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# A CONTRIBUTION TO THE BIOLOGY OF *IANTHINA JANTHINA* (L.)

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(Plate I and Text-figs. 1 and 2)

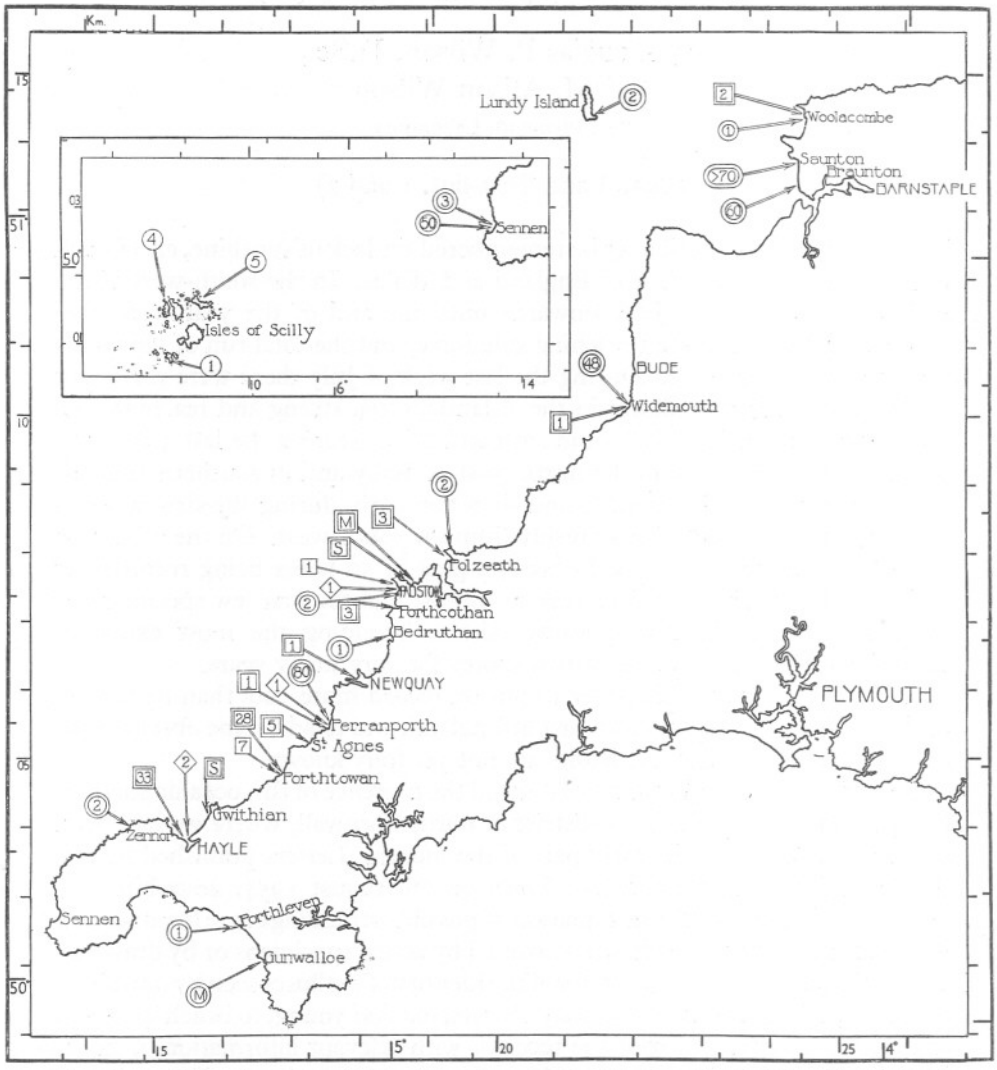
The summer of 1954 will long be remembered for lack of sunshine, excess rain and frequent high winds over England and Wales. In the south-west of the region the winds from June onwards until the end of the year were predominantly westerly, often reaching gale force, and the total run of the winds was often above average. During the last week of July there were persistent westerly winds from well out in the Atlantic, often strong and reaching gale force at times, particularly on the 27th and 28th. During the last 4 days the winds were generally from the north-west at Scilly and in southern Ireland. They were variable in strength and direction early during the first week in August, but occasionally blew freshly from the south-west. On the 7th it was often blowing strongly from the west, a gust of 50 knots being recorded at Scilly. It was during this first week in August that the first few specimens of *Ianthina janthina* (Linnaeus) came ashore, heralding the most extensive strandings of this species on British shores for very many years.

It is the purpose of this paper to put on record more data than have been available for any previous stranding in England, and to add some observations on the living animal, whose habits are not yet fully known.

