course the separation is merely functional. The vas deferens (*vd*) runs back, accompanied by the female part of the duct (*ov*), towards the posterior end of the body, lying to the right of the hermaphrodite duct. It is a deep gulley, V-shaped in transverse section and surrounded by a thick layer of subepithelial glands. During the proximal part of its course the apex of the V is directed ventrally, and the oviduct, a similar longitudinal glandular groove, lies on its left, the two passages having a common dorsal wall. A longitudinal ciliated flange (*lf*) on each side of the mouth of that gulley which acts as vas deferens, closes it off from the oviduct. On the dorsal wall of the female channel, above the flanges guarding the male section, is a longitudinal ciliated tract (*lt*) leading upwards to the receptaculum seminis (*rs*) and downwards to the duct of the bursa copulatrix (*dbc*). Near the origin of the male duct lies the opening (*op*) of the large prostate gland (*pr*). This is a sac-like outgrowth of the glandular walls of the vas deferens, and its walls are deeply folded. The gland cells here and in the vas deferens are grouped in clusters, bound together by connective tissue, and their long ducts open between ciliated cells which direct the secretion along the male duct. The gland cells have large spherical nuclei with very prominent nucleoli and the secretion spherules which fill the vacuolated cytoplasm stain with iron haematoxylin; those in the ducts take the stain most readily. After azan the spherules are red and the cytoplasm purple. In the vas deferens muscle fibres, circular and oblique in direction, pass through the connective tissue between the glands, and also form an external layer which is concentrated on the right side of the gulley and around the dorsal wall.

The common genital duct, with its parallel male and female divisions, passes back through the haemocoel and becomes twisted in such a way that the vas deferens appears to curve around the right side of the oviduct and then to pass across its dorsal surface to the left side. The twist causes the openings of the two channels to face not dorsally, as in the anterior region, but to the left. At this point the vas deferens becomes completely separated from the oviduct, and for the rest of its course it is a narrow, ciliated and non-glandular duct with muscular walls (vd_1). It passes beneath the female duct to the origin of the external ciliated groove (Fig. 1 A, *cg*). This leads from the female aperture (*fe*), and passes around the right side of the body near the junction of the foot and body wall, to the pedal mucous gland. The vas deferens enters the muscles above the groove and runs parallel with it. Just behind the male opening (*ma*), which is situated a short distance behind the right tentacle, it returns to the haemocoel and runs back in a sinuous course to the base of the retracted penis. During the final part of its course mucous cells, which are wedged between the fibres of the thick coat of circular muscles, open into the narrow tube; the penis sheath is also lubricated by subepithelial mucous and mucoid glands. The retractor muscle of the penis is very long, and from the base of the copulatory organ it runs straight back in a ventral position to its origin on the dorsal surface of the foot beneath the bursa copulatrix.

The oviduct is complicated in its anterior part by the development of six pouches which are outgrowths of the glandular wall (Fig. 4, I–VI), and which serve to increase the distance through which the eggs must travel on their way to the female aperture. The first of these pouches is very small; it overhangs the fertilization chamber and acts as a receptaculum seminis (*rs*). The walls at the blind end are an opaque white, and resemble in histological detail the glandular walls of the fertilization chamber. In all other parts the glandular area of the oviduct is yellow. The remaining five pouches are of increasing size, with the sixth very much broader and longer than the others—it is coiled in a spiral and may exceed the whole of the rest of the oviduct in length. The four pouches anterior to it (nos. II–V) lie over the proximal end of the female channel. In other members of the Onchidiidae more than one spirally wound outgrowth from the genital duct has been described: two are figured by Plate (1893) in *Onchidium verruculatum* and three in *O. nigrum*, and these extra spirals appear to correspond with some of the smaller pouches in *Onchidella celtica*.

The wall of the oviduct is composed of columnar ciliated epithelium resting upon a thick and compact layer of gland cells which pour their secretion into the lumen of the duct. Along each pouch the epithelium is folded to give an internal longitudinal ridge (*ilr*). In the long spiral caecum (no. VI) that part of the wall directly opposite the ridge is thin with few subepithelial glands (*tw*). The base of the first pouch and the second, into which are directed the fertilized eggs with their coat of albumen, produce a mucous secretion. In the two succeeding pouches (nos. III and IV) the secretion is similar, but stains less easily with mucicarmine and slightly with iron haematoxylin. In the last two pouches (nos. V and VI), the largest of the series, the same two kinds of cell occur, and also a third type of gland which gradually replaces the other two and is especially numerous in the spiral pouch. The protoplasm is vacuolated and the majority of the spherules contained in the vacuoles are untouched by mucicarmine, stain rather deeply with iron haematoxylin and deep blue with azan. At certain centres of activity within each cell clumps of mucoid spherules occur, though they are not found in the ducts of the glands, and the final secretion is untouched by stains which are considered to be specific for mucus. The subepithelial cells of the main channel of the oviduct, which passes from the spiral caecum towards the female aperture, are mucoid glands, and in the connective tissue which binds them together in groups run a few circular and oblique muscle fibres. Such fibres enable the oviduct to be closed off from the rest of the genital duct. The gland cells decrease in number after the separation of the male and female channels, and the oviduct becomes a ciliated tube which is surrounded by a very thick coat of muscles. It curves ventrally and then describes a slight dorsal loop which receives on its dorsal wall the duct of the bursa copulatrix (*dbc*). The longitudinal ciliated tract (*lt*), which arises anteriorly near the receptaculum seminis and runs back between the original dorsal wall of the genital duct and the ciliated folds over the vas deferens, curves to the right with the twisting of the common genital duct, and, after the separation of the vas deferens, runs along the dorsal wall of the ventral curve of the oviduct to the opening of the duct from the bursa. The bursa (*bc*) lies anteriorly beneath the common genital duct; it is a large spherical vesicle and on dissection appears strawberry-pink in colour and flecked with a white calcareous deposit. It is lined by tall glandular cells with oval, nucleolated nuclei lying in the lower half of the cytoplasm. This is vacuolated throughout and the small secretion spherules contained in the vacuoles are dissolved on fixation. The free ends of the cells often have an irregular outline due to the discharging of the secretion. Beneath the basement membrane of the epithelium are a few circular muscles, and outside these the connective tissue contains blood spaces surrounded by large cells which are laden with calcium granules. The lumen of the bursa is invariably filled with a reddish brown fluid and in this may be found irregularly shaped refringent masses of a similar colour. During spring and summer there are clumps of spermatozoa, and a few living sperm have been seen there in December. The fluid is derived from the prostate secretion and from the wall of the vesicle, though neither of these secretions are so deeply pigmented when first liberated. The duct from the bursa (*dbc*) is lined by tall, columnar, ciliated cells and surrounded by a thick coat of circular muscles, with which are interspersed longitudinal fibres. It runs beneath the posterior end of the oviduct, and around its right side, to open at a point which marks the beginning of the vagina (*v*). The vagina, a very muscular tube, passes ventrally to the female aperture which lies to the right of the anus. A long flagellum (*fl*), with yellow glandular walls, coils over its dorsal surface and opens into it ventrally by a short duct. The opening is just posterior to the opening of the duct from the bursa. Joyeux-Laffuie (1882) refers to the flagellum as the caecal appendage or mucous gland, though the latter name is misleading since the secretion is not of a mucous nature. A fine canal runs through the flagellum and is lined by gland cells and ciliated cells; in the duct a columnar ciliated epithelium occurs and there are no gland cells. The secreting cells, which have basal nuclei, contain spherules of varying sizes clustered at the distal end of the cytoplasm. The ciliated cells are constricted by the gland cells and the nuclei are elongated and situated in the mid-region of the cells. A coat of circular muscles underlies the basement membrane and forms a sphincter around the duct. In the vagina the epithelium is columnar and ciliated, and the connective tissue below is ramified by radial, circular and longitudinal fibres, between which are mucous cells; externally a thick and compact coat of circular muscles forms a sphincter.

The vagina opens to the right and slightly in front of the so-called anus (Fig. 1A, *fe*, *mco*). A groove connects the two apertures and the lips of the groove run into those of the vaginal aperture, on the one hand, and those of the anus on the other. The ciliated groove (*cg*), arising at the female aperture, is lined by a columnar epithelium with short cilia. The epithelium is ridged longitudinally, both because of the fact that the supporting connective tissue varies in thickness and because the cells are of unequal height; the surface is lubricated by a few subepithelial mucous glands. A muscle coat of considerable thickness lies in the connective tissue, the fibres being mainly circular in direction, and the groove can be deepened so that the longitudinal ridges are obliterated, and the two lips then approximate to form a virtual tube. Although several attempts have been made to study the ciliary currents on the walls, only on one occasion was movement observed—this was very slight and directed anteriorly. The groove leads to the pedal mucous gland, which lies above the anterior tip of the foot and is a deep pouch with an extensive transverse opening (*o*). At its inner end the pouch is divided into two by a horizontal muscular partition, and the ciliated groove, which passes into the gland on the right side, runs straight back and ends in the shallower, dorsal chamber (*dc*). A cuticularized epithelium lines the walls of the undivided part of the gland, and the whole dorsal chamber except for the right wall on which the ciliated groove runs. The cuticle is pierced by the ducts of subepithelial gland cells. The dorsal chamber is very muscular, most of the muscles being circular, a few longitudinal or oblique. The ventral chamber (*vc*) is glandular, and the secreting cells, which are subepithelial, surround the ventral and lateral walls, opening to the surface between ciliated cells, whilst the dorsal wall is cuticularized. The secreting cells are for the most part mucous and mucoid glands, the former being especially numerous laterally. In the undivided part of the pedal gland the secreting cells decrease in number. In addition to mucous and mucoid cells two other types of secreting cells are present, and a few of these spread into the ventral chamber: in one, which is ubiquitous in the tissues of the foot, and is also found around the ciliated groove and the dorsal chamber of the pedal gland, the secretion is in the form of large protein spherules; in the other the cytoplasm is homogeneous and granular, but contains one or two large vacuoles with no apparent contents.

Egg masses of *Onchidella celtica* are found in the crevices inhabited by the adults and several may occur together. Each mass, which is laid by one individual and contains from sixty to over a hundred eggs, is somewhat flattened and of an irregular outline, measuring about a centimetre in diameter. It is firmly cemented to the rock, in most cases to the roof of the slanting crevice, and consists of the irregular coilings of a long tubular capsule which is embedded in jelly, and which is expanded at regular intervals by the eggs. Each egg lies at the centre of an oval mass of transparent albumen, and that in its turn is covered by the capsule wall. Between one egg and the next the capsule narrows to a fine strand. The capsule wall is made up of three distinct layers: an inner mucoid coat and middle and outer layers which, though thin, are very tough, the former staining lightly with iron haematoxylin and the latter deeply. The strand between any two eggs has a similar structure: in the centre is the mucoid layer, enclosing perhaps a streak of albumen, but the two outer layers are thicker than elsewhere since they are not distended, and here they appear to be made up of concentric sheets of a similar secretion which, in the middle layer, are separated by mucoid fluid.

Joyeux-Laffuie (1882) states that fertilization is reciprocal and Hoffmann (1929) figures the position of two copulating individuals in which the right borders of the mantles are in contact, the anterior ends pointing in opposite directions, and in each the penis is protruded from beneath the anterior edge of the mantle on the right side and thrust into the female aperture of the other. Sperm, embedded in prostatic secretion, are deposited in the bursa copulatrix, and in mature individuals collected during early summer they are present there in large numbers. Joyeux-Laffuie (1882) assumes that the eggs are both fertilized and encapsulated in the vagina, but a more detailed knowledge of the genital duct shows that this cannot be the case. From the bursa (Fig. 4, *bc*) the sperm make their way to the receptaculum seminis (*rs*) via the longitudinal groove (*lt*) which connects these two regions of the female tract, and there they await the discharge of the eggs into the fertilization chamber (*fc*). It is not known how soon after copulation the formation of egg capsules may begin.

When the eggs are passed down the hermaphrodite duct the proximal end of the vas deferens is contracted and they proceed along the wider female channel to the fertilization chamber. This is distended with secretion from the albumen gland and, one by one, the eggs are discharged into the secretion and are also fertilized. The stream of eggs and albumen now starts on the circuitous journey down the oviduct entering each of the six pouches (I–VI) in turn and being directed through these by the ciliary currents on their walls. Meanwhile the encasing capsule wall is secreted. The actual secretion of this wall has not been observed, though the part played by the various types of glands may be conjectured.

Prior to the entry of the fertilized eggs the glands of the oviduct discharge their secretion. In the first two diverticula of the duct this is mucous, and together with the mucoid secretion from the two succeeding diverticula it supplies the material for the manufacture of the inner layer of the capsule wall. The two outer layers are produced by the fifth and sixth diverticula, the largest of the series, with the sixth providing the most extensive glandular area of the whole oviduct. In these diverticula the mucous and mucoid cells are gradually replaced by glands which furnish a secretion with the same staining properties as the outer layer of the egg capsule; in no other area of the oviduct do such glands occur. The outer layer of the capsule wall is composed entirely of this secretion, whilst the middle one is composite, being an admixture of the inner and outer layers. In the posterior part of the oviduct the subepithelial glands lubricate the passage for the stream of eggs and add to it a thin mucoid covering. The exact locus at which the whole mass is acted upon so that it acquires its moniliform appearance is uncertain. It may be in the muscular vagina, or even outside the female duct if the process is purely physical.

The contents of the oviduct are presumably discharged into the ciliated groove. The cilia may at such a time become more active and combine with the muscles in effecting the passage of eggs along the groove and into the dorsal chamber of the pedal mucous gland. Since this chamber is very muscular the egg string may be moulded here. It seems reasonable to assume that the secretion in which they are embedded, and which cements them to the substrate, is poured from the glandular walls of the pedal gland, for this secretion has the same texture and staining properties as that supplied by the gland.

EMBRYOLOGY

The newly laid capsules of *Onchidella celtica* may be collected in July, August and the beginning of September; it is doubtful whether any are produced later. Within the capsule the embryo passes through a prosobranch veliger stage, followed by a post-veliger which shows gradual detorsion and a recession of the visceral hump, so that before hatching the appearance of the adult is assumed. In December and January empty capsules have been found in the rock crevices, as well as capsules containing veligers and post-veligers. The development of these was presumably retarded by the low temperature of the winter months, which may also account for the number of malformed individuals among them. Joyeux-Laffuie (1882) alleges that embryos kept in the laboratory, if not carefully attended, take on abnormal shapes, such abnormalities occurring more frequently in *Onchidella* than in other gastropods. It is the earliest post-veliger stages of detorsion which are most frequently malformed and among which there is the highest mortality. Spawn has been obtained from animals in captivity and from this normal embryos developed.

In such egg masses laid during the first week in July the veligers were fully formed in seventeen days, and about a month later their embryonic development was near completion—they appeared as miniatures of the adult. They hatched a week or so after. Only those points in the development which help to elucidate the adult structure are considered here, and the stages leading up to the veliger are completely omitted.

The Veliger

The veliger measures about 0·3 mm. in length, and by means of the large bilobed velum (Fig. 5A, v_1) it swims in the surrounding albumen. A pair of eyes (*e*) is developed, each situated on a slight protuberance which represents the rudiment of an adult tentacle. The foot (*f*) has a triangular sole and bears a large operculum (*op*) which was not observed by Joyeux-Laffuie (1882); near the broad base are embedded two otocysts (*o*), symmetrically placed, one on each side. At the anterior end of the foot the pedal mucous gland is present. The visceral hump is covered by a thin transparent shell (*sh*), which shows an endogastric coiling through about 180°, and on the right side is the mantle cavity (Fig. 6A, *mc*). This communicates with the exterior by a wide opening and at its extreme inner end is the anus. Projecting into the mantle cavity above the anus is a transitory organ, the larval kidney (Fig. 5A, *lk*), which corresponds in structure and position with what Mazzarelli (1906) calls the secondary kidney of the opisthobranchs; Joyeux-Laffuie (1882) mistakes it for the hermaphrodite gland. Sections show that it comprises three cells (Fig. 6A, *lk*), one much larger than the others. They are held together by a fine layer of connective tissue and their bases are directed upwards towards the dorsal surface. The nuclei are large and deeply staining, each with two nucleoli, and the cytoplasm is highly vacuolated; in the vacuoles small granules occur. It is uncertain whether this kidney communicates with the exterior: the suggestion of a minute opening has sometimes been seen, and it may be that the aperture is only visible when a drop of excretory matter is expelled. The rudiments of the definitive kidney of the mollusc can be found in a somewhat undifferentiated mass of cells (Figs. 5A and 6A, *rdk*) which lies above the larval kidney and between it and the pericardium.

Behind the velum and on either side of the oesophagus, in the young veliger, is a small opaque rounded body with green-brown granules, the so-called larval organ of Joyeux-Laffuie (1882). These are also transitory structures which cannot be traced in later stages, and appear to be homologous with the primary or cephalic kidneys of opisthobranchs and other pulmonates (Mazzarelli, 1906).