It was in mid-August that we first noted the presence of this oceanic surface-living mollusc in the Padstow district of north Cornwall, where we had been shore-collecting since the early part of the month. Letters published in *The Western Morning News* and *The Times* on 26 August 1954, describing the mollusc and appealing for information of possible strandings in other districts, brought a number of replies, accompanied by actual specimens or by drawings or descriptions which left no doubt of the identity of molluscs seen by untrained observers, who ranged from holiday visitors, old and young, to beach-combers of long experience. A list of the records, with relevant information, is given below, together with our own observations on strandings. For a better appraisal of the extent and timing of the latter they are plotted on the chart reproduced in Text-fig. 1.

To check whether there had been strandings in southern Ireland a letter was sent to *The Irish Times* and published on 4 September 1954. Among replies from people who had found *Ianthina* there before the only one that gave

information for 1954 came from Miss Mildred Sheridan, Achill Island, Co. Mayo, who stated that in the previous May, after a particularly violent storm, the strand was covered with the shells. She picked up forty to fifty perfect




Text-fig. 1. Map to show positions of strandings of *Ianthina janthina* (L.) listed in Table I. Records for the same locality in the same week are summed. Figures indicate the numbers reported, and where actual numbers are not available S = several, and M = many. Numbers or letters within a single circle are strandings during the first week (1–7 August); within a double circle the second week (8–14 August); within a single square the third week (15–21 August); within a double square the fourth week (22–28 August); within a diamond the fifth week (29 August–4 September). Arrows point only approximately to the positions of strandings which are often not known to within 2 or 3 miles.

## TABLE I. STRANDINGS OF *IANTHINA JANTHINA* (L.) DURING AUGUST AND SEPTEMBER 1954

| Date | Locality | Number | Condition | Recorder |
|---|---|---|---|---|
| First week (1–7 Aug.) | | | | |
| Early Aug. | St Agnes, Isles of Scilly | 1 | Living | Mrs M. Hicks |
| First week Aug. | St Martins, Isles of Scilly | 5 | — | Mrs L. M. Hughes |
| Early Aug. | Tresco, Isles of Scilly | 4 | Empty shells | Mrs Ariadne Cook |
| Second week (8–14 Aug.) | | | | |
| 8 Aug. | Gwenver, near Sennen | 1 | Living | Rev. P. H. T. Hartley |
| 9 Aug. | Treveal Cove, Zennor | 2 | Living | Miss Tamsin and Master Timothy Procter |
| 9–10 Aug. | Constantine Bay, near Padstow | 2 | — | Mrs O. Woosnam-Mills |
| 10–11 Aug. | Widemouth Bay, near Bude | 48 | — | Mrs L. F. J. Gunn |
| 11 Aug. | Saunton Sands, near Barnstaple | *c.* 24 and more on following days | Living | Mrs Doris Wilson |
| 11 Aug. | Gwenver, near Sennen | 2 | Living | Rev. P. H. T. Hartley |
| 10 or 11 Aug. | Dollar Cove, Gunwalloe | Several dozen | Living | Mr Frank Sabin |
| About 10–12 Aug. | Sennen Cove | *c.* 50 | Living | Mr T. G. W. Fowler |
| 12 Aug. | Braunton Sands, near Barnstaple | *c.* 60 | — | Mrs Wiseman |
| About 12 Aug. | Saunton Sands, near Barnstaple | 40–50 | Empty shells | Lt.-Col. L. T. G. Ricketts |
| Second week | Lundy Island | 2 | One dead | Miss J. L. Bloom |
| Second week | Woolacombe | 1 | — | Mr J. Crowder |
| Estimated second week | Perranporth | *c.* 80 | Living | Mr S. Chenoweth |
| Second week | Coast near Polzeath | 2 | Living | Mr G. Pym |
| 14 Aug. | Porthleven | 1 | Living | Mr H. B. Sargent |
| 14 Aug. | Bedruthan Steps, near Padstow | 1 | Living | Mr T. Roberts |
| Third week (15–21 Aug.) | | | | |
| 14–21 Aug. | Porthtowan | About 1 a day | Living | Mr N. A. Wesley |
| 15 Aug. | Trevone Bay, near Padstow | 3 or 4 | Living | Mr C. Roberts |
| 15 Aug. | Trevone Bay, near Padstow | 1 | Living | Master R. J. H. Wilson |
| 19 Aug. | Trevone Bay, near Padstow | Several | Living | M. A. and D. P. Wilson |
| 19–20 Aug. | Trevone Bay, near Padstow | Several | Living | Miss Bridget Hickey |
| 20 Aug. | Constantine Bay, near Padstow | 1 | Living | Mrs O. Woosnam-Mills |
| 20 Aug. | Harlyn Bay, near Padstow | Many | Living | Miss H. Bibby |
| 21 Aug. | Harlyn Bay, near Padstow | *c.* 36 | Living and recently dead | M. A. and D. P. Wilson |
| Fourth week (22–28 Aug.) | | | | |
| 22–28 Aug. | Porthtowan | About 4 a day | Living | Mr N. A. Wesley |
| 22 Aug. | Hayle | 3 | Living | Miss Hartnoll |
| 22 Aug. | Mother Ivey's Bay, near Padstow | 2 | Living | Mrs O. Woosnam-Mills |
| 22–24 Aug. | St Agnes, near Perranporth | 3–5 | — | Mr W. E. Williams |
| 23 Aug. | Mother Ivey's Bay, near Padstow | 1 | Empty shell | Mrs O. Woosnam-Mills |
| 23 Aug. | Daymer Bay, near Padstow | 1 | Living | Mr S. Lees |
| 23 Aug. | Trevone Bay, near Padstow | Several | Living | M. A. and D. P. Wilson |
| 24 Aug. | Polzeath | 2 | One living | Mrs E. M. Davies |
| 24 Aug. | Gwithian | 1 | Living | Dr W. D. Oliver |
| About 24 Aug. | Widemouth Bay, near Bude | 1 | Living | Dr E. N. Rudland |
| 24 Aug. | Constantine Bay, near Padstow | 1 | Empty shell | Mrs O. Woosnam-Mills |
| 24 Aug. | Gwithian | Several | Living | Mrs S. Bennett |
| 25 Aug. | Trevone and Harlyn Bays, near Padstow | Few | Living | M. A. and D. P. Wilson |
| 25 Aug. | Holywell Beach, Newquay | 1 | Living | Mr P. Rayner-Smith |
| 25 Aug. | Perranporth | 1 | Living | Miss D. W. Hill |
| 25 Aug. | Porth Kidney Sands, Hayle | *c.* 30 | Some living, some empty | Miss Tamsin and Master Timothy Procter |
| 27 Aug. | Gwithian | 6 | — | Mrs S. Bennett |
| 27 Aug. | Porth Mear, Porthcothan | 3 | — | Miss H. M. Spittle |
| 27 Aug. | St Agnes, Isles of Scilly | 1 | Empty shell | Mrs M. Hiels |
| Before 28 Aug. | Woolacombe | 1 or 2 | Living | Miss Jane Asher |
| Fifth week (29 Aug.–4 Sept.) | | | | |
| 29 Aug. | Lelant, near Hayle | 2 | Empty shells | Mrs D. C. Bazeley |
| 29 Aug. | Constantine Bay, near Padstow | 1 | Living | Mrs O. Woosnam-Mills |
| End of Aug. | Perranporth | 1 | — | Mr S. Chenoweth |
| End of Aug. | Bryher, Isles of Scilly | 1 | Empty shell | The late Major A. A. Dorrien Smith |
| About 1 Sept. | Marloes sand, Dale Fort, Pembrokeshire | 1 | Empty shell | Mr J. H. Barrett |

TABLE I (*continued*)

| Date | Locality | Number | Condition | Recorder |
|---|---|---|---|---|
| Sixth week (5–11 Sept.) | | | | |
| 5 Sept. | Carbis Bay | 1 | Empty shell | Mr A. Hutton |
| 5 Sept. | Braunton Sands, near Barnstaple | Few | Empty shells | Mrs Wiseman |
| Seventh week (12–18 Sept.) | | | | |
| 12 Sept. | Sennen Cove | 1 | Living | Mr and Mrs H. H. Sheldon |

specimens and many more were broken. She enclosed the remains of a shell to confirm the identification. Dr J. R. Bruce found one living *Ianthina* sp. washed up in White Park Bay, Co. Antrim, early in July, along with thousands of dead, but fresh, *Velella* skeletons.

It may be assumed therefore that the shoal which stranded in Cornwall in August came in from the Atlantic to the south of Ireland without touching its shores. It seems most unlikely that it was part of the shoal that stranded on Achill Island in May, probably early. The stormiest weather in May was during the first week, and for the rest of that month the winds were mostly below the average.

Records of strandings during the first week of August (see Table I) are scanty. Even though the appeal for information did not appear in the press until 3 weeks later it seems clear that there were indeed few strandings at this time and all were on the Isles of Scilly. One of these was definitely a living mollusc; four of the others were empty shells when found; information is incomplete for the other five. Immediately after the appearance of the press appeal the late Major A. A. Dorrien Smith of Tresco organized a search; only one shell (presumably empty) was found (on Bryher) and was kept by the finder. From these few records it can be inferred that the oncoming shoal, drifting before the wind, almost entirely missed the Isles of Scilly, and passed, in view of what happened later, north of them.

The second week of August brought many strandings on the mainland. Early in the week a living *Ianthina* was found in the Land's End district, near Sennen, and two at Zennor a little farther north; from the middle of the week onwards large numbers were stranded along an extensive length of coastline from Land's End to north Devon. There appear to have been particularly dense concentrations near Bude and in Bideford Bay, but there were also some heavy strandings farther south at Perranporth, Sennen, and on the western shore of the Lizard peninsula. None were recorded at any time farther up the English Channel. The Perranporth record is a little vague as to date, but most probably refers to this period.