The mouth, which is median and situated beneath the velum, is surrounded by long cilia. It leads into the buccal cavity, a ventral diverticulum from which forms the rudiment of the odontophore. The oesophagus (Fig. 5A, *oe*) passes through the nerve ring (*g*), where the ganglia are concentrated as in

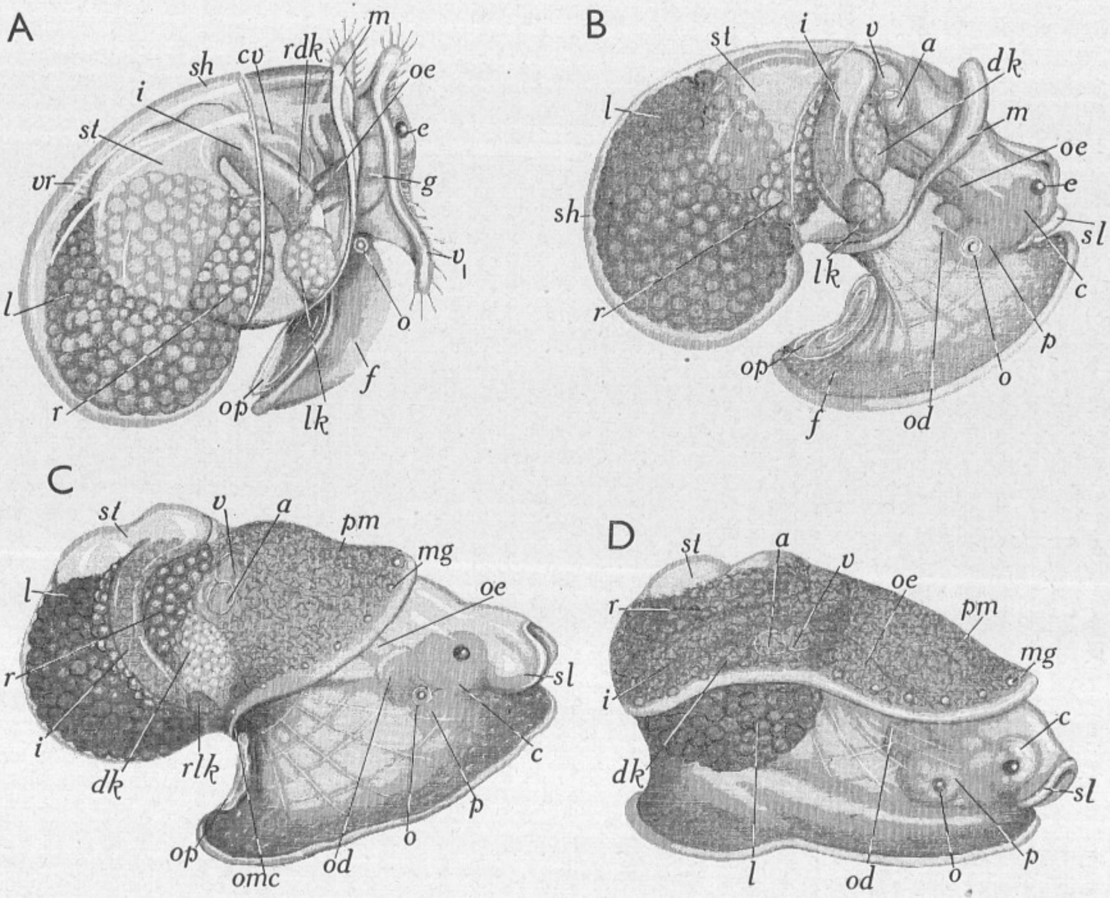


Fig. 5.

A. Veliger from the right side: × 170.

B. Early post-veliger: × 150.

C. Embryo at mid-detorsion: × 120.

D. Embryo near completion of detorsion: × 110.

a, auricle; *c*, cerebral ganglion; *cv*, cardiac vesicle; *dk*, definitive kidney; *e*, eye; *f*, foot; *g*, ganglia of nerve ring; *i*, intestine; *l*, left lobe of digestive gland; *lk*, larval kidney or secondary kidney; *m*, mantle; *mg*, marginal gland; *o*, otocyst; *od*, odontophore; *oe*, oesophagus; *omc*, opening of mantle cavity; *op*, operculum; *p*, pedal ganglion; *pm*, pigment of mantle; *r*, right lobe of digestive gland; *rdk*, rudiments of definitive kidney; *rlk*, remains of larval kidney; *sh*, shell; *sl*, sensory lobe; *st*, stomach; *v*, ventricle; v_1, velum; *vr*, velar retractor muscle.

the adult, and runs straight back to the stomach (*st*), into which it opens ventrally on the right side. The stomach and digestive gland comprise the visceral mass, the latter not yet constricted from the stomach. The gland is divided into two unequal lobes—a larger left one (Figs. 5A and 6A, *l*) which occupies the whole left wall and spreads posteriorly and ventrally around the gastric sac, and a smaller right lobe (*r*) which is restricted to an anterior strip on the right wall. The intestine (Fig. 5A, *i*) leaves the stomach dorsally, on the right side, above the point of entry of the oesophagus, and passes below the dorsal integument to the anus. The heart is dorsal and towards the right side: in the early veliger it is indicated only by a vesicle (Figs. 5A and 6A, *cv*) which contracts at rather irregular intervals; but later the auricle and ventricle can be distinguished, the latter lying to the left and slightly posterior to the auricle. The velar retractor muscle (Fig. 5A, *vr*) is situated on the left side of the larva and is inserted anteriorly around the foregut and the posterior part of the velum. It passes back on the left side of the stomach to its posterior attachment near the median part of the shell. The velum is withdrawn into the shell when the muscle contracts—a movement which will also help the circulation of the blood.

The organization of the veliger is typically prosobranch, as is indicated by the following points: the mantle cavity lies on the right side, the rudiments of the definitive kidney are anterior to the rectum, and it is the hepatic area on the left which is enlarged.

The Post-veliger

During early post-veliger life (Fig. 5B) the foot (*f*), now covered by ciliated epithelium except in the region of the operculum, develops a large, oval, creeping sole which enables the embryo to cling to and creep around the capsule wall, the path being lubricated by the pedal mucous gland. The otocysts (*o*) persist and Joyeux-Laffuie (1882) has traced them into the adult; in the later stages of development, at the time when the operculum is lost, they are far less obvious. The velum is not cast off as a whole, its ciliated covering is gradually lost and the two halves appear to be transformed into the sensory lobes which border the mouth (Figs. 5 B, C, D, *sl*) and have been described in the adult. The tentacles are still represented by the broad bosses with an eye situated in the middle of each. Later the shell (Fig. 5B, *sh*) is cast off and the velar retractor muscle lost.

When detorsion takes place it is effected slowly, and, as may be seen from Figs. 5 B, C and D, it is accompanied by an increase in the diameter of the neck region connecting the head and foot to the visceral hump, mainly in an antero-posterior direction, and also by the gradual recession of the visceral hump as the viscera come to project into this neck. While the mantle cavity migrates along the right side to a more posterior position its opening to the exterior is reduced in size; the blind end, which receives at its extremity the opening of the rectum, and is at first directed posteriorly, becomes ciliated. Black pigment is developed in the subepithelial tissues of the mantle (Fig. 5 C, D, *pm*), appearing at first around the anterior border and immediately behind the rudimentary marginal glands, which are just visible, and then extending laterally so as to reach the posterior end, leaving the visceral hump light in colour because here the mantle is thin and there is little or no subepithelial tissue. As the visceral mass is reduced in size so the mantle which covers it thickens and then becomes pigmented.

During detorsion the stomach and digestive gland rotate through approximately 90°, so that the right side becomes dorsal and the dorsal surface lies towards the left. It must be emphasized that this movement is not one of detorsion, but is forced upon the alimentary canal so that it can accommodate itself to changes in the disposition of viscera elsewhere, due to movements of detorsion. The left lobe of the digestive gland (Fig. 5 C, D, *l*) becomes ventral and the smaller right lobe dorsal (*r*). They have both been gradually constricted from the stomach and are now completely separated from it at the posterior end, where it forms a closed sac lined by columnar epithelium. The original left lobe opens into the stomach by an aperture occupying the greater part of the ventral wall (Fig. 6B, *vo*), and the original right one has a dorsal and less extensive opening into the anterior end and towards the right side (*do*). Each extends forwards for a short distance in front of the stomach, and the oesophagus is now directed dorsally over the broad anterior diverticulum from the ventral lobe, and opens into the stomach between this and the small anterior diverticulum from the dorsal lobe. The intestine, lined by ciliated epithelium, still arises dorsally, but on the left side (*oi*), a short distance behind the oesophageal opening. It passes over the oesophagus, as in the adult, to describe a slight anterior loop, and then leads back on the right side, behind the definitive kidney, to the anus (Fig. 5 C, D). During its whole course it lies dorsal to the digestive gland and at times the beating of the cilia of the epithelium and the sudden contraction of muscle cells, which are developing around the intestinal wall, can be seen through the mantle.

In the early stages of detorsion there are only two openings of the digestive gland into the stomach, one for each lobe. Later a third appears at the posterior end of the stomach. It is ventral (Fig. 6C, *po*) and communicates with the posterior portion of the original left liver lobe, which has become divided from the anterior part and forms the posterior liver lobe of the adult. The writer cannot agree with Joyeux-Laffuie's (1882) statement that the posterior lobe of the adult is derived from the original right: here, as in *Aeolis* (Fischer, 1892), it is the larger left lobe which divides to give the left and posterior lobes of the adult.

By this time the cilia around the mouth have been lost and the radula is developed. As soon as the odontophore muscles are functional the tongue is, at intervals, rhythmically protruded through the mouth; at first the action is only feeble, but later the radula draws in some of the surrounding albumen which is used as food. The salivary glands are distinguishable in the late veliger, when they appear as clumps of mucous cells pressed against the oesophageal tube and behind the nerve ring, one clump lying against the ventral wall of the oesophagus and the other against the dorsal. With detorsion the oesophagus rotates through 90° so that the ventral clump of mucous cells becomes the left salivary gland of the adult, and the dorsal group the right salivary gland.

The secondary kidney (Fig. 5C, *rlk*) degenerates as the definitive kidney (*dk*) is differentiated. The latter forms a rather elongated mass of cells, one end of which lies on the median side of the larval kidney and abuts on to the mantle cavity, whilst the other end is directed dorsally. The kidney is in communication with the pericardium by the renopericardial duct, which at this stage is relatively much wider and shorter than in the adult and is not ciliated. It is given off from the auricular end of the pericardium and runs towards the mantle cavity. At the point where it reaches the ventral end of the definitive kidney it opens into the primary ureter which discharges into the mantle cavity in front of and dorsal to the anus. It is thus seen that whereas in the typical mollusc the excretory tissue is developed on the walls of the original coelomoduct, connecting the pericardium and mantle cavity, in *Onchidella* these remain always relatively undifferentiated, and the definitive excretory cells are formed from the block of tissue lying alongside the duct. At a later stage this block of tissue cavitates and the lumen is placed in connexion with the pericardium by way of the renopericardial canal, and with the mantle cavity by means of the primary ureter. The heart is at first transverse and the auricle lies to the right of the ventricle and in front of the anterior loop of the intestine. During detorsion it moves back along the right side and the auricle comes to lie behind the ventricle (Fig. 5B, D, *a*, *v*).

The Embryo at the time of Hatching

Some days before the embryo frees itself from the capsule it has attained the superficial appearance of the adult: it is oval in outline, a flat creeping foot covers the ventral surface and the pigmented mantle covers the dorsal. All traces of the projecting visceral hump have disappeared. The tentacles are still broad lobes bearing the eyes and they are invaginable. The head can be withdrawn into the shelter of the mantle which has grown down over it, and also overhangs the foot, so that the side walls of the body (Hoffmann, 1929) are hidden. As the mantle edge grows downwards these side walls rotate from their original vertical position to one where they slope upwards and outwards at an angle of 45°. The edge of the mantle turns under and inwards to join them and the two surfaces lie in the same plane. The marginal glands (Fig. 5D, *mg*), developed in the tissues of the thickened edge of the mantle, open on to the dorsal surface; as yet no papillae are developed. The opening of the mantle cavity (Fig. 6C, *omc*) has the appearance of a small

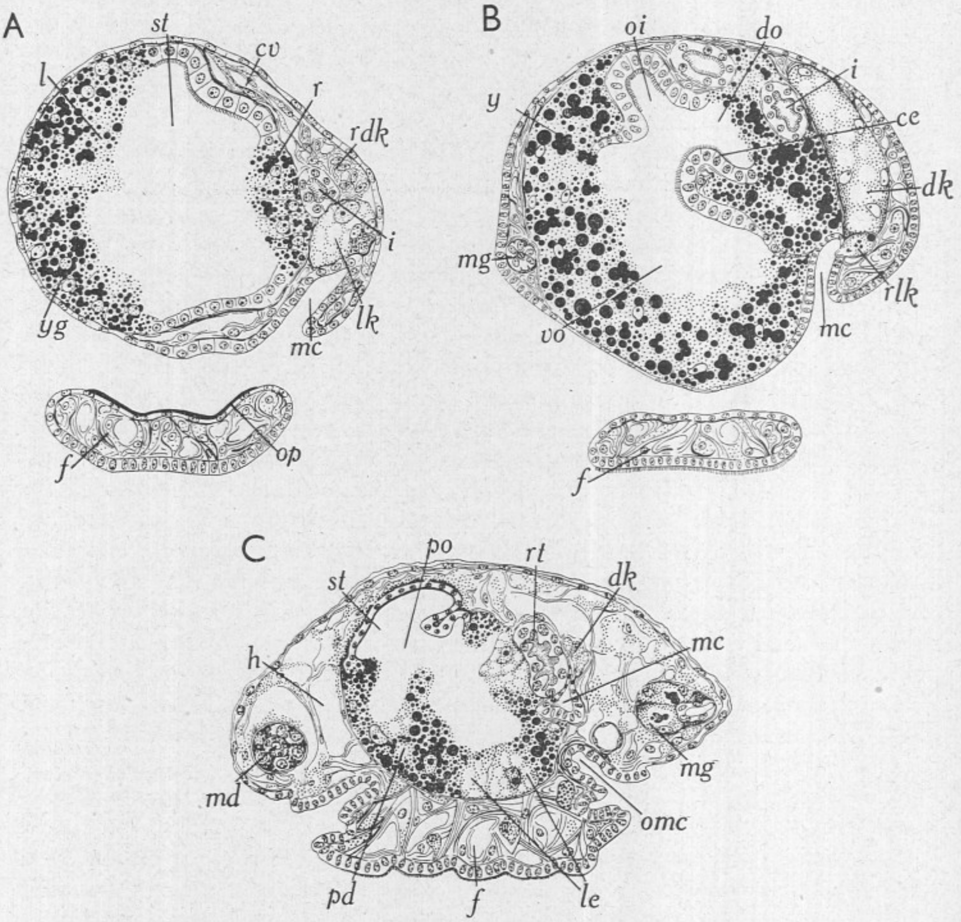


Fig. 6. A. Veliger. Transverse section through stomach and larval kidney: × 240. B. Embryo at mid-detorsion. Transverse section through stomach and kidney: × 230. C. Embryo at time of hatching. Transverse section to show kidney opening into tubular mantle cavity and opening of posterior lobe of digestive gland: × 207. *ce*, ciliated epithelium of stomach; *do*, opening of right lobe of digestive gland; *h*, haemocoelic space; *le*, lime and excretory cells forming; *mc*, mantle cavity; *md*, duct of marginal gland; *oi*, origin of intestine; *pd*, posterior lobe of digestive gland; *po*, opening of posterior lobe of digestive gland; *rt*, rectum; *vo*, opening of left lobe of digestive gland; *yg*, yolk granules. Other letters as in Fig. 5.

round hole at the posterior end of the body, between the foot and the mantle, and to the right of the middle line. The heart is in the adult position, on the right side and posterior, the auricle lying behind the ventricle, and the pulsation of the two chambers can be seen through the mantle.

The capsule wall is gradually weakened by the action of the radula, perhaps assisted by an enzyme, and as soon as it is punctured the embryo emerges. It is difficult to find these young animals in the sandy rock crevices. Only three have been seen in their natural habitat and these were creeping over the egg masses from which they had just emerged. They do not appear to cluster with the rest of the community in the crevice, for the smallest individuals found in any community were 2·6 mm. in length and showed the characteristics of the adult, whereas the newly hatched forms are 1·2 mm. in length, and in them neither lung nor reproductive organs are formed and the kidney is a simple, unbranched sac lying on the right side posteriorly.

The alimentary canal shows all the features of the adult. A jaw is developed in the roof of the buccal cavity and behind this the dorsal ciliated channel runs back to the oesophagus; the rest of the buccal cavity is lined by a cuticle. Before passing through the nerve ring the oesophagus receives the openings of the salivary glands which have now migrated through the nerve ring; as yet no salivary duct is developed. The epithelium of the crop is covered by a cuticle, and the crop is closed from the stomach by a sphincter. Because of differential growth of the stomach wall the anterior liver openings, which occupied a dorsal and ventral position during detorsion, are now gradually regaining their original orientation of right and left, and are opening into the initial chamber. At this stage they are wide, with no duct. Behind them the triturating stomach is differentiated, the epithelium being covered by a thickening cuticle beneath which the dorsal and ventral plates are formed. The posterior liver opening is still ventral (Fig. 6C, *po*). The lobes of the digestive gland are branching to form the initial tubules, and in the crypts of these lime cells and excretory cells are forming (*le*). The body cavity is approximately circular in transverse section and bounded on each side by a muscular diaphragm; it is filled for the most part by the digestive system. The greater part of the digestive gland lies ventral to the gut and has not as yet spread over the intestine. This has lengthened and assumes the coilings of the adult, though the ventral caecum of the anterior intestine and the typhlosole cannot be distinguished. At the posterior end of the gizzard, and on the right side, the rectum (*rt*) passes ventrally to open into the mantle cavity (*mc*). This is a short tube which runs dorsally to the anus, and is ciliated except around its opening to the exterior (*omc*), where it is surrounded by a sphincter. To the right of the anus it sends a small diverticulum to the opening of the definitive kidney (*dk*), and from this is derived the secondary ureter. In the adult this cavity has previously been called the rectum and its opening to the exterior the anus, but from its development it is clear that it is a reduced mantle cavity, and this explains the fact that both the alimentary canal and the kidney open into it (Fig. 1B, *mc*), and that its opening is connected to the vaginal opening by a groove, the two being surrounded by common lips. The kidney is still a compact, pear-shaped mass, with a small central cavity, lying on the right of the rectum just behind the heart; the broader end is dorsal and the ventral end opens into the incipient secondary ureter. The heart and kidney are separated from the general body cavity by the right diaphragm. It is not until later in development that the kidney branches and spreads around the posterior wall of the rectum to the left side of the body, where it penetrates the haemocoelic spaces (Fig. 6C, *h*) between the left diaphragm and the body wall. Carried round by this growth the secondary ureter comes to open into the posterior wall of the mantle cavity (Fig. 1B, *su*) instead of its right side, and into it the primary ureter projects as a long papilla (*u*) which is slung from the walls by two lateral sheets of tissue. A small mass of undifferentiated cells which will give rise to the reproductive organs lies posterior to the stomach. No lung has yet been formed, and it would seem that as it opens separately from the mantle cavity it must arise as a separate and independent invagination of the mantle epithelium which grows inwards and forwards to come into intimate contact with the haemocoelic blood spaces around the kidney.