During this second week winds were at first more or less westerly, light to moderate, increasing in strength on the 9th to blow strongly from the north-west and continuing fresh from the same quarter on the 10th. Early on the 11th it was a little north of west, later swinging round to the south. It was on

the 10th–11th that most strandings seem to have taken place, and it was most probably on the 11th at Gunwalloe. The wind continued light south-westerly over the 12th, becoming almost due west on the 13th and dropping in strength.

Relatively few strandings were recorded during the third week and these were mostly in the Padstow district, and towards the end of the week. Winds were at first light to moderate, variable in direction, freshening on the 17th and 18th, until they were blowing strongly from almost due west, veering later to north and decreasing somewhat. They remained fresh and northerly until the end of the week. Northerly winds blow straight onshore in Trevone and Harlyn Bays, but they would also strand *Ianthina* on other parts of the coast if any were sufficiently close offshore.

During the fourth week there were strandings over a longer length of coastline, that from St Ives Bay to Woolacombe. The single record from the Isles of Scilly was of an empty shell which had undoubtedly stranded earlier. Most of the records are of living specimens, never in any great number. The largest number recorded was from near Hayle on 25 August, but an unknown proportion of these were empty and must have been from earlier strandings. Until the 25th the winds were north and north-westerly, mainly moderate; they died away on the 26th, and on the 27th and 28th were light westerly veering north.

For the fifth week the only living mollusc recorded was from Constantine Bay on the first day of the week. Thereafter only empty shells, or presumed empty shells, were found. These were most probably from earlier strandings; and although a living specimen was found at Sennen on 12 September, the invasion was over. That this was due to absence in the area of further living specimens and not to the wind is certain. The week had opened with light or moderate winds from the west, veering to the south-east on 31 August and 1 September. They were moderate and mainly from the south-west on 2 September, increasing in strength and becoming westerly and strong on the 3rd. On 4 September there was a calm. Light to fresh rather southerly winds followed, becoming westerly. On 9 September it blew strongly from the west and remained fresh and strong until the 12th, on which day the living specimen was found at Sennen. Thereafter, for the remainder of the month winds were often strong from a westerly direction, the total run of the winds being substantially above the average. No more *Ianthina* came in, but they were followed from mid-September onwards by large numbers of *Physalia physalis*, which was also abundant on the coast of southern England.

To sum up: excepting for the one notable find of an empty shell at Dale Fort in Pembrokeshire, the strandings were confined to the north coasts of Cornwall and Devon and, in the south, the west coast of the Lizard peninsula. The shoal, or shoals, blown in from the west, missed southern Ireland and barely touched the Isles of Scilly; the main strandings were in the second week of August during a time of fresh or strong north-westerly winds.

During the third week more, but apparently smaller numbers, came ashore in the middle of the region at a time of northerly winds. Thereafter, the number of living animals found quickly declined and one only was taken at Sennen after the end of August.

## Some Previous Strandings in South-west England and Wales

It is known that three species of *Ianthina*—in current nomenclature *I. exigua* Lamarck, *I. pallida* Thompson, *I. janthina* (L.)—strand from time to time in south-west England and Wales (Forbes & Hanley, 1853; Fowler, 1947, 1948, 1949; Graham, 1954) as well as in Ireland and Scotland. Mr T. G. W. Fowler, who has searched the beaches at Sennen regularly for many years, tells us, in a personal letter, that the 1954 specimens were 'the first for quite two years'. He remarks that he knows 'there were a few at Constantine Bay in September 1937 or '38'. The main interest in the 1954 strandings is the unusually long length of coastline affected, and probably the numbers stranded were, for that locality, far greater than for very many years. Some correspondents who live on or visit the north Cornish coast and regularly search the beaches there assured us that they had never seen these shells before. We ourselves on numerous visits to the Padstow district from about 1933 had never encountered them. A few older people remembered having seen some washed up about fifty years previously. Mr C. Roberts of Trevone told us he had seen similar shells at Harlyn Bay in 1903 or 1904. Mrs Doris Wilson, writing from Braunton, remarked that her friend 'Mrs Wiseman had found some, only much smaller specimens, about fifty years ago in much the same place' (at Braunton). Miss E. M. Ferguson, writing from Somerset, mentioned finding six empty *Ianthina* shells at Croyde in North Devon, in 1903 she thinks. There are thus three quite independent witnesses to a stranding about that time, and fairly good evidence that there has not been an extensive stranding of *Ianthina* along the north coasts of Cornwall and Devon since then.

Mr J. H. Barrett, writing from Dale Fort Field Centre, Pembrokeshire, notified us that about a dozen dead shells and one live specimen were found at West Dale on 6 September 1950. Another dead, but with float, was found on Marloes sands on 20 August 1953. All were identified as *I. britannica* (= *I. janthina*).

## Coincident Strandings of *Velella*

One of the main foods of *Ianthina* is *Velella*, and it was to be expected that this latter organism would strand with it. We ourselves found a considerable number of living and recently dead *Velella* stranded at Trevone and Harlyn Bay at the same time. Mr T. G. W. Fowler reported to us 'hundreds and thousands of live *Velella*' at about the same time as the *Ianthina* strandings at Sennen. The Rev. P. H. T. Hartley saw many living *Velella* on Gwenver

beach on 8 August, and stated that they were 'at a density of about one to the yard of tide edge'. Mrs Doris Wilson also saw a few at Saunton at the same time as *Ianthina*. Mr S. R. Nutman had seen many fresh skeletons, one with remains of living tissues, on 30 July at Polzeath. During the first few days of August a small number of living ones were stranded at Wembury near Plymouth. No doubt *Velella* were seen elsewhere but not reported; in order to avoid confusion no mention of *Velella* was made in the letters to the press.

## Shell Shape and Growth

The very extensive and confusing synonymy of the genus has recently been clarified by Laursen (1953). Of the many species of *Ianthina* described he recognizes only five, of which only *I. janthina* is viviparous. He figures variations in shell shape, showing how two series diverge from the two large specimens which, of the four shells in the Linnean collection, he regards as representing the type. At one extreme are trochoid shells (narrow in proportion to height), at the other they are flattened (wide in proportion to height). It was on the basis of these varied shapes alone that so many species were described; anatomically they are similar.

Although among the 1954 specimens there was a considerable range of shell shape it was clear that all intermediate varieties between the extremes were present and that only one species was involved. The majority of these fragile shells were damaged but there were a fair number unbroken. Their heights and widths were measured with calipers graduated in hundredths of an inch. The width recorded was the maximum distance across the last whorl and is inclined at an angle to the height (Text-fig. 2). These measurements are recorded in Table II. No broken shell was larger or smaller. In the graph (Text-fig. 2) the height is plotted against the ratio width/height, and it will be seen that in spite of much variation between individuals of similar heights the general tendency is for the ratio to get smaller as the shell grows. Mr G. M. Spooner has kindly estimated the regression of width on height and finds that this tendency is significant. The line drawn through the points in Text-fig. 2 represents the best fit, assuming a linear relation between the ratio and height, through the plots of the thirty-eight observations listed in Table II. It will be seen that the additional points also fall on either side of this line, including the projected portion beyond a height of 1·1. Wide flattened types (= *I. planispirata* Adams & Reeve) are commoner among the smaller shells than the larger. The only shell in which height and width were equal came from Saunton, and it is interesting that four of the eight measurable shells from that district were somewhat taller types than those from elsewhere. This may be without significance; on the other hand, the shells stranded at Saunton may have come from the borders of the shoal, for *Ianthina* was not reported farther east along the coast.

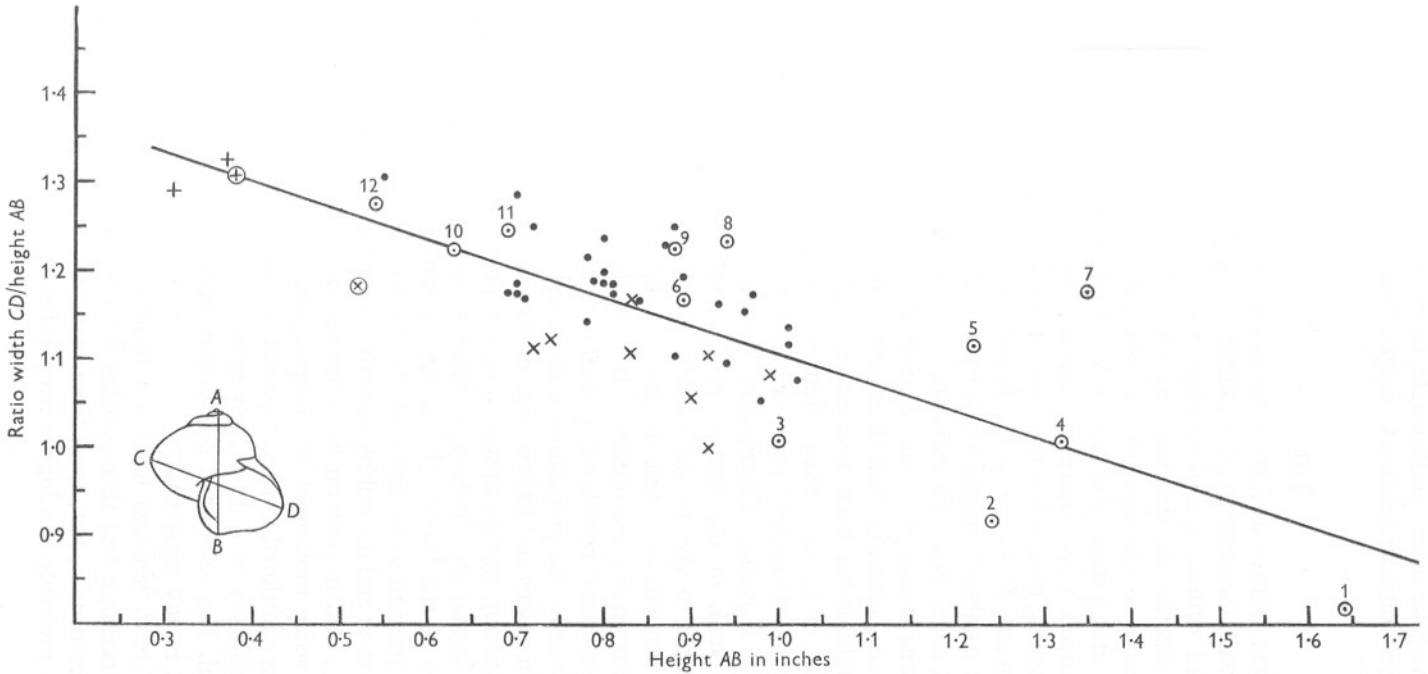
The diagrams of shells given by Laursen in his fig. 15 (1953) have been carefully drawn and are reproduced natural size. Nos. 3, 7 and 12 are from the original material of Linnaeus. These diagrams have been measured with the calipers and the results plotted in Text-fig. 2, along with those for the 1954 shells. It will be seen that they lie about the same curve, though it is noteworthy that the large and relatively broad shell no. 7 (identical with the type from the Linnean collection) falls farther to one side of it than do any of the others. Also plotted are measurements of two shells of *I. planispirata*