The smallest individual which has been seen in any adult community measured, as previously stated, 2·6 mm. in length. It was found during mid-August and was presumably hatched from eggs laid in the previous season. The mantle cavity was relatively wide and still opened on the right side of the body, receiving just within the mouth of the opening, and anterior to the anus, the female aperture, and posteriorly the opening of the ureter. From the kidney a small diverticulum had spread around the posterior end of the body and penetrated the haemocoelic spaces on the left side. The pneumostome was posterior and to the right of the opening of the mantle cavity, and led through a short duct to a small and comparatively unbranched pulmonary sac. This was in contact with the kidney on the right side, and a tendency to spread around the posterior diverticulum was indicated.

Discussion

The mantle cavity of the typical mollusc contains a definite series of organs and into it opens a definite number of apertures. The structure of the veliger of *Onchidella celtica* is essentially comparable with that of a monotocardian prosobranch, except that no ctenidium and hence no osphradium are present, so that if it possesses a cavity homologous with the molluscan mantle cavity we should expect to find opening into it a single kidney, the anus and the genital aperture. The cavity which has already been described on the right side of the veliger agrees with this, except that no genital aperture has yet appeared. The cavity can therefore be taken as a true mantle cavity. During the metamorphosis of the larva into the adult the rotation due to detorsion rotates it from its original position on the right side of the body to a median position posteriorly, carrying the anus and kidney opening with it, and meanwhile it becomes converted into a narrow tubular space with its opening contracted into a small pore. The kidney spreads posteriorly around the mantle cavity and on to the left side of the body, bringing about the consequent migration of its opening into the mantle cavity which has already been described. The net result of all these changes is that at the end of metamorphosis the animal has a secondary bilateral symmetry, a type of reorganization which is of frequent occurrence in detorted gastropods accompanying the loss of shell and reduction of the visceral hump. The median opening at the posterior end of the body of *Onchidella*, which has previously been called the anus, is thus seen to be nothing more nor less than the opening of the mantle cavity in its new position, and what has been called the secondary opening of the excretory system into the rectum is nothing but a retention of the original opening of the kidney into the mantle cavity, as in all molluscs. The former interpretation of the relationship of these parts was obviously possible only so long as the real nature of the cavity was unknown. In the adult animal the female aperture also opens into the mouth of the mantle cavity and on its right side, providing a further clue as to the identity of this space. As the penis lies on the side of the animal's head anterior to the region affected by detorsion, it retains this position in the adult.

Since it is clear that the space into which the digestive, excretory and genital systems open is the homologue of the mantle cavity of other molluscs, then the cavity called the lung—the possession of which is one of the main reasons for regarding the Onchidiidae as pulmonate gastropods—must be a new structure, independently evolved and not homologous with the lung of the pulmonates. This being so the question now arises as to whether the Onchidiidae should not be regarded as opisthobranchs which have acquired a pulmonary cavity. Both Plate (1893) and Hoffmann (1929) would agree that whatever the anatomical specialization of the genus *Onchidella* may be it is at least typical of the Onchidiidae as regards its habitat; were the Onchidiidae, as Bergh (1885) suggests, true pulmonates they must be regarded as attempting to invade the sea from the land: on the former view the direction of migration would be reversed.

The opisthobranch affinities of the group have previously been recognized by Plate (1893) and Labbé (1934). The former assumes a tectibranch origin for the pulmonates and proposes to derive the Onchidiidae from the base of the pulmonate stem; the latter actually regards them as a group of opisthobranchs. The most important points in which these molluscs agree with the opisthobranchs are: (1) the reduction in size of the visceral hump; (2) the loss of the shell; (3) the posterior position of the mantle cavity; (4) the position of the auricle behind the ventricle; (5) the reduction of ganglia in the visceral loop to three; (6) the possession of three liver lobes, two anterior and one posterior; (7) the general disposition of the reproductive organs; (8) the veliger larva with its primary and secondary kidneys. On the other hand, it may be said with Bergh (1885) that the Onchidiidae possess a number of characters in common with the pulmonates, the most important of which are: (1) the possession of a lung; (2) the shortening of the visceral loop; (3) the retractile tentacles bearing eyes at their summits; (4) the loss of a seminal groove; (5) the development of thick chitinous plates in the stomach; (6) the number of lateral teeth on the radula. The occurrence of these features may, however, be explained in other ways: the lung in the two groups is not homologous; the shortening of the visceral loop is not confined to pulmonates, but is found in many nudibranchs; the development of eyes on the tentacles is indicated even in the prosobranch molluscs such as *Buccinum* and *Nucella*, though here the tentacles are not invaginable; in dorids the seminal groove is lost and these nudibranchs have also numerous lateral teeth on the radula. The stomach of the Onchidiidae is built on the typical prosobranch plan in that the crushing plates are developed in the stomach itself, and differs from that of the tectibranch where the plates are oesophageal and the stomach is reduced (Fretter, 1939). Its distinguishing features can be directly attributed to the quantities of sand which are ingested with the food (Heidermanns, 1924).

It is generally recognized that the opisthobranchs are derived from monotocardian prosobranchs. The pulmonates and the opisthobranchs have retained only one set of the organs associated with the mantle cavity and so may have come either from closely related prosobranch groups or the pulmonates may have originated from an early group of the opisthobranchs themselves. If the latter be the case, then it may be suggested that the Onchidiidae separated from the opisthobranch stem at about the same time. From this origin, however, the Onchidiidae have evolved along different lines from the pulmonates, retaining more opisthobranch characters. Owing to adaptation to similar habitats they have acquired a superficial resemblance to the nudibranchs, and the acquisition of a lung, a structure independent of the true mantle cavity, has enabled them to become most active during intertidal periods, and so to exploit a habitat at a time when it is closed to other littoral gastropods. Even with this organ of terrestrial respiration their range is still restricted by their dependence on a relatively high humidity, although it is doubtful how serious this factor would be in limiting activity on the seashore. Many of the features which the Onchidiidae share with the pulmonates may be attributed to the close origin of the two groups, the similarity of their diet and their air-breathing habit. The pulmonary respiration of *Onchidella celtica* is by itself insufficient for the respiratory needs of the animal, but is a necessary supplement to pallial respiration when the animal is active.

The distribution of the Onchidiidae, the northern limit of which is the extreme south-western coasts of England, and likewise their inactivity during the winter months, suggest that they are unable to endure a low temperature. The tendency towards the adoption of a terrestrial mode of life has been intensified in other members of the group: some live above the intertidal zone and *Onchis montana* is definitely terrestrial.

On the whole it would seem that the most suitable place to assign the group is with the opisthobranchs, regarding it as a small twig from the base of the main stem. This is in agreement with Labbé (1934), though he prefers the name Silicodermatae to Onchidacea. He states that in *O. celtica* spicules of silica are found in the connective tissue under the epidermis, the largest measuring 25μ and occupying a large part of the dermal tissue. In other species he describes the spicules as being much larger. No suggestion of such spicules has been found in *O. celtica*, nor could they be identified in the examination, which was kindly made by Mr A. G. Lowndes, of the nota of forty newly collected specimens. Unless the spicules are much more conspicuous in the other genera, the name Silicodermatae would appear to be a misnomer.

Mr Lowndes has given me the following note:

> The material given to me was weighed, 3·397 g. It was placed in a Kjeldahl flask together with about 100 ml. of concentrated sulphuric acid and a sufficient quantity of potassium sulphate. After boiling up the mixture for an hour a drop of mercury was added and the whole again boiled till the liquid in the flask became quite clear and colourless. When the contents of the flask were cool they were washed out into a 1000 ml. beaker and allowed to remain overnight. A small amount of sediment was to be seen on the bottom of the beaker. Nearly all the liquid was poured off and about 50 ml. of concentrated nitric acid added. The beaker was then filled with distilled water and allowed to stand for 4 hr. There was a small amount of sediment and it was examined in water both in a watch-glass and on a slide under a Zeiss D objective. The sediment was seen to consist of a few sand grains, a few identifiable sponge spicules and a very large number of diatom frustules. The length of the diatoms was found to be 8μ in most cases. There was also a small amount of matrix consisting of amorphous silica but no recognizable spicules other than those mentioned were found. [*A. G. Lowndes.*]

SUMMARY

Onchidella celtica lives in communities in intertidal rock crevices, emerging only when uncovered by the tide during the milder months (March–November). It feeds on young algae and diatoms, rasping them from the rock with the radula which is lubricated by a mucous saliva. The distensible crop and stomach afford ample storage space for the food. The stomach consists of three chambers (Fig. 2), and the dorsal (*d*) and ventral (*v*) chitinous plates of the posterior one, the gizzard, crush the contents and help to direct the soluble portion towards the ducts of the digestive gland. There are three of these—the two anterior (*ld*, *rd*) are large and lead from the initial chamber of the stomach (*ic*), the third (*pd*) is small and joins the posterior wall of the gizzard (*pw*). The digestive gland secretes into the stomach; no cellulase occurs. Feeding experiments suggest that the digestive cells of the gland absorb only fluid. Lime and excretory cells occur in the crypts of the digestive epithelium, the latter concerned with taking up excretory matter from the blood and elaborating it into spherical masses for evacuation with the faeces. From the anterior ducts this waste matter, and that from the

digestive cells, is directed to a small caecum (*c*), and so prevented from mixing with food in the stomach, and there is consolidated and cemented to the faecal rod which fills the intestine a few hours after a meal. The large quantity of indigestible and undigested food in the stomach is directed into the intestine by the mechanical action of the gizzard.

The mantle is solely responsible for respiration when the mollusc is covered by water or is inactive at low tide. At other times pulmonary supplements pallial respiration—the pneumostome (Fig. 1A, *p*) is widely open during periods of activity and the cavity of the lung distended. The lung follows the course of the kidney; its walls are produced into fine diverticula which penetrate the nearby haemocoelic spaces (Fig. 3A), and the respiratory surface consists of parallel blood channels lined by squamous epithelium (*os*, *is*, *sc*). *O. celtica* will survive in an atmosphere of 90% R.H. for three days without apparent effect.

The period of sexual activity extends over the summer months; egg capsules are laid during July, August and the beginning of September. The upper part of the hermaphrodite duct acts as a vesicula seminalis and here there is evidence of sperm absorption. Distally the duct divides into two channels, the oviduct (Fig. 4, *ov*) and vas deferens (*vd*), which are glandular and share a common dorsal wall. Both are ciliated and the gland cells are subepithelial. At the beginning of the vas deferens a large diverticulum forms the prostate (*pr*). The upper part of the oviduct bears six diverticula (I–VI) along which the eggs must travel. The first of these, the smallest, overhangs the fertilization chamber (*fc*) and acts as a receptaculum seminis (*rs*); the other five are of increasing size, and the sixth is wound into a spiral. The fertilization chamber receives the ducts of the albumen gland (*dag*). The two channels of the genital duct become entirely separated: the vas deferens forms a narrow non-glandular tube (vd_1) and follows the external ciliated groove (Fig. 1A, *cg*) on its way to the penis; the oviduct becomes less glandular and at the beginning of the muscular vagina (Fig. 4, *v*) it receives the duct from the bursa copulatrix (*dbc*) and, approximately opposite this, the duct of a glandular flagellum (*fl*).

The egg capsules are cemented to the walls of the rock crevices. Each is an elongated tube distended at regular intervals by an egg and coiled in a mucoid secretion. Each egg is surrounded by albumen, and by a capsule wall made of three distinct layers; the consistency and staining properties of these suggest that they are secreted by the diverticula of the oviduct (I–VI). The embedding mucoid secretion is probably produced by the pedal mucous gland (Fig. 1A, *dc*, *vc*). Whilst in the egg capsule the egg develops into a typical prosobranch monotocardian veliger (Fig. 5A) which undergoes detorsion and assumes the external appearance of the adult (Fig. 5B, C, D). At this stage it hatches. There is no lung and the kidney is a simple sac behind the heart. The lung appears to develop not from the mantle cavity, but as a separate invagination of the mantle epithelium behind this cavity.

The embryological study shows that the tube which has previously been called the rectum is a reduced mantle cavity receiving the openings of the anus, the ureter and, at its mouth, the vagina. The new interpretation of the homologies of these parts calls for a revision of the systematic position of the Onchidiidae; its affinities with the prosobranchs are discussed and it is concluded that the family should be regarded as an early offshoot from the main stem of the opisthobranchs.

REFERENCES

AREY, L. B. & CROZIER, W. J., 1921. On the natural history of *Onchidium*. *Journ. Exp. Zool.*, Vol. XXXII, pp. 443–502.

BERGH, R., 1885. Ueber die Verwandtschaftsbeziehungen der Onchidien. *Morph. Jb.*, Bd. X, pp. 172–81.

BROCK, J., 1883. Besprechung der Arbeit von Joyeux-Laffuie. *Biol. Zbl.*, Bd. III, pp. 370–4.

CUVIER, G., 1804. Mémoire sur l'Onchidie, genre de mollusques nus, voisin des Limaces, et sur une espèce nouvelle, *Onchidium Peronii*. *Paris, Ann. Mus. Hist. nat.*, T. V, pp. 99–122.

ELLIS, A. E., 1926. *British Snails*. Oxford, Clarendon Press.

FISCHER, H., 1892. Recherches sur la morphologie du foie des Gastéropodes. *Bull. sci. Fr. Belg.*, T. XXIV (ser. 4, T. III), pp. 260–346.

FORBES, E. & HANLEY, S., 1853. *A History of British Mollusca and their Shells*. London.

FRETTER, V., 1937. The structure and function of the alimentary canal of some species of Polyplacophora (Mollusca). *Trans. Roy. Soc. Edinb.*, Vol. LIX, pp. 119–64.

—— 1939. The structure and function of the alimentary canal of some tectibranch molluscs, with a note on excretion. *Trans. Roy. Soc. Edinb.*, Vol. LIX, pp. 599–646.

—— 1941. The genital ducts of some British stenoglossan prosobranchs. *Journ. Mar. Biol. Assoc. U.K.*, Vol. XXV, pp. 173–211.

GRAHAM, A., 1932. On the structure and function of the alimentary canal of the limpet. *Trans. Roy. Soc. Edinb.*, Vol. LVII, pp. 287–308.

HALLER, B., 1894. Betrachtungen über die Nieren von *Onchidium celticum* Cuv. *Verh. naturh.-med. Ver. Heidelberg*, N.F. Bd. V, pp. 1–10.

HEIDERMANNS, C., 1924. Über den Muskelmagen der Süsswasserlungenschnecken. *Zool. Jb. Abt.* 3 *Allg. Zool.*, Bd. XLI, pp. 335–424.

HIRASAKA, K., 1922. On the structure of the dorsal eyes of *Onchidium* with notes on their formation. *Annot. zool. jap.*, Vol. X, pp. 171–81.

HOFFMANN, H., 1929. Zur Kenntnis der Oncidiiden (Gastrop. Pulmonés). Teil II. Phylogenie und Verbreitung. *Zool. Jb. Abt.* I *Syst.*, Bd. LVII, pp. 253–302.

HOWELLS, H. H., 1942. The structure and function of the alimentary canal of *Aplysia punctata*. *Quart. Journ. Micr. Sci.*, Vol. LXXXIII, pp. 357–97.

JHERING, H. VON, 1877. Ueber die systematische Stellung von *Peronia*, und die Ordnung der Nephropneusta. *Erlangen, Sitzber. Phys. Med. Soc.*, Bd. 9, pp. 131–68.

JOYEUX-LAFFUIE, J., 1882. Organisation et développement de l'Oncidie *Oncidium celticum* Cuv. *Arch. Zool. exp. gén.*, Vol. X, pp. 225–383.

LABBÉ, A., 1934. Opisthobranches et Silicodermes (Oncidiades). *Rés. sci. Voy. Indes orientales néerl. Prince Léopold Belg.*, Vol. II, fasc. 14 (i), pp. 1–83.

LINKE, O., 1933. Morphologie und Physiologie des Genitalapparates des Nordseelittorinen. *Wiss. Meeresuntersuch.*, Vol. XIX, no. 5, 60 pp.

MAZZARELLI, G., 1906. Contributo alla conoscenza delle larve libere degli opisthobranchi. *Arch. zool. ital. Napoli*, Vol. II, pp. 19–78.

PLATE, L., 1893. Studien über opisthopneumone Lungenschnecken. II. Die Oncidiiden. *Zool. Jb. Abt.* 2 *Anat.*, Bd. VII, pp. 93–234.

SEMPER, C., 1876–7. Einige Bemerkungen über die "Nephropneusten" von v. Jherings. *Arb. Zool. zool. Inst. Würzburg*, Bd. III.

WISSEL, K. VON, 1898. Beiträge zur Anatomie der Gattung *Oncidiella*. *Zool. Jb.*, suppl. Bd. IV (*Fauna Chilensis*, Bd. I), pp. 583–640.

THE LARVAE OF THE GENUS *PORCELLANA* (CRUSTACEA DECAPODA) AND RELATED FORMS

By Marie V. Lebour, D.Sc.
Naturalist at the Plymouth Laboratory

(Text-figs. 1–12)

Although the larva of *Porcellana* is one of the earliest known decapod larvae and at a later date the different stages of *P. longicornis* were well described by Sars (1889), there is yet much that is unknown. Few larvae have been actually hatched from the egg and in no case has the number of larval stages been definitely ascertained. In order to fill in some of the gaps in our knowledge a detailed study of the two common Plymouth species was begun (*P. longicornis* and *P. platycheles*). Unfortunately, war conditions made it difficult to obtain material and many specimens were lost as the result of air-raids; it was therefore not until the summer of 1942 that the work could be finished.

It is now possible to distinguish between the two species in all stages. Both have been hatched from the egg, larvae from the plankton have moulted and the post-larvae have been obtained from the last larvae. A comparison with Gurney's (1938*a*) notes on the species from the Red Sea and his general comments on the larvae of the genus and its relatives (1942) is of much use. These, with the first larvae of *Petrolisthes armatus* hatched by myself at Bermuda and certain larvae described by other workers, have made it possible to make some progress in the elucidation of the relationships of the larvae.

Porcellana longicornis and *P. platycheles* are both common at Plymouth; but whereas the latter is confined to coastal waters and lives between tidemarks and down to about 3 fathoms, the former has a much wider range and although occurring with *P. platycheles* between tidemarks extends to well beyond the Eddystone grounds. It was thought that a third species was present in the outside waters (see Gurney, 1942), but this larva has now been proved to belong to *P. platycheles*.

Large numbers of *Porcellana* larvae are caught in the tow-nets from between the Breakwater and the Rame-Eddystone grounds. It has always been assumed that these represented the two species. All the late larvae, with the exception of a very few specimens, rarely obtained, possessed three pairs of pleopods and this fact gave rise to the assumption that both species had only three pairs. The few specimens with four pairs of pleopods were regarded as a new species. It is now certain that all those with three pairs of pleopods belong to *P. longicornis* and the few rare specimens with four pairs belong to *P. platycheles*. The fact that under present conditions tow-nettings were unobtainable beyond the Breakwater led to the detailed study of the plankton of the inshore waters—hitherto rather neglected for the richer outside hauls. Larvae of *P. platycheles* (recognized from comparison with those hatched from the parent) were collected in these hauls and moults from the first to the second stages obtained, proving without a doubt that *P. platycheles* has four pairs of pleopods and is identical with the form rarely present in the outside hauls. The larvae of *P. platycheles*, however, are never plentiful even in the inshore samples, probably because of their large size and because only small tow-nets can at present be used. Larvae of *P. longicornis* are more abundant, but they are not caught in large numbers. It is samples taken with the 2 m. ring trawl at Station L_4 and beyond, which at times are so full of the larvae of *P. longicornis*.

P. longicornis breeds from January to November, the larvae being most abundant in spring and summer. *P. platycheles* has a shorter breeding season beginning in April or May (very rarely March) and finishing by September, June to the end of July being its usual maximum breeding period.

Sars (1889) has described the larvae of *P. longicornis* in detail; he found two distinct stages in the plankton, but suggested that the earliest was not the first—a suggestion which is supported by hatching the larvae at Plymouth. A later stage than his last also occurs at Plymouth although the post-larvae obtained all moulted from the less developed form similar to his last. His description of the two stages of *P. longicornis* may be taken as typical of the two main stages of a Porcellanid larva. As is shown below, however, there are three or four stages (possibly five) in *P. longicornis* and two (possibly three) in *P. platycheles*.

In all Porcellanid larvae known there are two main stages (I and II). Stage I is exemplified by Sars's earliest stage, in which the exopods of the first and second maxillipedes bear 4 setae and the telson 7+7 setae, the third maxillipede and legs being rudimentary and very small. Stage II is exemplified by Sars's last stage, in which the exopods of the first and second maxillipedes bear 10–12 setae, that of the third either having setae (usually 4) or not, the endopod and also the legs being non-functional, but more developed. The telson either has 8+8 setae (*Porcellana*) or 7+7 with a central tooth (*Petrolisthes*). The first of the main stages may include two, called here I*a* and I*b*, and the second may include two or three, called here II*a*, II*b* and II*c*. Gurney (1938*a*) found only two stages in *Porcellana inaequalis* and *Petrolisthes*? sp. from the Red Sea. Menon (1937) concluded that there were probably three in his Indian Porcellanids.

The young is hatched as a pre-zoea (Fig. 1*a*) which is much the same in all the species in which it is known. It lives for some hours, coming up to the light and to the surface and swimming vigorously. The antennule has two large feathered apical spines with aesthetes showing at the base, and may or may not have a lateral spine (Fig. 1*b*). The antenna (Fig. 1*c*) has 5 large spines covering the zoeal exopod and a single spine over the endopod (*Porcellana longicornis*, *P. platycheles* and *P. inaequalis*) or 6 over the exopod in

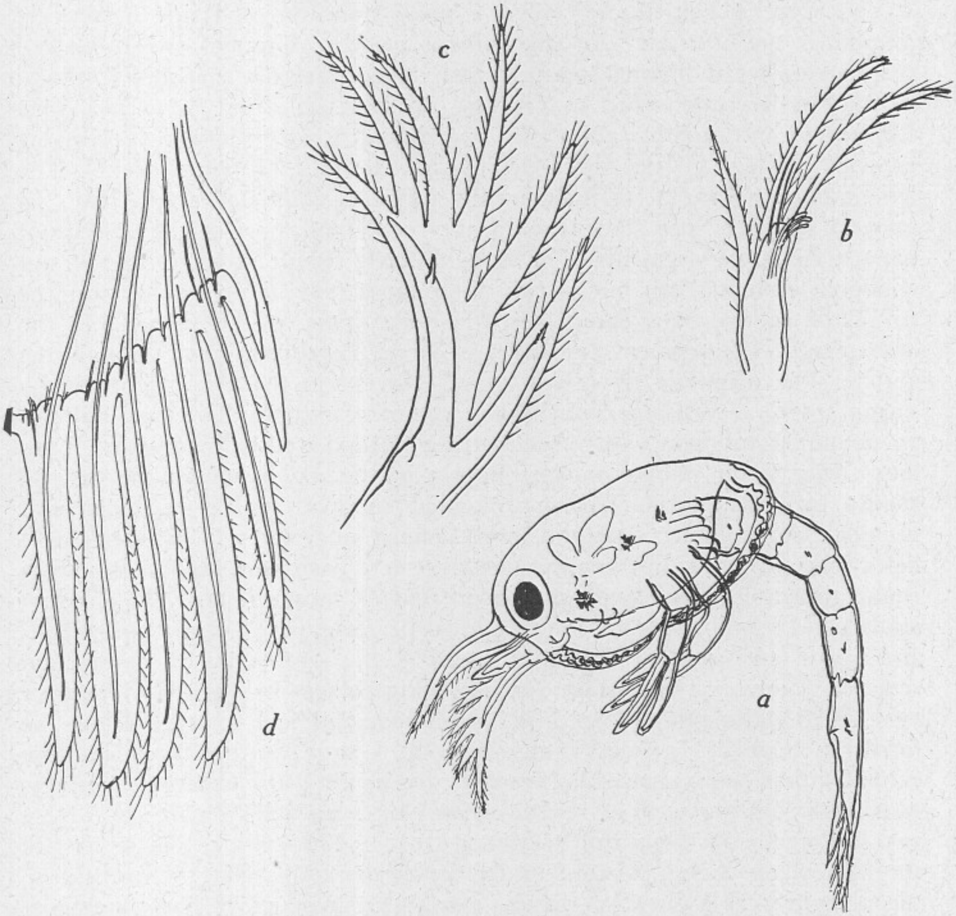


Fig. 1. Pre-zoea of *Porcellana platycheles*: *a*, side view, 2·4 mm. long without long spines; *b*, antennule; *c*, antenna; *d*, telson.

a species from Samoa described by Gurney (1926, 1942) in which there is also a lateral spine on the endopod. The telson has 6+6 spines, the first small and smooth, the others long and feathered. There is no trace of the second zoeal spine until just before the pre-zoeal cuticle is shed, when it may be present as a minute rudiment. The small posterior spine of the zoea internal to the seventh spine is included in the sixth pre-zoeal spine (Fig. 1*d*;

see also Gurney, 1942, p. 53, fig. 14*a*). The rostral and posterior carapace spines of stage I are crumpled up under the pre-zoeal cuticle.

The pre-zoea moults into stage I, either *a* or *b* (*a* in *P. longicornis*, *b* in *P. platycheles*). The zoea in all stages has a very long rostral spine and the posterior angles of the carapace are drawn out into long spines, the posterior carapace spines. The telson is triangular and bluntly pointed posteriorly. The second spine is hair-like. There is a small spine on each side posteriorly internal to the fifth seta. An anal spine is present. Uropods are absent and there are only 5 abdominal somites which may or may not have lateral spines. [A curious larva described by Gurney (1924*c*, 1942) from the *Terra Nova* Expedition and possibly not a true Porcellanid, is exceptional in possessing uropods in stage II, the telson deeply forked and an antennal scale.] The antennule is a simple rod armed with aesthetes and setae at the tips. In stage II segments may show through the cuticle and there may be groups of hairs to mark the segments. The antenna has a simple rod-like exopod and endopod without setae, but usually there are a few minute spines near the tip of the endopod and sometimes a hair-like spine on the exopod. In the latest stages the segments of the post-larval flagellum show through the cuticle. The mandible is without a palp (except in the form identified by Faxon (1879) as *Polyonyx*, which has a rudimentary one). The maxillule has an unjointed endopod with 3 setae at the tip and well-defined setose inner lobes. The outer margin bulges slightly in the region where the exopod should be. The maxilla has an unjointed endopod with 3 terminal and, usually, 2 pairs of inner setae and 4 well-defined inner setose lobes; the exopod has a long posterior lobe bearing one large seta posteriorly and 5 or 6 setae round the anterior and outer margin in stage I, more in stage II. The first and second maxillipedes are functional with 4 setae on the exopod in stage I, and 10–12 setae in stage II, and an endopod of 4 segments with no external setae on segments 1–3 in stage I, these being present in stage II. There are very small rudiments of the third maxillipede and legs in stage I, but the former is bilobed. In stage II the endopod is large, but not functional, the exopod either being unarmed (*Porcellana inaequalis*, *Petrolisthes* sp. (Gurney, 1939*a*)) or bearing setae (4 in *Porcellana longicornis* and *P. platycheles*, 3, 4 or 6 in Porcellanids described by Menon (1937)). The legs are non-functional, the fifth being curved forward under the others and chelate. There are no pleopods in stage I, but there may be 3 or 4 pairs in stage II. These are never setose, but are long in the stage (II*b* or II*c*) which changes to the post-larva. The post-larva differs markedly from the adult and certain characters have not yet appeared. There are now six abdominal somites and setose uropods; 3 or 4 pairs of setose pleopods are present. The telson is a plain plate. The legs are functional and the antennal flagellum long.

The number of larval stages varies in different species and even in the same species, but stages I and II are always present. Stage I may consist of two stages (I*a*, I*b*) or of one stage only (I*b*), stage II may consist of three stages (II*a*, II*b*, II*c*) or two (II*b*, II*c*) or of one only (II*b*). It is impossible to be certain that there is a moult between I*a* and I*b* or between II*b* and II*c* and a very wide range of individual variation is indicated. It is probable that the normal life-history of the genus is I*b*–II*b*–post-larva, as in *P. platycheles* (II*c* also being present as an alternative to II*b*) and possibly others, and these are more or less stable, but in *P. longicornis* (I*a* or *b*–II*a*–II*b* or *c*–post-larva) there exists a state of great variability not as yet settled down to normal.

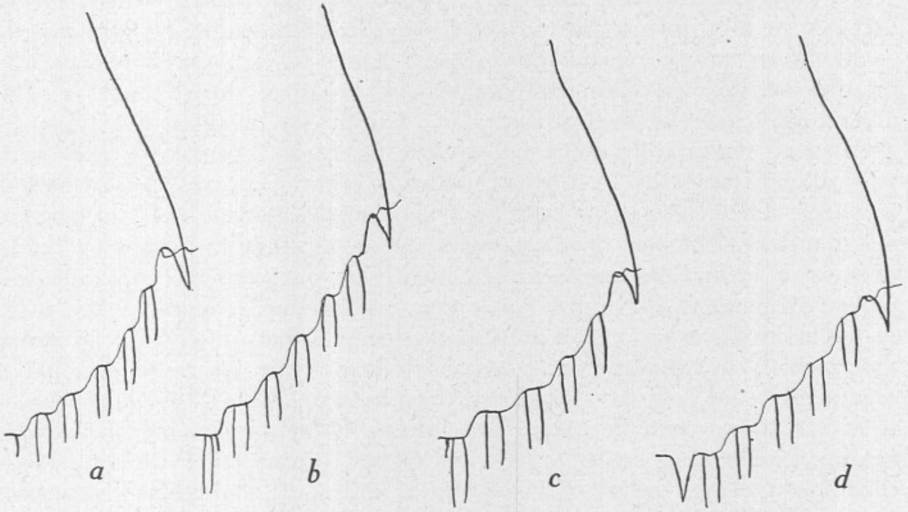


Fig. 2. Diagram of telson of *Porcellana* and *Petrolisthes*: *a*, *Porcellana longicornis*, stage I; *b*, *P. longicornis*, stage II; *c*, *Petrolisthes armatus*, stage I; *d*, *Petrolisthes* sp. (after Gurney), stage II.

Gurney (1938*a*) has shown that there are 4 pairs of pleopods in the larvae of *Porcellana inaequalis* and in *Petrolisthes* sp., and it is now found that there are also 4 pairs in *Porcellana platycheles*; therefore, as he truly remarks, this is not a generic character as there are 3 pairs in *P. longicornis*. He has also shown that *Porcellana* and *Petrolisthes* have a different type of telson respectively. *Porcellana* in stage I has the fifth long seta situated outside the central prominence, *Petrolisthes* has it on the central prominence (Fig. 2). In stage II *Porcellana* has a sixth long seta on the central prominence, whereas in *Petrolisthes* there is no sixth seta but a central tooth. As *Petrolisthes armatus* from Bermuda, moulted from the pre-zoea hatched from the egg, has a similar type of telson to Gurney's *Petrolisthes* it may safely be assumed that he is right in attributing his form to that genus. The type of telson thus appears to be a good generic character.

References to the early descriptions of unidentified Porcellanid larvae are here omitted, but Hesse (1884) has described the larva of what he regarded as *Porcellana platycheles* from the stomach of a mackerel. It appears from his description and figures that this is clearly *P. longicornis*.

THE LARVAE OF THE GENUS *PORCELLANA*

Of this genus we know the pre-zoea, stage I and stage II and post-larva of *Porcellana longicornis* (see Sars (1889) and the present work), *P. platycheles* (the present work) and *P. inaequalis* (pre-zoea and larvae only) from the Red Sea (see Gurney, 1938*a*). Menon (1937, 1940) describes what he believes to be the larva and post-larva of *P. serratifrons* from India. Other larvae ascribed by him provisionally to *Petrolisthes* probably belong to *Porcellana*.

All the larvae are transparent with red, orange or yellow pigment, usually on the rostrum, posterior carapace spines, region of the stomach, on the abdominal somites and telson and at the base of the maxillipedes. The pre-zoea swims actively for some hours. The larvae are very active and swim vertically, horizontally or sideways, usually front foremost, dorsal surface upwards. They swim up to the light and usually remain near the surface when healthy. The main food consists of debris, but they are capable of eating dead or moribund organisms and frequently devour their own brothers and sisters. Sometimes the empty long spines can be seen emerging at the anus. A specimen was seen to eat a moribund copepod. The contents of the gut in specimens from the plankton are entirely detritus with no visible remains of organisms. The post-larva feeds on detritus also, picking up small pieces from the stones with its chelae and putting them into its mouth, besides feeding by the filter on its third maxillipedes as is usual in the adult Porcellanids. The post-larvae of *P. longicornis* and of *P. platycheles* which were watched used the third maxillipedes alternately as described by Nicol (1932) or both together. The fifth legs were used to pick off any extraneous substance from the body which was kept scrupulously clean.

All the known larvae of *Porcellana* agree in having the telson with the fifth long seta outside the central prominence in stage I, and in stage II having a sixth seta situated on the central prominence. The third maxillipede in stage II may bear 4 setae on its exopod (*P. longicornis*, *P. platycheles*) or be unarmed (*P. inaequalis*, see Gurney, 1938*a*). According to Menon (1937, 1940) there are 6 setae in the larva attributed to *P. serratifrons*.

Porcellana longicornis (L.) (Figs. 3, 5–7, 8*a*, *b*, 9)

The earliest recorded female in berry occurred at the end of January (28. i. 38) in a *Chaetopterus* tube from the outside grounds. The eggs were nearly ready to hatch. The earliest larvae recorded in the plankton were at the end of February (24. ii. 38). In subsequent years they were later and they usually begin about March with a maximum from May to August and continue until October, rarely November. Early larvae were still in the inshore plankton in the middle of November 1941. The eggs when ready to hatch measure 0·48 × 0·40 mm. The pre-zoea is about 1·6 mm. in length, exclusive of the long spines on the antennae and telson. After swimming about for some hours at the surface nearest the light the pre-zoea moulted to the first larval stage, I*a*.

Stage Ia (Fig. 3*a*, *b*). This stage is distinctly smaller than Sars's first stage, the legs are not so well developed, but the posterior carapace spines are slightly longer. The newly moulted larva measures 4·5–4·8 mm. from spine to spine. Rostrum 2·9 mm., posterior carapace spines 1·1 mm., or rather more, body 1·6 mm. in length. Red pigment occurs on the rostrum, chiefly at the tip and in the centre so as to form bars, in the mouth region, on the sides of the abdominal somites, on the base of the first and second maxillipedes and on the tips of the posterior carapace spines. The region of the liver is usually greenish. There are fine spines on the rostrum; the posterior spines each have two conspicuous spines ventrally near the origin, the first the larger of the two, and small spines behind. This is an important difference in distinguishing the species from *Porcellana platycheles*, for in stage I of the latter the large spines are absent. The rudiments of the third maxillipedes are bilobed, but the legs are mere buds (Fig. 3*b*). The third seta of the telson (=the first long seta) is armed at the tip in a peculiar manner with large and conspicuous hook-like spines (Fig. 4*a*). The significance of these spines as a specific character was suggested by Dr Gurney (private communication) and is of importance, as here again we have a distinguishing character from *P. platycheles* in which the armature of the seta is quite different with long fine spines. *Petrolisthes armatus* has long fine spines at the ends of all the setae.