TABLE II. MEASUREMENTS OF SHELLS OF *IANTHINA JANTHINA* (L.)

| Height (in.) | Width (in.) | Ratio: width / height |
|---|---|---|
| Shells from Trevone and Harlyn Bays, 1954 | | |
| 0·55 | 0·72 | 1·309 |
| 0·69 | 0·81 | 1·174 |
| 0·70 | 0·83 | 1·186 |
| 0·70 | 0·90 | 1·286 |
| 0·71 | 0·83 | 1·169 |
| 0·72 | 0·90 | 1·250 |
| 0·78 | 0·95 | 1·218 |
| 0·78 | 0·89 | 1·141 |
| 0·79 | 0·94 | 1·190 |
| 0·80 | 0·95 | 1·188 |
| 0·80 | 0·99 | 1·238 |
| 0·81 | 0·96 | 1·185 |
| 0·81 | 0·95 | 1·173 |
| 0·84 | 0·98 | 1·167 |
| 0·87 | 1·07 | 1·230 |
| 0·88 | 1·10 | 1·250 |
| 0·89 | 1·06 | 1·191 |
| 0·93 | 1·08 | 1·161 |
| 0·94 | 1·03 | 1·096 |
| 0·96 | 1·11 | 1·156 |
| 0·97 | 1·13 | 1·165 |
| 0·98 | 1·03 | 1·051 |
| 1·01 | 1·12 | 1·109 |
| 1·01 | 1·15 | 1·139 |
| 1·02 | 1·10 | 1·078 |
| Shell from Porthcothan, 1954 | | |
| 0·70 | 0·82 | 1·171 |
| Shell from Lelant, 1954 | | |
| 0·80 | 0·96 | 1·200 |
| Shell from St Agnes, 1954 | | |
| 0·88 | 0·97 | 1·102 |
| Shells from Saunton, 1954 | | |
| 0·72 | 0·80 | 1·111 |
| 0·74 | 0·83 | 1·122 |
| 0·83 | 0·92 | 1·108 |
| 0·83 | 0·97 | 1·169 |
| 0·90 | 0·95 | 1·056 |
| 0·92 | 0·92 | 1·000 |
| 0·92 | 1·03 | 1·120 |
| 0·99 | 1·07 | 1·081 |
| Shells sent from Sennen by Mr T. G. W. Fowler some years ago (*planispirata* variety) | | |
| 0·31 | 0·40 | 1·290 |
| 0·37 | 0·49 | 1·324 |

Adams & Reeve, collected by Mr T. G. W. Fowler near Sennen and sent to us some years ago; his figures of a similar shell (1946) and one of *I. britannica* Forbes & Hanley (1948) from near Sennen Cove, were measured with calipers, and the results, adjusted according to the scale given on the plates, are also plotted.