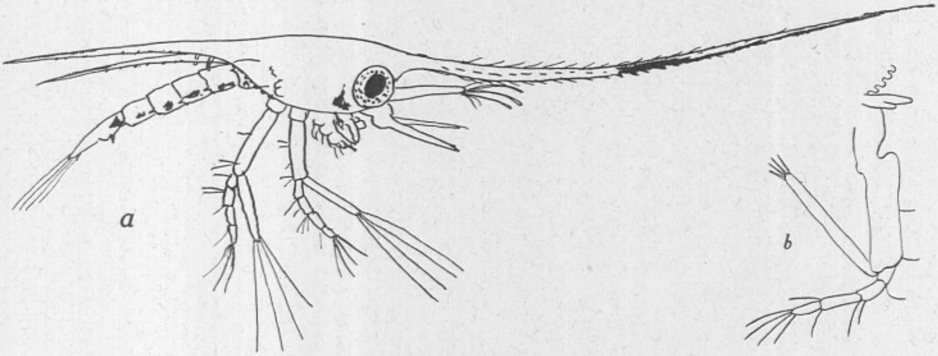


Fig. 3. *Porcellana longicornis*: *a*, stage I*a* from pre-zoea from egg, 4·6 mm. from spine to spine; *b*, second and third maxillipede and legs of same.

The pre-zoea in my experience has always moulted to I*a* and never to I*b*. I*a* has once moulted to II*a* which in all other cases came from I*b*. Thus *a* and *b* may be alternative stages. No moult has been observed from I*a* to I*b* and the way in which I*b* arises is consequently uncertain. The specimen of II*a* derived from I*a* was smaller than those from I*b* and this may account for the great variation in size in the later stages.

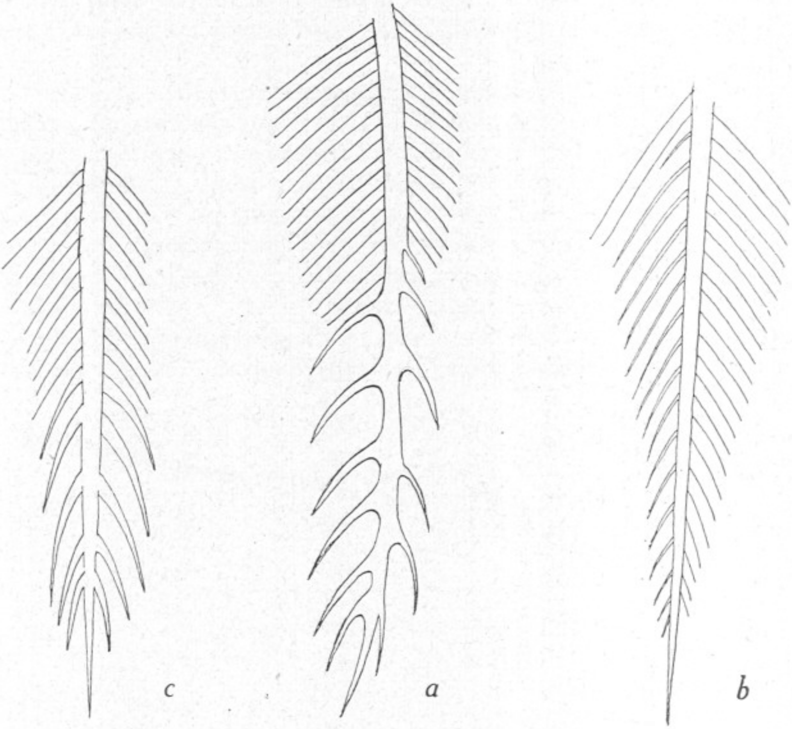


Fig. 4. Third seta of telson: *a*, *Porcellana longicornis*; *b*, *P. platycheles*; *c*, *Petrolisthes armatus*.

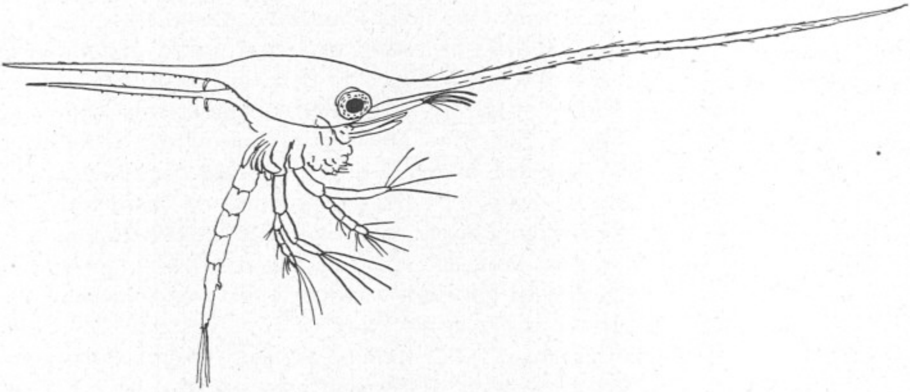


Fig. 5. *Porcellana longicornis*. Stage I *b*, from plankton, 5·8 mm. from spine to spine.

Stage Ib (Fig. 5). This stage agrees exactly with Sars's first stage and is the commonest stage of I in the plankton. The length of a typical specimen is 5·84 mm. from spine to spine, but the specimens may be longer or shorter. The rostrum is 3·3 mm.; the posterior carapace spines 1·5 mm; the length of the body, without rostrum, 2·2 mm. The form is the same as I*a* and the armature of the spines is the same, but the third maxillipede and legs are more developed. This stage from the plankton moulted into II*a* many times in finger bowls. It has never been seen to moult into II*b*.

Stage IIa (Figs. 6, 7 *a–f*). This stage is earlier than Sars's last stage, but of much the same form. It is frequently found in the plankton, and has moulted once from I*a* and many times from I*b* and itself moults to II*b*. The large ventral spines on the posterior carapace spines have now disappeared and only a few short spines remain. It has all the characters of stage II. The pleopods are very small and occur on somites 2–4. The telson has a sixth pair of long setae situated on the central prominence between the two short hairs. There are 11 setae on the exopods of the first and second maxillipedes and 4 on the exopod of the third maxillipede. The length of the long spines is very variable. A specimen which moulted from I*a* (4·5 mm. from spine to spine) measured 7·5 mm. from spine to spine. A typical specimen moulted from I*b* measured 8·8 mm. from spine to spine, the rostrum measured 5·6 mm., the posterior spines 2·5 mm., the body 2·6 mm. As a rule the posterior spines are about one-third the length of the rostrum, sometimes more, but never so much as half as they are in *Porcellana platycheles*. The legs are much more developed than they are in stage I, but still slender. Their lengths and the length of the pleopods are very variable. The endopod of the first leg shows signs of a chela, as also does the fifth leg which is hidden under the others. This stage moulted several times in finger bowls to stage II*b*. It is the stage figured by Gurney (1942, p. 256) as *Porcellana* sp.

Fig. 6. *Porcellana longicornis*. Stage II*a* from I*b*, 9·3 mm. from spine to spine.

Stage II*b* (Fig. 7, *g–l*). This is similar to Sars's last stage and may be taken to be its equivalent although the third maxillipede and legs are rather longer. It differs little from II*a*, but the pleopods are distinctly longer and the third maxillipede and legs more developed. The rostrum and posterior spines vary much in length. A specimen may measure 9 mm. from spine to

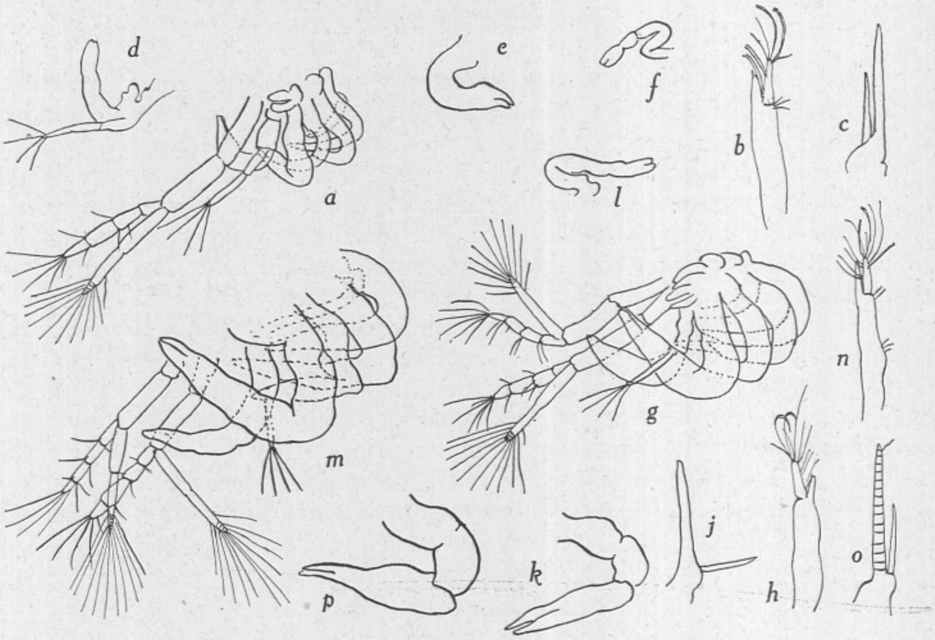


Fig. 7. *Porcellana longicornis*: *a*, stage II *a*, rather more developed than Fig. 6 from plankton; *b*, antennule; *c*, antenna; *d*, third maxillipede; *e*, first leg; *f*, fifth leg; *g*, stage II *b*; *h*, antennule; *j*, antenna; *k*, first leg; *l*, fifth leg; *m*, stage II *c* or late *b*; *n*, antennule; *o*, antenna; *p*, first leg.

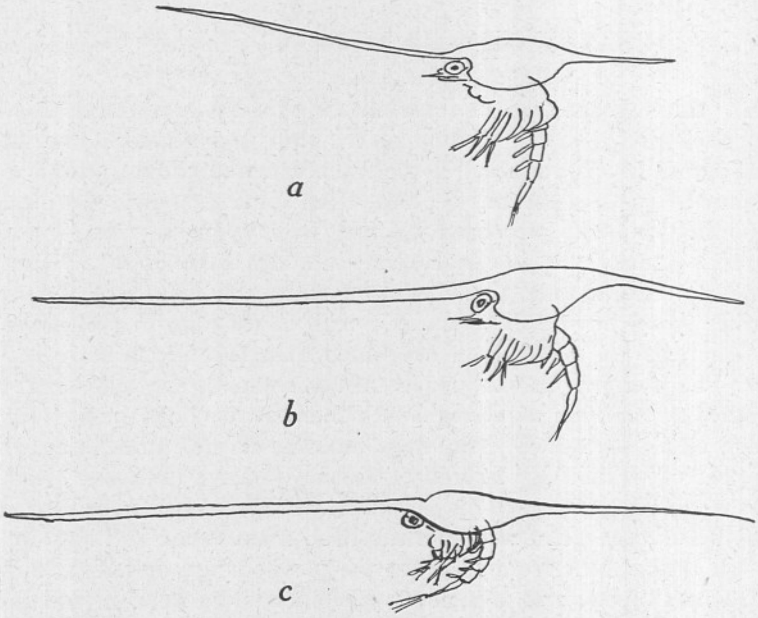


Fig. 8. *a*, *b*. *Porcellana longicornis*, last stage: *a*, with short spines; *b*, with long spines; *c*, *Porcellana platycheles*, last stage.

spine, but 11 mm. is not uncommon (Fig. 8). In some specimens the posterior spines are nearly double the length they are in others. In one measuring 9 mm. from spine to spine the rostrum is 5 mm.; posterior spine 2·5 mm.; body 3 mm. in length. Thus it is only the body and appendages which are larger than II *a*. This stage moulted several times to the post-larva, but there is a more advanced stage frequently found in the plankton which is here called II *c*. It has not been reared from II *b* nor has the post-larva been obtained from it. In lengths of spines and body it differs little from II *b*, but the third maxillipedes and legs are considerably larger (Fig. 7, *m–p*) making the thoracic region very heavy. The pleopods are larger and longer and the antennal flagellum is conspicuously jointed under the cuticle. It is possible that this is an alternative stage to II *b* or perhaps merely II *b* grown much more than usual before moulting to the post-larva, or it may be that a moult has taken place because conditions were unsuitable for an early change to post-larva.

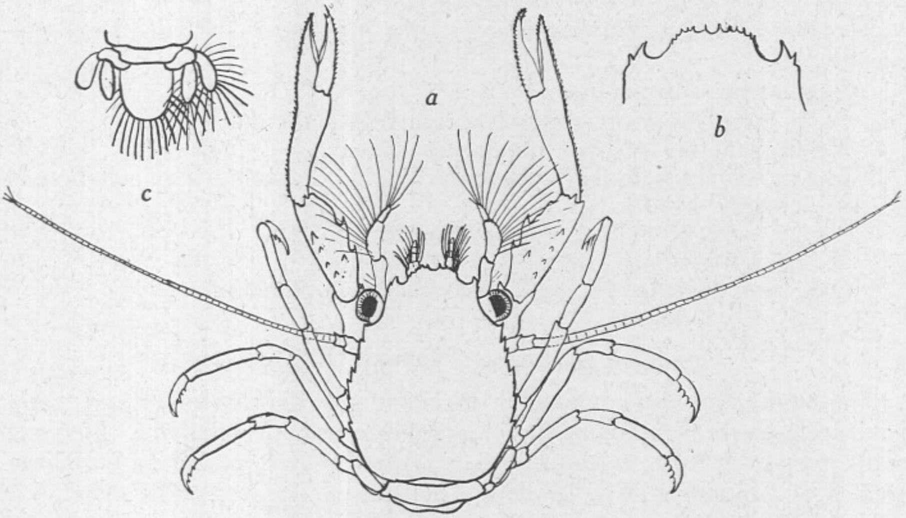


Fig. 9. *Porcellana longicornis*: *a*, post-larva from II *b*, carapace 1·6 mm. long; *b*, front of carapace; *c*, telson and uropods.

The Post-larva (Fig. 9 *a*, *b*, *c*). This was obtained several times by moult from II *b*. It is clear and transparent with small red chromatophores scattered about the body, especially in the front of the carapace and on the legs. Most of the chromatophores appear yellow by reflected light except those in the abdominal region which remain red. The post-larva can be recognized as a *Porcellana*, but is not very like the adult. The carapace measures 1·6 mm. in length and 1·3 mm. in breadth. The front is 3-lobed, the middle portion minutely toothed, whilst the lateral parts end in a strong tooth with small laterals. The sides of the carapace have strong teeth for nearly the whole length. The legs are functional, the chelae held out in front of the body when swimming, like a *Galathea*. The carpus of the chela is armed with 2 strong internal teeth, the propodus being fairly slender with hardly any hairs and bordered externally with small teeth. The dactyl has a similar armature. The dactyls of the remaining legs end in fairly strong claws and have 3 or 4 additional teeth. The sixth abdominal somite is now separated from the telson and bears setose uropods. There are 3 pairs of setose pleopods, on somites 2–4. The telson is not yet divided by sutures. It is rounded posteriorly and bordered by many setae. Although specimens lived for some time in bowls and plunger jars they all died before any moult was obtained.

The post-larval stage figured by Stebbing (1893) and attributed by him to this species is correctly identified, although Williamson (1915) regards it as probably belonging to *Porcellana platycheles*. Williamson has roughly described the larvae of *P. longicornis* and *P. platycheles*, but the details are insufficient to identify the two species accurately.

We thus have the following stages in the life history of *Porcellana longicornis*:

Egg hatches as a pre-zoea.
I*a* by moult from pre-zoea, also, rarely, in plankton.
II*b* in plankton only (not obtained by moult).
II*a* by moult from I*a* (once only) and I*b* (usually), also common in plankton.
II*b* by moult from II*a*, also common in plankton.
II*c* in plankton only (not obtained by moult).
Post-larva from II*b* by moult, also, rarely, in plankton.

Porcellana platycheles (Pennant) (Figs. 10, 11)

The adults are very common in the Plymouth district under stones between tide-marks on all rocky shores and down to about 3 fathoms. Breeding takes place from April to August, rarely earlier or later. No larvae have been seen after September. The larvae are present in the late spring and in the summer plankton inside the Breakwater, very rarely outside. The eggs are brownish green, measuring when ready to hatch 0·48–0·52 mm. in length and 0·42–0·45 mm. in breadth. The egg hatches as a pre-zoea measuring 2·5 mm. in length without the long spines. The rostral and posterior spines are folded in and much wrinkled (Fig. 1). There is red and orange pigment on the rostrum and spines and red and orange chromatophores show beneath the cuticle on the thorax and red on the abdominal somites. The antennule has long feathered spines, two at the tip and one on the side, the aesthetes of the first larva protruding slightly but not covered by spines. The antenna has 5 long feathered spines on the exopod and one on the endopod. The third maxillipede and legs are further developed than they are even in stage I*a* of *P. longicornis*.

The First Larva (stage I*b*, Fig. 10*a*). The first larva which moulted from the pre-zoea is in a later stage than in *P. longicornis*, stage I*a* being omitted. The rostral and posterior spines are very long and coloured red for nearly the whole length without bars. The red is, however, masked by a dull brown so that it rarely appears bright. The length from spine to spine in a typical specimen is 7·5–8 mm. In some of 8 mm. the rostrum measures 4·5 mm.; posterior spines 2·5 mm.; body 2·2 mm. The posterior spines are always half or more the length of the rostrum. The animal is clear and colourless except for a faintish pink tinge in the thorax, patches of red on the thorax and at the base of the maxillipedes, on the sides of the abdominal somites and base of telson. The rostrum curves upwards slightly and is covered with fine spines. The posterior spines reach a long way beyond the telson and have a few short spines, but no large spines such as distinguish the first stage of *P. longicornis*. The third telson spine (first long seta) has long fine spines, coarser however than on the main part, at its tip (Fig. 4*a*), in contrast to the hook-like spines of *P. longicornis*. Rudiments of the third maxillipede and legs are well advanced. This stage from the plankton moulted to the second stage similar to II*b* of *P. longicornis*, II*a* being omitted.

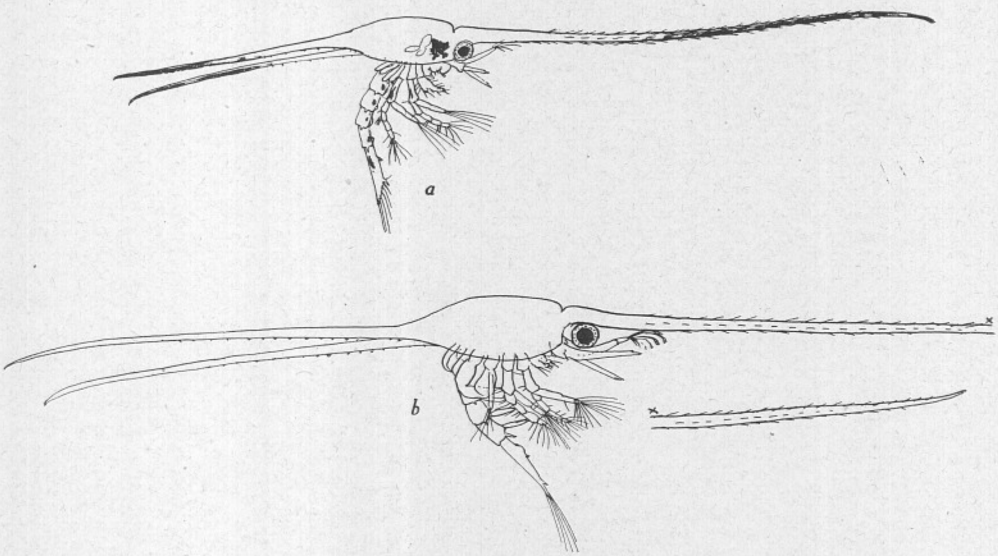


Fig. 10. *Porcellana platycheles*: *a*, stage I*b* from plankton, 8 mm. from spine to spine; *b*, stage II*b* from plankton, 11·5 mm. from spine to spine.

Stage IIb (Fig. 10*b*) moulted from I*b*, and was also obtained from the plankton. It is similar to II*b* of *P. longicornis*, but is variable in size. There are 4 pairs of pleopods, on somites 2–5, and these vary in length. In a specimen 11·5 mm. in length from spine to spine the rostrum was 7 mm.; posterior spine 4·2 mm.; body 3·5 mm. The telson has the sixth long seta situated on the central prominence as in all the species of *Porcellana*. There are 12 setae + a very small one on the exopods of the first and second maxillipedes and 4 on the third. There is a trace of the chela on the first leg and on the fifth leg and the legs are not very well developed. A specimen belonging to this stage from the plankton moulted to the post-larva in July and another one a few days afterwards. A third and a fourth died whilst moulting. There is a later stage similar to stage II*c* of *P. longicornis* in which the limbs are much more developed than in II*b*, but no moult was obtained from II*b*. One of these later stages died whilst moulting to the post-larva.

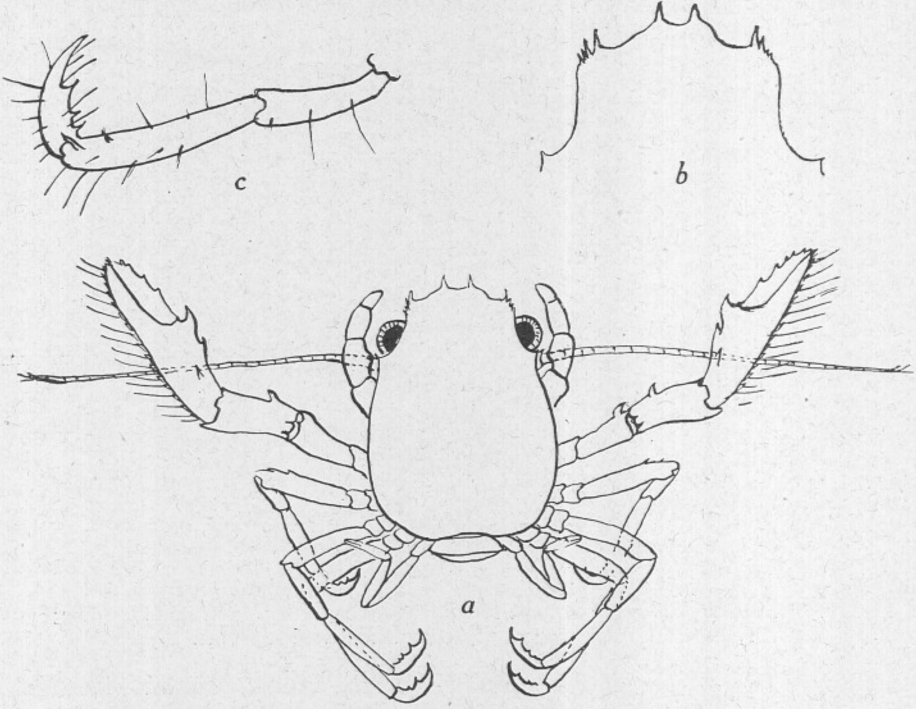


Fig. 11. *Porcellana platycheles*: *a*, post-larva from II*b*, 9·6 mm. across carapace; *b*, front of carapace; *c*, end of last leg.

The Post-larva (Fig. 11). This was obtained by moult from II*b* from the plankton. It is smaller than *P. longicornis* and the chelae are much more hairy and shorter. The telson is a simple plate. There are four pairs of setose pleopods and setose uropods. It is nearly colourless, but there are small scattered red chromatophores which become more conspicuous after the first day of moulting from the larva. No further stages were obtained. The carapace measured 1·44 mm. in length and 0·96 mm. in breadth. The front although roughly three-lobed projects more in the centre than in *P. longicornis* and has only 2 teeth, the lateral part having 4 teeth, the front one the largest. The third maxillipedes and first legs are shorter and broader than in *P. longicornis*, the first leg with only one internal tooth on the carpus and the propodus thick and stout with a fringe of thick hairs externally besides fine teeth. The dactylus is armed with a few strong teeth. The chelae in the two species foreshadow the form of the adult and it is easy to distinguish between them. The dactyls of the remaining legs have 3 teeth internal to the terminal claw.

The stages in the life history of *P. platycheles* may be summed up as follows:

Egg hatches as a pre-zoea.
I*b* by moult from pre-zoea.
II*b* from I*b* by moult.
II*c* in plankton (not obtained by moult).
Post-larva from II*b* and II*c* by moult.

P. platycheles thus has fewer stages than *P. longicornis*, I*a* and II*a* being omitted.

We are now in a position to compare the two species and the following table shows the chief differences:

	P. longicornis	*P. platycheles*
Number of larval stages	3 essential (2 alternative, making 5 in all) I*a*, I*b*, II*a*, II*b*, II*c*	2 essential (1 alternative, making 3 in all) I*b*, II*b*, II*c*
Posterior spines	about ⅓ rostrum, never ½	about ½ rostrum, never less
Third telson spine	with hooks at end	with fine setae at end
Pleopods (stage II)	3 pairs on somites 2–4	4 pairs on somites 2–5
Armature of posterior spines (stage I)	2 conspicuous spines ventrally near the origin	these spines absent
Rostrum	red in wide bars	red, masked with brown evenly, not in bars

The Larvae of the Genus *Petrolisthes*

Petrolisthes armatus was hatched from the egg in Bermuda, but the late stages are as yet unknown. Gurney (1938*a*) describes an early and a late stage of a Porcellanid from the Red Sea which he attributes to this genus with a query. As from the reason he gives it is extremely likely that this is so, and the early larva agrees in essentials with that of *P. armatus*, we may assume that it really is a *Petrolisthes*. They differ from *Porcellana* in two points: (i) in the first larva the seventh seta of the telson (fifth long seta) arises from the central prominence, and (ii) (in the Red Sea form and, presumably, in *Petrolisthes armatus*) there is a central spine instead of an extra pair of setae in the late larva. The Red Sea form has 4 pairs of pleopods. The three larvae ascribed to *Petrolisthes* by Menon (1937) have all the characters of *Porcellana*, but, on the other hand, his *Porcellanella* larva agrees with *Petrolisthes* in essentials.

Petrolisthes armatus (Gibbes) (Fig. 12)

This species was hatched from the egg as a pre-zoea which swam about for some hours before moulting to the first larva. It was unfortunately impossible to be sure of the characters of the pre-zoea as the cuticle was so extremely delicate that it was always damaged.

The First Stage (I*a*). The rostrum and posterior spines are colourless, but there are patches of red chromatophores in the mouth region, on the base of the second maxillipedes, on the sides of the abdominal somites and dorsally on the telson. The length from spine to spine is 9 mm.; posterior spines 1·6 mm.; rostrum 6 mm.; body 2 mm. The rostrum is covered with small spines and minute protuberances. The posterior spines are covered with small spines which continue on to the posterior edge of the carapace. The telson is as broad as it is long. The appendages are very similar to those of *Porcellana*. The rudiments of the third maxillipedes and legs are exceedingly small. The long setae on the telson all have coarse spines at the tip, but the third seta (first long seta) has them larger and more numerous. No further stages of this species were obtained.

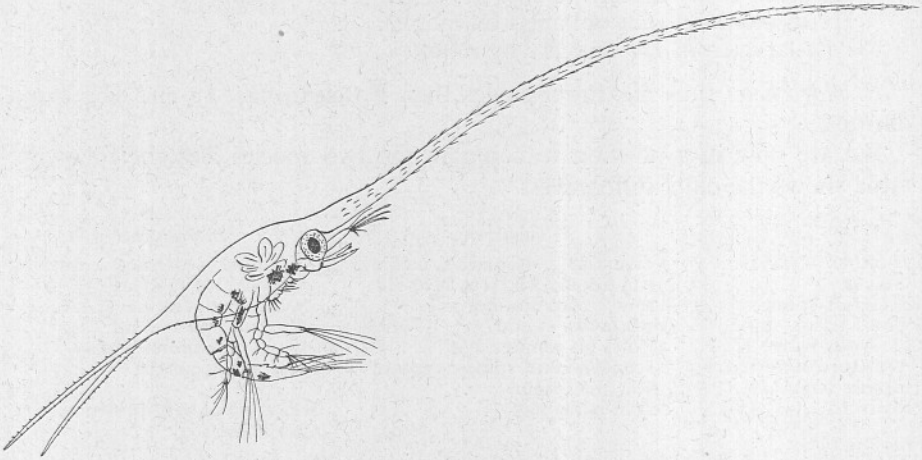


Fig. 12. *Petrolisthes armatus* from Bermuda. Stage I*a* from pre-zoea from egg, 9 mm. from spine to spine.

Gurney's (1938*a*) description of stage II of *Petrolisthes* sp. shows that it differs little from stage II of *Porcellana* except in the telson as noted above. The exopod of the third maxillipede has no setae. He regards the species as having only two stages.

Faxon (1879) describes a larva which he attributes to *Polyonyx macrocheles* which resembles *Porcellana* in its telson and has pleopods on somites 2–5, thus resembling *P. platycheles*.

The known Porcellanid larvae thus fall into two groups divided by the form of telson:

A. Fifth long seta of telson situated outside the central prominence, a sixth seta on the prominence in stage II.

  I. Pleopods on abdominal somites 2, 3 and 4
  [*Porcellana longicornis*. Menon's *Petrolisthes* sp. 1 and 2, and his Porcellanid forms 1 and 2 (probably all *Porcellana*) (see Menon, 1937, 1940)]

  II. Pleopods on abdominal somites 2, 3, 4 and 5
  [*Porcellana platycheles*, *P. inaequalis*, Menon's Porcellanid, form 3 (=*P. serratifrons*?), Faxon's *Polyonyx macrocheles*]

B. Fifth long seta of telson on the central prominence, in late stages, no sixth seta, but a central tooth present

  Pleopods on abdominal somites 2, 3, 4 and 5 (so far as is known)
  [*Petrolisthes armatus*, only first larva known, so number of pleopods not ascertained, Gurney's *Petrolisthes* (?) sp., Menon's *Porcellanella* (probably *Petrolisthes*)]

LITERATURE

The references to the larvae will be found in Gurney's (1939) *Bibliography of the Larvae of Decapod Crustacea*, Ray Society, and (1942) *The Larvae of Decapod Crustacea*, Ray Society.

The following work is not included in the above:

NICOL, E. A. T., 1932. The feeding habits of the Galatheidae. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 87–106.

MEASUREMENT OF PHYTOPLANKTON POPULATION BY THE PIGMENT EXTRACTION METHOD

By A. C. Gardiner

The Laboratories, Metropolitan Water Board, London

Harvey's method of estimating concentration of planktonic algae was used by him to study seasonal abundance of net-caught algae in the waters around Plymouth (Harvey, 1934). His data showed that, in these circumstances, good agreement was to be expected between depth of tint of an acetone extract of algal pigments and the amount of algae, reckoned in terms of number multiplied by area or volume of individual cells (Harvey, 1935, p. 182). It does not necessarily follow, however, that agreement will be equally good in different circumstances. It is known, for instance, firstly, that the 'Harvey Standard' has not the same colour composition as acetone extracts from freshwater phytoplankton and, secondly, that extracts from phytoplankton collected at different seasons or from different localities are not of uniform colour (Riley, 1938, p. 371; Kozminski, 1938, p. 144). The colour of an acetone extract varies with the qualitative composition of the plankton; hence in the sea, as in fresh water, it is not to be expected that extracts from collections in which Bacillariophyceae (diatoms), Chrysophyceae (e.g. *Phaeocystis*, see Savage & Hardy, 1934) or Dinophyceae predominate will be of the same colour. It is the object of this paper, firstly, to specify two essential conditions which must be satisfied before the pigment-extraction method can estimate without avoidable error the concentrations of marine or freshwater phytoplankton and, secondly, both to indicate certain problems in need of further investigation and to suggest some lines of approach to these problems.

THE PIGMENTS IN PLANKTONIC ALGAE

Recent work by Kylin (1927), Seybold & Egle (1938), Carter, Heilbron & Lythgoe (1939) and Heilbron (1942) on the pigments present in the various classes of algae must be the starting point for a critical examination of the reliability of any modification of the Harvey method. The following composite table, abridged from the works referred to above, summarizes the chief differences between some classes of algae, members of which are likely to form the major part of a marine or freshwater plankton.

Seybold & Egle (1938) are of the opinion that chlorophyll B is completely absent from all classes of algae examined by them, save the Chlorophyceae. This view is not shared either by Kylin (1927) or by Dutton & Manning (1941, p. 521), and the latter authors prefer to write about the 'near absence' rather than the absence of chlorophyll B in the diatom *Nitzschia closterium*.

	Chlorophyll A	Chlorophyll B	'Xanthophyll'	Carotin	Fucoxanthin	Flavoxanthin	Phycoerythrin	Phycoxanthin Myxoxanthophyll Aphanizophyll	Peridinin (Kylin, 1927)
CHLOROPHYCEAE	+	+	+	+	−	−	−	−	−
BACILLARIOPHYCEAE	+	−	+	+	+	−	−	−	−
CHRYSOPHYCEAE	+	−?	+	+	+	−	−	−	−
MYXOPHYCEAE	+	−	+	+	−	+	+	+	−
DINOPHYCEAE	+	−	+?	+	−	−	−	−	+

All workers are agreed, however, that in algae other than the Chlorophyceae the amount of chlorophyll B is very small indeed.

The pigments common to the classes of algae in the above table are chlorophyll A, 'xanthophyll' and carotin, and further work may show that these three are common to all aquatic algae. *The first essential condition, then, is that the estimate of algal abundance must be based on the concentration of one (or more) of these common pigments.*

THE SOLUBILITY OF ALGAL PIGMENTS IN ACETONE

If a mixed sample of freshwater algae be extracted for 12–24 hr. either with pure or 80% acetone in the cold, it is immediately apparent from examination under the microscope that only certain species have been completely decolorized. Virtually all diatoms will appear colourless; very many species of Chlorophyceae will apparently have lost but little of their original colour; certain of the Myxophyceae, including *Aphanizomenon*, *Anabaena* and *Microcystis* will be pale or dark blue; *Tribonema* (Xanthophyceae) and *Ceratium* (Dinophyceae) will be far from completely decolorized. Methyl alcohol is somewhat superior to acetone in its solvent action upon Chlorophyceae and Myxophyceae; it is inferior to acetone for diatoms. A mixture of equal parts of methyl alcohol and benzene has proved a good solvent. Pigments should be extracted as soon as possible after collection, for there is a loss of certain pigments when algae are dried in air (Seybold & Egle, 1938, p. 56). *The second essential condition, then, is that the solvent must extract completely the chlorophyll A, 'xanthophyll' or carotin from all members of a phytoplankton.*

THE CONSTANCY OF THE AMOUNTS OF THE COMMON PIGMENTS IN THE ALGAL CELL

In higher plants it is known, firstly, that 'the amount of chlorophyll A and B is not far from being constant, namely 0·6 to 1·4 grm. per 100 grm. of dried leaves', secondly, that 'the total weight of carotin and xanthophyll is from 0·07 to 0·2 grm. per 100 grm. of dried leaves, the ratio of carotin to xanthophyll being about 0·6' (Baly, 1940, p. 14). Excluding plants living in deep shade, it is probably not far from the truth to assert that the leaves of all terrestrial plants in this country receive light of the same spectral composition. In waters of widely differing colour and turbidity it is quite certain that the spectral composition of the subsurface light will not be constant (James & Birge, 1938, pp. 56–7; Cooper & Milne, 1938, p. 526). Stanbury (1931, p. 650) has shown that the colour of the diatom *Nitzschia closterium* varies from 'a rich dark brown shade to a decided greenish tint', when grown under light of different wave-length. Since the pigments normally present in diatoms are chlorophyll A, 'xanthophyll', carotin and fucoxanthin, it is, perhaps, legitimate to conclude by analogy from higher plants (Egle, 1937, p. 573) that any induced colour change will be the result of a shift in the ratios of the pigments. It follows, then, that in waters of widely differing colour and turbidity estimates of algal abundance based upon the extraction of one or more common pigments might be subject to considerable errors.