Measurements of the 1954 shells thus confirm Laursen's conclusion, based on comparative evidence, that these varied types belong to one species. He was unable to explain their origin, suggesting that it might be related to variations in shell shape at the veliger stage brought about by differing spatial conditions during embryonic growth. Measurements of veliger larvae obtained




Text-fig. 2. Graph to illustrate the relation of shell width to shell height in *Ianthina janthina*, expressed as ratio of width to height, based on specimens and drawings. The diagram at the side indicates the shell dimensions measured: *AB* the height, *CD* the width. Shells collected in August 1954 at Trevone, Harlyn Bay, Porthcothan, Lelant and St Agnes are indicated by dots; shells collected the same month at Saunton are shown by ×'s. A dot within a circle with a number over it indicates a similarly numbered drawing in Laursen (1953, fig. 15). Two shells of the synonymous *I. planispirata* collected by Mr T. G. W. Fowler at Sennen prior to 1954 are shown by +'s. A similar cross in a circle indicates Fowler's *I. planispirata* from *J. Conch.*, Vol. 22, p. 186, plate I. A × in a circle indicates Fowler's *I. britannica* from the same volume, p. 308. For explanation of the line see text, p. 297.

in 1954 (see below) gave ratios width/height between 1·54 and 1·75. Veligers are thus considerably broader relative to height than any of the shells plotted in Text-fig. 2.

## The Float

The size of the float relative to that of the animal varied greatly, sometimes being quite large with the older portion ragged and worn as in Pl. I, fig. 1, in others smaller and without a degenerating end as in Pl. I, figs. 2 and 3. Mr Peter David regards the degenerating end as atypical, and informs us that in the hundred or so specimens he has taken at sea while in *Discovery II* he has never seen such a thing, and he wonders if it is due to an unfavourable environment. Laursen (1953) figures the curved float of *I. exigua*, and shows such an end, remarking that 'when the parts of the float grow old, they go to pieces and are broken off' (*loc. cit.* p. 6). It may be noted here that while the greater part of the combined animal and float is under water quite a light puff of breath directed at the float will make the snail scud along before it.

A few of the least damaged of our specimens, which had been gathered directly from the sea, added to their floats while kept in dishes of sea water. The method of building has been described several times before, the earliest account being that of Coates (1825). Jeffreys (1867) gives a good account of early observations. Fraenkel (1927) watched a species that appeared at Naples (apparently *I. pallida* Thompson). We proved, as others had done, that an *Ianthina* sunk to the bottom of a vessel by partial destruction of its float is unable to rise to the surface, but that if the water-level be lowered until the propodium is able to break through the water surface, the snail will be afloat again in a few minutes. It is the function of this part of the foot to form mucus-coated bubbles of air and to attach them to the proximal end of the float—briefly, the propodium is stretched upwards, the upper part bends back at right angles and flattens out on the water-surface film, with its intensely black secreting surface upwards, in contact with the air. Its centre is then depressed so that the whole organ becomes spoon-shaped, then hood-shaped; the edges of the 'hood' (Pl. I, fig. 2) contract together, meeting closely enough to prevent water entering the cavity. The propodium is then drawn under the water and the bubble smartly clapped against the base of the float (Pl. I, fig. 3), held in position for a few seconds and then cemented in place by a side-to-side motion of the propodium, wiping over it and presumably spreading additional mucus. Sometimes the new bubble fails to be attached and floats away as a tiny glassy sphere. By pressure the bubbles become polyhedral. The completed float is firm between the fingers, springy and dry—it is not in any sense sticky.

One individual of *I. janthina* formed a bubble in about 65 sec, making perhaps ten in succession and then pausing for a while. Fraenkel's animals took only 30–40 sec over it, but, apart from being another species, at Naples in May they were probably at a higher temperature.

## The Epipodium

When the animal is alive the shell is very slippery. Possibly this may bear some relation to the lateral extension of the foot—the epipodium. As described by Adams (1862), in lively individuals it is 'reflexed on the right side on the penultimate whorl of the shell' (Pl. I, figs. 1–3). The margin is irregularly notched, when fully expanded the right-hand lobe is thin and transparent; only the left-hand lobe is pigmented. Master Richard Wilson noticed rippling movements of the expanded right-hand lobe and suggested a possible connexion with the passage of water over the gills.

Laursen (1953) thinks the epipodium may serve to give the animal a better balance in the water: we saw no sign of its acting as a fin for balance or propulsion, and our specimens never of their own accord moved away from any position where they happened to be floating against the side of the jar or basin, even after many hours. Incidentally, Adams in his 1862 paper did not make the statement attributed to him by Laursen that it co-operated in the animal's movements. It had been made by earlier writers, and the point was discussed by Moerch (1860). Movements of the animal are mainly contractions and extensions of the body, bringing the shell close to the float or about its width lower in the water, and also twisting the body. We had an impression that although *Ianthina* has no eyes the expanded animal when in a glass jar could perceive our near approach and would contract into the shell. Our animals discharged red-violet liquid when handled, but the amount was small. The ink streamed downwards and was soon dispersed.