It has been suggested that the chlorophyll content not only varies with the physiological state of the algal cell, but also is not constant in different classes of algae (Riley, 1940, pp. 286–7). Chlorophyll separated by saponification with KOH, the method used by Riley, will be a mixture of chlorophylls A and B at those times when Chlorophyceae predominate; when other classes of algae are dominant it will be chlorophyll A only. The difference in the solvent action of acetone towards the several classes of algae must also be taken into account before the amounts actually present can be compared.

The reliability of the pigment-extraction method will depend to a great extent upon the constancy of the ratios of the common pigments both at different seasons and in different classes of algae, and it is imperative that measurements designed to put these points to the test shall be made. The selection of the common pigment should be influenced not only by the relative amount present in the different classes of algae, but also by the ease of separation (*vide infra*).

THE SEPARATION OF PLANT PIGMENTS

Complete separation of algal pigments is possible by the Tswett chromatographic technique (Carter, Heilbron & Lythgoe, 1939; Cook, 1941; Zechmeister & Cholnoky, 1941). Of the various algal pigments, chlorophyll A is present in the greatest concentration, whence it follows that extracts from smaller quantities of algae would give more easily readable colours than would be the case if another pigment were selected as the common pigment. Owing to the ease with which carotin can be separated, however, the selection of carotin has much to recommend it. One of the real advantages of the Harvey method is the speed with which determinations can be made, and it is very desirable to retain this feature if possible. Methods for the separation of carotin in silage are modifications of the Tswett technique and details will be found in a recent paper by Bolton & Common (1942, p. 51). Should, however, chlorophyll A be selected, the standard for comparison must either be an artificial one or a solution of chlorophyll A, as used by Krey (1939, p. 205). Commercial chlorophyll being almost certainly prepared from higher plants (and hence a mixture of chlorophylls A and B) cannot be used as a standard except for Chlorophyceae.

GENERAL CONSIDERATIONS

There is insufficient evidence at the moment upon which to base an opinion as to the magnitude of the error likely to arise from seasonal or specific variations in the content of a common algal pigment. Gillam, El Ridi & Wimpenny (1939, p. 86), it is true, have stated that 'it seems unlikely that any arbitrary colorimetric measurement based on the amount of chlorophyll present in an acetone or ether suspension will give more than a rough estimate of the diatoms present in any sample', but it seems essential to obtain further data. If it may be assumed for the moment that the concentration of a common pigment is relatively constant in all classes of algae, there is little doubt that estimates based upon the complete extraction of one or more common pigments will tend to approach nearer the truth than will estimates expressed in terms of numbers multiplied by area or volume of individual cells. The difficulties of making such weighted counts are considerable; at seasons when Myxophyceae are dominant in a plankton they are very great. If it should turn out that wide differences are characteristic of the several classes of algae, it may be necessary to know the relative proportions of the different classes present. The chlorophyll B, fucoxanthin, 'phycocyanin' ratio would provide an approximate estimate of the proportions of Chlorophyceae, Bacillariophyceae plus Chrysophyceae and of Myxophyceae.

Although, admittedly, there are times, particularly in the spring, when agreement between weighted counts and depth of tint of an acetone extract is good, it is very unlikely that any modification of the Harvey method proposed to date, including that in use in these Laboratories, is sufficiently free from avoidable error to be more than an approximation. Hence, regional surveys in which chlorophyll is used as a measure of phytoplankton production (Deevey, 1940) may well give a misleading impression. It is essential not only to recognize the limitations of the method, as Riley has done (1939), but also to appreciate the factors, which in all probability, are responsible for a large part of these limitations. There is little doubt that certain sources of error can be eliminated and no time should be lost in seeking an improved technique. Unless this be done there is danger that much field work will later be found to have been of doubtful value.

My thanks are due to Lt.-Col. E. F. W. Mackenzie, O.B.E., M.C., Director of Water Examination, Metropolitan Water Board, for permission to submit this article for publication.

SUMMARY

1. In order that the Harvey method shall estimate without avoidable error the concentration of marine or freshwater phytoplankton, it is essential, firstly,

that the estimate be based upon the concentration of one or more pigments common to all classes of algae, secondly, that the solvent selected shall extract completely the common pigments.

2. Attention is directed to the possible influence of the spectral composition of subsurface light upon the pigment ratios in algal cells.

3. The use of carotin as the common pigment is suggested owing to the ease with which this pigment can be separated.

4. Failure to recognize the limitations of the method may materially reduce the value of certain types of field work.

REFERENCES

BALY, E. C. C., 1940. *Photosynthesis*. London.

BOLTON, W. & COMMON, R. H., 1942. Modifications of Moon's method for the estimation of Carotene in silage. *Journ. Soc. Chem. Ind.*, Vol. LXI, p. 50.

CARTER, P. W., HEILBRON, I. M. & LYTHGOE, B., 1939. The Lipochromes and Sterols of the algal Classes. *Proc. Roy. Soc.* B, Vol. CXXVIII, p. 82.

COOK, A. H., 1941. *Chromatographic Analysis*. Institute of Chemistry, London.

COOPER, L. H. N. & MILNE, A., 1938. The ecology of the Tamar Estuary. II. Underwater illumination. *Journ. Mar. Biol. Assoc.*, Vol. XXII, p. 509.

DEEVEY, E. S. Jr., 1940. Limnological studies in Connecticut. V. A contribution to regional limnology. *Amer. Journ. Sci.*, Vol. CCXXXVIII, p. 717.

DUTTON, H. J. & MANNING, W. M., 1941. Evidence for carotenoid-sensitized photosynthesis in the diatom *Nitzschia closterium*. *Amer. Journ. Bot.*, Vol. XXVIII, p. 516.

EGLE, K., 1937. Zur Kenntnis des Lichtfeldes der Pflanze und der Blattfarbstoffe. *Planta*, Bd. XXVI, p. 546.

GILLAM, A. E., EL RIDI, M. S. & WIMPENNY, R. S., 1939. The seasonal variation in biological composition of certain plankton samples from the North Sea in relation to their content of Vitamin A, Carotenoids, Chlorophyll and total fatty matter. *Journ. Exper. Biol.*, Vol. XVI, p. 71.

HARVEY, H. W., 1934. Measurement of phytoplankton population. *Journ. Mar. Biol. Assoc.*, Vol. XIX, p. 761.

—— 1935. Note concerning a measuring plankton-net. *Journ. d. Cons. Internat.*, Vol. X, p. 179.

HEILBRON, I. M., 1942. Some aspects of algal chemistry. *Journ. Chem. Soc.*, Feb. 1942, p. 79.

JAMES, H. R. & BIRGE, E. A., 1938. A laboratory study of the absorption of light by lake waters. *Trans. Wis. Acad. Sci.*, Vol. XXXI, pp. 1–154.

KOZMINSKI, Z., 1938. Ueber die Chlorophyllverteilung in einigen Seen von Nordost-Wisconsin (U.S.A.). *Arch. d'Hydrobiol. et d'Ichthyol.* T. XI, p. 120.

KREY, J., 1939. Die Bestimmung des Chlorophylls in Meerwasser-Schöpfproben. *Journ. d. Cons. Internat.*, Vol. XIV, p. 201.

KYLIN, H., 1927. Ueber die karotenoiden Farbstoffe der Algen. *Hoppe-Seyler's Zeitschr. f. Physiolog. Chem.*, Bd. CLXVI, p. 38.

RILEY, G. A., 1938. The measurement of phytoplankton. *Int. Rev. d. ges. Hydrobiol. u. Hydrog.*, Bd. XXXVI, p. 371.

—— 1939. Correlations in aquatic ecology. *Journ. Mar. Res.*, Vol. II, p. 56.

—— 1940. Limnological studies in Connecticut. III. The Plankton of Linsley Pond. *Ecol. Monog.*, Vol. X, p. 279.

Savage, R. E. & Hardy, A. C., 1934. Phytoplankton and the Herring. *Fish. Invest., England*, Ser. 2, Vol. xiv, pp. 1–73.

Seybold, A. & Egle, K., 1938. Quantitative Untersuchungen über Chlorophyll und Carotenoide der Meeresalgen. *Jahrb. f. Wiss. Botanik*, Bd. lxxxvi, p. 50.

Stanbury, F. A., 1931. The effect of light of different intensities, reduced selectively and non-selectively, upon rate of growth of *Nitzschia closterium*. *Journ. Mar. Biol. Assoc.*, Vol. xvii, p. 633.

Zechmeister, L. & Cholnoky, L., 1941. *Principles and Practice of Chromatography*. London.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1941–42

The Council and the Officers.

During the year the Association has suffered a heavy loss in the death of Dr Guy Wood, who had been a Governor representing the Fishmongers' Company since 1931 and had been Honorary Treasurer for the past seven years. The Council also regret to note the death of Dr Cresswell Shearer, F.R.S., a Founder of the Association.

Major E. G. Christie-Miller has been nominated by the Fishmongers' Company to succeed Dr Guy Wood as a Governor, and at the meeting held in October he was elected Honorary Treasurer.

Four ordinary meetings of the Council were held during the year. Three of these were held in the rooms of the Royal Society and the thanks of the Association are due to the Society for this privilege. One meeting, in April, was held at Plymouth: it took place in the Grand Hotel since there were at the time unexploded bombs in and near the laboratory premises. The average attendance at the four meetings was twelve.

Air Raid Damage to the Plymouth Laboratory.

No additional damage of any consequence has been incurred during the year, though a few windows have been broken. The delayed action bombs which fell shortly before the April meeting were safely removed.

For the first three months of the year the staff of the Laboratory was largely engaged in repairing the damage occasioned in the March raids and though much will need to be done before the buildings are fully restored most of the laboratories have been made usable. Emergency repairs have been carried out in all the buildings: roofs have been made water-tight, and that of the specimen store has been renewed in corrugated iron; slating has been replaced, new rain-water gutters and pipes have been supplied and in nearly all the research rooms one window has been glazed. The heavily damaged southern end of the Easter class house has been removed and the northern part boarded in for use as a store, the roof of the constant temperature rooms has been boarded and a temporary roof has been put on the garage. The tank room cannot be restored until the end of the war: it has been closed throughout the year, thus depriving the Association of a valuable source of income.

Claims for compensation under the War Damage Act have been submitted on behalf of the Association. The claim under Part I of the Act (buildings) has been prepared by the Association's Architects and it is understood that, since the Laboratory comes under the heading of a Charity for the advancement of science or research, the amount of compensation will be determined by the War Damage Commission in consultation with representatives of the Association. No insurance premiums are payable under Part I of the Act. Under Part II (movable property) the Association is fully insured and a claim for property damaged or destroyed has been made.

The Council wishes to acknowledge with gratitude the receipt of a grant of £250 from a sum given by the American Philosophical Society to aid science and learning in Britain. The grant, which was made by the Royal Society, was given for emergency measures necessitated by recent air raid damage and essential for the maintenance of research work in the Laboratory.

Early in the year a house near Tavistock was rented by the Association. The house is used as accommodation for the Director, and for the storage of the Association's library. The Council decided at their April meeting that the library should be moved to a place of greater safety and it was transferred in May, certain reference books and recent volumes of some of the more important serials being retained at the Laboratory.

Plans for the rehabilitation of the Laboratory are being prepared, though it is evident that no work of this kind can be undertaken until the war is ended and that financial difficulties are likely to be considerable. The most urgent items will be (i) the renovation of the tank room, in order to restore the income derived from this source, (ii) the rebuilding of the south-eastern end of the North building, which was heavily damaged, and (iii) the provision of accommodation for the Easter class.

The Ship and Motor Boat.

The *Salpa* is still under requisition by the Admiralty and has not been available for the work of the Laboratory. The rate of hire for the ship has now been agreed with the Ministry of War Transport, the sums received from this source being credited to the *Salpa* Depreciation Fund. The motor boat *Gammarus* continues to work in restricted areas in Plymouth Sound and Cawsand Bay.

The Staff.

Since the date of the last Report the Association has temporarily lost the services of two more members of the scientific staff. Dr W. R. G. Atkins left the Laboratory on 7 July 1941, to take a commission in the Royal Army Medical Corps. Mr E. Ford has been given a commission in the Royal Air Force, in which he is assisting Mr F. S. Russell: he left on 20 November 1941. Seven members of the scientific staff are now away on National Service.

During the year the scientific staff of the Laboratory has been re-graded in accordance with a scheme recently approved for the Agricultural Research and Advisory Services. Under this scheme Dr W. R. G. Atkins and Mr E. Ford become Principal Scientific Officers, Mr F. S. Russell, Dr H. W. Harvey and

Dr M. V. Lebour become Senior Scientific Officers, while Dr A. Sand, Mr D. P. Wilson, Mr G. A. Steven, Mr G. M. Spooner and Dr L. H. N. Cooper are Scientific Officers.

The Association has lost the services of an old and highly valued member of the Laboratory staff during 1941. Captain V. Lord, who has been suffering from continued ill-health during the past two years, expressed the wish to retire from his post, and his resignation was accepted by the Council at their meeting in October. Captain Lord has been in the employment of the Association for twenty-eight and a half years, and all those who have worked with him have recognized his sterling qualities and the very valuable service he has rendered to the Laboratory.

Occupation of Tables.

The following have occupied tables at the Plymouth Laboratory during the year:

J. Cochemé (Self-retrieving spinner for mackerel).
P. G. Corbin (Plankton on mackerel grounds).
L. R. Crawshay, Plymouth (Sponges).
Dr Vera Fretter, London (Embryology of *Onchidella*).
A. T. Goodman (Library).
Dr M. Jepps, Glasgow (Life history of *Polystomella*).
A. G. Lowndes (Density of aquatic organisms).
Dr N. K. Panikkar, U.C., London (Osmoregulation in marine animals).
Dr M. W. Parke & Miss E. Clay (Algae).
W. J. Rees (Hydroids and Medusae).
Miss N. G. Sproston (Parasites of fishes).

Dr Paul Haas and Dr E. H. Thierry visited the Laboratory during the year in connexion with the investigations on marine algae.

No vacation courses were held during the year.

Special Research.

During the year there has been an increase in the work which the Laboratory has been asked to undertake on behalf of the Government. Advice has been given on a number of matters in reply to enquiries from service departments, and Dr Atkins, while at the Laboratory, continued to carry out confidential work on behalf of the Admiralty.

The curtailment of imported supplies of fish owing to war conditions has brought difficulties to a number of the colonies, and in several of them attempts to develop the local fisheries, some of them of considerable richness, are being made. Unfortunately information about these fisheries is most inadequate; their administration has been sadly neglected and even of the most important species of fish little or nothing is known of the life-history, growth-rate, migrations and other important factors. The Director of the Plymouth Laboratory has given some assistance to the Colonial Office in devising plans to meet war-time emergencies and it is hoped that the establishment of a number of suitably equipped fishery research stations will be included in post-war schemes for colonial development.

An extensive programme of work on marine algae has been put in hand during the year. Red algae are now in demand for the manufacture of bacteriological agar, while large quantities of brown algae are being used as raw material for national service requirements. Our knowledge of the biology of the brown algae is unfortunately scanty, and series of experiments have been begun at Wembury and on the west coast of Scotland. These experiments are being carried out by Dr Mary Parke, whose services were transferred to the Plymouth Laboratory at the beginning of the war, and others on the same lines are being conducted by Dr Margery Knight in the Isle of Man. Strips of beach have been cleared of weed in order to observe the new growth and many plants have been measured and marked, some being cut in order to follow the extent of regeneration.

The Association has also been asked to undertake surveys in south-west England, in Wales and in Scotland to ascertain the areas where brown algae are to be found in the greatest abundance. This work, which is beyond the resources of the greatly depleted laboratory staff, is being carried out for the Association by Dr V. J. Chapman and a party of research students from the School of Botany at Cambridge.

With one possible exception the red algae which can be employed in making agar occur in such small quantities that they cannot be used commercially. Dr A. P. Orr, of the Scottish Marine Biological Association, has taken a leading part in this work and experiments which he has made on the production of an agar substitute from other red algae have given very promising results. The Laboratory is co-operating in the developments which are now taking place and it is to be expected that satisfactory methods of producing culture media will shortly be evolved.

Tests on the durability under sea water of cords, textiles and netting, manufactured for service requirements, are now in progress. It would have been difficult or impossible to carry out these tests, which are on a far larger scale than any hitherto attempted by the Laboratory, but for the helpful assistance of Mr F. Payne, Manager of the Constructive Department, Devonport Dockyard, through whom the Association has obtained the loan of a large raft belonging to the Admiralty. Tests on the durability of the insulation in submarine cables are also being made and plates for the study of antifouling problems have been exposed.

Scientific Work of the Plymouth Laboratory Staff.

Interruptions due to air raids, and the absence of a large proportion of the scientific staff, have resulted in a greatly reduced output of scientific work.

H. W. Harvey has been engaged in investigating the phosphate set free from organic matter in solution in sea water by bacterial action and hydrolysis. These experiments were interrupted and the opportunity was taken to collate the results of published observations relating to factors which control the production of plant life in the sea. A review of recent developments in this field is being published in *Biological Reviews*.

Miss Lebour has published a paper in the *Annals and Magazine of Natural History* on the larval *Processa* of Bermuda, with a description of a new species, with which the Plymouth species are compared. The same paper deals with the larval Thalassinids of Bermuda. She has also published a joint paper with Dr R. Gurney on various larval decapods from Bermuda. Whenever possible she has continued her work on larval decapods and Mollusca from Plymouth; but she has been hampered by war-time restrictions in collecting and some of the material on which she was working was destroyed in air raids. Work on larval Porcellanids, crab larvae and *Teredo* has progressed, and tow-nettings from inside the Sound are examined regularly, the object being to ascertain the general contents of the hauls, and especially to identify the larvae in order to continue the study of life-histories of the decapod Crustacea and Mollusca and to add to our knowledge of the breeding seasons.

Mr D. P. Wilson has continued his observations and experiments on *Nitzschia closterium* in culture. There is now evidence that in addition to the formation of normal spindle-shaped cells from triradiate cells through an intermediate oval form without horns, there sometimes occurs in triradiate cultures a transformation into the spindle-shape by a direct elimination of one of the three horns. This appears to have taken place in a clone triradiate culture rather suddenly and on a large scale. Since the last report some triradiate cells have been obtained by the growth of hornless forms derived from normal spindle-shaped cells; change in this direction is much rarer than in the opposite. So far no consistent correlation between cell shape and the physical conditions under which growth has proceeded has been found, although it has appeared that light intensity or its duration may not be without effect. Experiments are still in progress.

Since last mentioned in these reports, considerable progress has been made in the study of the effect of winter tank temperatures on *Sepia officinalis* in captivity. The temperature of the aquarium water fluctuates with the air temperature and during frosty weather cuttle-fish are quickly killed. During the last two winters a small tank has been electrically heated and the temperature stabilized at about 13·5° C. In it a few cuttlefish have been kept in healthy condition much longer than before. When death took place in this tank it was found to be due to egg-binding in a solitary and fully mature female, or to injuries incurred during severe fighting between fully mature males at a time when females were not available. It seems probable that in order to keep *Sepia* in health for long periods under aquarium conditions, winter temperatures must be controlled and the sexes suitably balanced. A preliminary examination of *Sepia* shells collected over a period of years has indicated that most interesting results would be obtained by a more intensive study when material can again be obtained in quantity.

Mr Wilson has again assisted Mr J. Kingcome with the rearing of oysters in tanks at his fishery on the River Yealm. The summer of 1941 proved to be a very late season, due perhaps to the unusually cold weather in the spring when the parents were known to be very late in commencing shell growth. Eventually a small spat-fall was obtained. Last year's brood is growing well in cages in the estuary.

Since Mr Ford left, Mr Wilson has been sub-editor of the Journal, and he has also been engaged on plans for the restoration of the tank room.

Mrs Sexton has been engaged throughout the year with further detailed study of the genus *Gammarus*, particularly of the estuarine species and their relations with freshwater and purely marine forms. It is important to have the different species and their so-called varieties more strictly defined in view of their constant citation in ecological work. Particular attention has been paid to *Gammarus zaddachi* Sexton, a widespread species ranging from fresh to salt water, often confused with *G. locusta* (L.) at the seaward limit of its range, with *G. duebeni* Lillj. in the brackish water and with *G. pulex* in the freshwater. *G. zaddachi* develops an increase in the number of the sensory outgrowths of the cuticle in the freshwater environment, and at first glance, appears to be specifically different from the more spinose estuarine form; but the figures which have been prepared prove that structurally they are identical.

The Library.

As explained earlier in this Report the library has been moved out of Plymouth, only a small amount of recent literature being retained at the Laboratory. Accessions, as was to be expected, are less numerous than in times of peace, but current numbers of many periodicals have been received and some books have been added. The thanks of the Association are due to those institutions and authors who have presented books and papers.

For purposes of insurance under the War Damage Act the Council decided to obtain a professional valuation of the library. The work was carried out early in the year by Mr R. Ridgill Trout, and the total amount of the valuation, including stocks of back numbers of the Journal, is £15,750.

Published Memoirs.

Vol. XXV, No. 2 of the Journal of the Association was issued in November 1941.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association:

FRETTER, VERA, 1941. An abnormal male *Sepia officinalis*. *Proc. Malacol. Soc.*, Vol. XXIV, pp. 154–5.

GURNEY, ROBERT & LEBOUR, MARIE V., 1941. On the larvae of certain Crustacea Macrura, mainly from Bermuda. *Journ. Linn. Soc. Zool.*, Vol. XLI, pp. 89–181.

LEBOUR, MARIE V., 1941. Notes on Thalassinid and Processid Larvae (Crustacea Decapoda) from Bermuda. *Ann. Mag. Nat. Hist.*, Ser. 11, Vol. VII, pp. 401–20.

Lowndes, A. G., 1941. Rapid determination of water in animals and plants. *Nature*, Vol. cxlviii, p. 79.

Panikkar, N. Kesava, 1941. Osmotic behaviour of the fairy shrimp *Chirocephalus diaphanus* Prevost. *Journ. Exp. Biol.*, Vol. xviii, pp. 110–14.

Panikkar, N. Kesava & Sproston, Nora G., 1941. Osmotic relations of some metazoan parasites. *Parasitology*, Vol. xxxiii, pp. 214–23.

Rees, W. J., 1941. The hydroid of the medusa *Cosmetira pilosella* Forbes. *Proc. Roy. Soc. Edinb.*, B, Vol. lxi, pp. 55–8.

Waterman, T. H., 1941. A comparative study of the effects of ions on whole nerve and isolated single nerve fibre preparations of crustacean neuromuscular systems. *Journ. Cell. Comp. Phys.*, Vol. xviii, pp. 109–26.

Wells, G. P., 1942. The action of potassium on echinoderm, molluscan and crustacean muscle. *Journ. Exp. Biol.*, Vol. xviii, pp. 213–22.

Wilson, D. P. & Lucas, C. E., 1942. *Nitzschia* cultures at Hull and at Plymouth. *Nature*, Vol. cxlix, p. 331.

Membership of the Association.

There have been no changes in the lists of Vice-Presidents and Associate Members. The total number of members of the Association on 31 March 1942 was 312 as compared with 313 at the corresponding date in 1941. During the year one life member was elected and two annual members compounded for their annual subscriptions.

Finance.

Grant from Development Fund. The Council have again to express their thanks to the Development Commissioners for their continued support of the general work of the Laboratory.

Private Income. The Council gratefully acknowledges the following generous grants for the year:

From the Fishmongers' Company (£600), the Royal Society (£50), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the Laboratory: The Universities of Cambridge (£105), London (£105), Oxford (£52. 10*s.*), Bristol (£25), Birmingham (£15. 15*s.*), Manchester (£10. 10*s.*), Leeds (£10. 10*s.*), Sheffield (£5); the British Association (£50), the Physiological Society (£30), and the Ray Lankester Fund (£20).

President, Vice-Presidents, Officers and Council.

The following is the list of those proposed by the Council for election for the year 1942–43.

President

G. P. Bidder, Sc.D.

Vice-Presidents

The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholas Waterhouse, K.B.E.
The Lord Moyne, P.C., D.S.O.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. Peel, D.S.O., M.C.
Lord Mildmay of Flete, P.C.
The Right Hon. Sir Reginald Dorman-Smith, M.P.
Sir Joseph Barcroft, C.B.E., F.R.S.
Prof. J. Stanley Gardiner, F.R.S.
Prof. Walter Garstang, D.Sc.

COUNCIL

To retire in 1943

- Prof. D. Keilin, Sc.D., F.R.S.
- E. S. Russell, O.B.E., D.Sc.
- Prof. E. J. Salisbury, D.Sc., F.R.S.
- L. A. Harvey
- H. Cary Gilson

To retire in 1944

- C. F. A. Pantin, Sc.D., F.R.S.
- Prof. T. A. Stephenson, D.Sc.
- Prof. W. M. Tattersall, D.Sc.
- Prof. C. M. Yonge, D.Sc.
- J. Z. Young

To retire in 1945

- Prof. A. V. Hill, O.B.E., Sc.D., Sec.R.S., M.P.
- Prof. H. Graham Cannon, Sc.D., F.R.S.
- The Hon. Miriam Rothschild
- C. Forster-Cooper, M.A., Sc.D., F.R.S.
- Prof. A. C. Hardy, D.Sc., F.R.S.

Chairman of Council

Prof. James Gray, M.C., Sc.D., F.R.S.

Hon. Treasurer

Major E. G. Christie-Miller, 71 Park Street, London, W. 1

Secretary

Stanley Kemp, Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Sc.D.
The Lord Moyne, P.C., D.S.O.
A. T. A. Dobson, C.B., C.V.O., C.B.E. (Ministry of Agriculture & Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.
  Major E. G. Christie-Miller
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
H. G. Maurice, C.B. (Zoological Society)
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S. (Royal Society)
E. J. Allen, C.B.E., D.Sc., F.R.S. (*Honorary*)

BALANCE SHEET 1941–42

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1942

	£	s.	d.	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:									
Re-instatement of War Damage				272	19	1			
Staff Tax Deductions due to Inland Revenue ...				240	12	4			
Accrued Expenses				80	6	11			
Subscriptions received in advance				18	16	0			
Grant received in advance				150	0	0			
							762	14	4
INCOME TAX SUSPENSE ACCOUNT:									
As at 31st March 1941							53	9	8
AQUARIUM GUIDE PRINTING FUND:									
As at 31st March 1941							22	1	6
SPECIAL APPARATUS FUND:									
As at 31st March 1941				55	4	11			
Less: Expenditure				45	0	0			
							10	4	11
MACKEREL RESEARCH FUND:									
As at 31st March 1941				56	9	8			
Less: Expenditure				16	1	3			
							40	8	5
ALGAL RESOURCES SURVEY FUND:									
Grant Received				800	0	0			
Less: Expenditure	582	13	4						
Remuneration credited to Income and Expenditure Account	29	2	8						
				611	16	0			
							188	4	0
E. T. BROWNE BEQUESTS FUNDS:									
Building Fund, as at 31st March 1941	1050	8	5						
Interest on Investment	32	1	2						
				1082	9	7			
Library Fund, as at 31st March 1941	1030	19	7						
Interest on Investment	31	9	4						
				1062	8	11			
Special Apparatus Fund, as at 31st March 1941	2110	4	5						
Interest on Investment	64	8	0						
				2174	12	5			
Scientific Publications Fund, as at 31st March 1941	1582	13	3						
Interest on Investment	48	6	0						
				1630	19	3			
							5950	10	2

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director as at 31st March 1941:						
S/S "Salpa"	2000	0	0			
Motor Boat "Gammarus"	100	0	0			
Nets, Gear and General Equipment	30	0	0			
				2130	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director as at 31st March 1941				4000	0	0
LIBRARY, at valuation of Mr Ridgill Trout in January 1941				15750	0	0
STOCKS ON HAND, as valued by the Director:						
Specimens	1050	0	0			
Chemicals	150	0	0			
Journals	400	0	0			
				1600	0	0
SUNDRY DEBTORS:						
Sales of Specimens and Journals	217	17	6			
Sundries	126	13	6			
Income Tax Recoverable	54	13	4			
				399	4	4
PREPAYMENTS				48	2	0
GENERAL FUND INVESTMENT, at market value as at 31st March 1931:						
£352. 2*s.* 3*d.* Local Loans 3% ... ... (Market value at date £339. 15*s.* 9*d.*)				232	7	10
E. T. BROWNE BEQUEST FUNDS INVESTMENT, at cost:						
£6047. 9*s.* 10*d.* Conversion Loan 3% ... ... (Market value at date £6138. 4*s.* 1*d.*)				5950	10	2
"SALPA" DEPRECIATION FUND INVESTMENTS, at cost:						
£590. 6*s.* 0*d.* Local Loans 3%	506	10	9			
£3124. 9*s.* 1*d.* Conversion Loan 3%	3168	19	6			
(Market value at date £3740. 19*s.* 2*d.*)				3675	10	3
REPAIRS AND RENOVATION FUND INVESTMENT, at cost:						
£206. 12*s.* 1*d.* Conversion Loan 3% ... ... (Market value at date £209. 14*s.* 1*d.*)				208	10	7
COMPOSITION FEES FUND INVESTMENTS, at cost:						
£18. 8*s.* 6*d.* Local Loans 3%	15	15	0			
£200. 18*s.* 11*d.* Conversion Loan 3%	204	15	0			
(Market value at date £221. 14*s.* 9*d.*)				220	10	0

"SALPA" DEPRECIATION FUND:		
As at 31st March 1941	3062 11 9	
Add: Amount receivable from Ministry of War Transport on account of Hire	638 0 0	
Interest on Investments	91 18 6	
Less: Transfer to Repairs and Renovations Fund	50 0 0	
		3742 10 3
REPAIRS AND RENOVATIONS FUND:		
As at 31st March 1941	258 4 3	
Add: Transfer from "Salpa" Depreciation Fund	50 0 0	
Interest on Investment	4 12 0	
		312 16 3
COMPOSITION FEES FUND:		
As at 31st March 1941	157 10 0	
Add: Fees Received	63 0 0	
		220 10 0
CAPITAL RESERVE ACCOUNT:		
As at 31st March 1941		17311 8 2
SURPLUS:		
As at 31st March 1941	6872 19 10	
Add: Surplus for the year, as per Income and Expenditure Account	247 14 6	
		7120 14 4
		£35,735 12 0

CASH AT BANK AND IN HAND:			
Coutts & Company		1229 2 6	
Lloyds Bank Limited		141 4 8	
Cash in Hand		51 9 7	
			1421 16 9
RECOVERABLE EXPENDITURE:			
M. Parke Fund:	£ s. d.		
As at 31st March 1941	110 19 2		
Expenditure	388 9 8		
	499 8 10		
Less: Grant Received	495 0 0		
		4 8 10	
Biological Investigations in Algae:			
Expenditure	504 9 9		
Less: Amounts Recovered ...	436 15 9		
		67 14 0	
Celanese Account:			
Expenditure		26 17 3	
			99 0 1
			£35,735 12 0

L. A. HARVEY
T. A. STEPHENSON } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1942 according to the best of our information and the explanations given to us and as shown by the books of the Association.

Shinners Bridge, Totnes, S. Devon.
13*th May*, 1942.

PRICE, WATERHOUSE & CO.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1942

	£	s.	d.	£	s.	d.
To SALARIES, including the Association's Contributions to Superannuation				6505	18	8
,, LABORATORY WAGES, including National Insurance and the Association's Contributions to Superannuation				2496	17	6
,, UPKEEP OF LIBRARY				156	9	5
,, SCIENTIFIC PUBLICATIONS, LESS SALES				286	5	9
,, UPKEEP OF LABORATORIES AND TANK ROOMS:						
Buildings and Machinery	79	14	8			
Electricity, Gas, Coal, Oil and Water	399	18	6			
Chemicals and Apparatus	109	19	0			
Rates, Taxes and Insurance	137	7	6			
Travelling Expenses	53	11	4			
Stationery, Postages, Telephone, Carriage and Sundries	249	4	10			
Specimens	136	11	11			
				1166	7	9
,, MAINTENANCE AND HIRE OF BOATS:						
Wages, including Diet Allowance, National Insurance and Casual Labour	874	1	0			
Coal, Water, Oil, Petrol, etc.	20	19	6			
Maintenance and Repairs, with Nets, Gear and Apparatus	16	1	7			
Purchase of Material for Nets for Sale, excluding Labour	63	19	1			
Boat Hire and Collecting Expenses	2	15	4			
Insurance	48	17	11			
				1026	14	5
,, BANK CHARGES				12	2	0
,, BUILDINGS EXTENSION FUND—BALANCE AS AT 31ST MARCH 1941 WRITTEN OFF				54	3	2
,, WAR TIME EXPENDITURE:						
War Damage Contributions	418	3	3			
War Risk Insurance	78	15	0			
Accommodation for Director and Removal and Storage of Library	185	17	0			
Amounts payable to Firewatchers	60	5	0			
Re-instatement of War Damage to Buildings and Machinery (including Professional Fees)	477	5	2			
	1220	5	5			
Less: Grant received from American Philosophical Society and Sundry Donations	273	13	3			
				946	12	2
,, BALANCE, BEING SURPLUS FOR THE YEAR				247	14	6
				£12,899	5	4

	£	s.	d.	£	s.	d.
BY GRANTS:						
Ministry of Agriculture and Fisheries Grant from Development Fund	10713	0	0			
Fishmongers' Company	600	0	0			
Royal Society	50	0	0			
British Association	50	0	0			
Physiological Society	60	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				11483	0	0
,, SUBSCRIPTIONS (excluding Subscriptions received in advance)				259	7	0
,, DONATIONS				140	15	0
,, SALES:						
Specimens	526	10	9			
Fish	–	–	–			
Nets, Gear and Hydrographical Apparatus	21	10	3			
				548	1	0
,, TABLE RENTS (including University of Cambridge £105; Oxford £105; London £105; Bristol £25; Birmingham £15. 15*s.* 0*d.*; Leeds £10.10*s.*0*d.*; Manchester £10.10*s.*0*d.*; Sheffield £5; Imperial College £10; Trustees of Ray Lankester Fund £20)				422	5	0
,, TANK ROOM RECEIPTS				–	–	–
,, INTEREST ON INVESTMENTS (GROSS)				15	5	10
,, SALE OF DR M. V. LEBOUR'S BOOK				1	0	10
,, SALE OF "PLYMOUTH MARINE FAUNA"					8	0
,, REMUNERATION IN CONNECTION WITH ALGAL RESOURCES SURVEY				29	2	8
				£12,899	5	4

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. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. 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 and physiology Marine animals and plants are supplied to educational institutions and at the close of the war arrangements will be made for the resumption of the courses for advanced students formerly held at Easter and in September.

Research work at sea is undertaken by a motor boat, and, in normal times, by a steam drifter, 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 Officers 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.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

CONTENTS

LONDON
CAMBRIDGE UNIVERSITY PRESS
BENTLEY HOUSE, N.W. 1

BOMBAY • CALCUTTA • MADRAS • MACMILLAN

PRINTED IN GREAT BRITAIN BY WALTER LEWIS, M.A., AT THE UNIVERSITY PRESS, CAMBRIDGE