## Feeding

*Ianthina* is said to feed on a number of pelagic animals (see Laursen, 1953, p. 14 for brief summary), but appears to subsist mainly on *Velella*. As the adult has, so far as is known, no power of swimming it can only attack its prey when by chance it drifts against it. We introduced our specimens to living, though battered, *Velella* which had come ashore with them, but the *Ianthina* did not eat them even when their snouts were fully expanded, with the forked tentacles erect, and mandibles and teeth exposed as if ready for food.

We are indebted to Mr Peter David for permission to publish the following notes, which he made in 1954 aboard *Discovery II* when watching *I. janthina* collected at Station 3098, 42° 36′ N., 20° 43′ W. The species was identified by Dr J. E. Morton from specimens brought back by Mr David.

Several large specimens were found with *Velella* tentacles adhering to them and several *Velella* were taken with small *Ianthina* attached to the under surface. Some of these were kept alive for two days, and at the end of this time the *Ianthina* were still quite active, and apparently browsing on the *Velella*; the latter seemed to be lifeless, but from previous experience of *Velella*, it was known that, when dead, their tentacles drop off; the specimens with *Ianthina* on them did not break up in this way.

It was observed that the *Ianthina* exuded their purple dye periodically (fairly frequently) while feeding, and it seems possible the dye may be used to anaesthetize the *Velella*. Clean *Velella* floats were seen and taken, and may be all that *Ianthina* leaves of its food. . . . The small individuals feeding on *Velella* had no floats in most cases, though in one case a detached float was attached to the rim of the *Velella*; the float would be in the way while the animal was eating, as it seems to be attached to the foot, and the normal gastropod eating habits are used.

Mr David adds that on the November 1954 cruise of *Discovery II* he also observed an unidentified ovigerous species.

To quote from his letter. 'This animal also feeds on *Velella*, but in a different way; instead of abandoning its float and browsing on the under side of the *Velella*, this species is held by surface tension against the rim of *Velella*, and proceeds to chew semicircular pieces from it, in much the same way as a caterpillar does on the edge of a leaf. As far as I could determine no purple was released, but then the *Ianthina* is out of reach of the *Velella* tentacles.'

## Reproduction

On not very complete evidence the Ianthinidae are thought to be protandrous hermaphrodites. *I. janthina* is viviparous, the other species attach egg capsules to the under-surface of the float. In Graham's material (1954) of *I. janthina* the males were all markedly smaller than the females. This was in agreement with earlier observations of Ankel (1930) on another species. Laursen (1953), however, could find males and females of the same size in the one collection, and also saw very large males, sterile individuals and hermaphrodites; it would seem that *Ianthina* can pass through more than one breeding cycle.

We had two active specimens gathered from the margin of the sea, which respectively shed male and 'female' genital products. Both were of about the maximum size we saw. In the later part of the day after collection one animal shed singly at intervals at least thirty-six dark brown cylindric pellets, about $\frac{1}{10}$ in. long, and at first thought to be faecal. They fell to the bottom of the container (a white china basin) and quickly disintegrated, releasing a number of fully developed veliger larvae with brownish purple shells, swimming with a bilobed velum. Twenty or more were in each packet, varying from 100 to 230 $\mu$ across the shell at its maximum width. They gyrated actively over the bottom, neither moving upwards, nor congregating towards nor away from the light. Fraenkel's veligers (1927) (probably *I. pallida* Thompson) swam evenly in the aquarium, showing neither geotaxis nor phototaxis, although they had eye-spots.

As a prelude to the shedding of a packet the propodium was withdrawn from its normal resting position appressed to the base of the float, and was furled up and twisted from side to side.

Extrusion was so rapid that it could be missed in the momentary shifting of

the gaze, so that only once was it seen. Master Richard Wilson was looking down on this animal when from between the bottom of the foot and the gills a 'little bullet' suddenly shot upwards and out over the (morphologically) left-hand side of the shell, that which is not covered over by the epipodium (Pl. I, figs. 2, 3). Several packets were seen shortly after emergence and there was no doubt that they came out from this side.

The organization of larvae into packets which are violently extruded seems not before to have been noted. Laursen (1953), having described the embryoduct as leading to the inside of the mantle cavity some distance from the rectum, says only that 'the embryos now leave the mother animal and swim freely into the ocean'. This only happened in our animal the next day, when it was less active, and a small number of veligers emerged singly at their own pace.

The second animal, which was in another container, several times shed over the left-hand side of the shell a quantity of mucus containing a number of elongated whitish droplets, about the same length as the larval pellets. They fell gently to the bottom. Further observation was impossible without a microscope, but preserved material showed they must have been aggregates of spermatozeugmata. These seem not to have been seen alive in *I. janthina*, but closely resemble those of a species (probably *I. pallida*) described in detail by Ankel (1930). Each is made up of an oligopyrene spermatozoan, whose head is a flat lanceolate plate with a thicker densely granular base from which emerges a tail. To this are attached by their heads so many eupyrene spermatozoa as to give it the appearance of a fox's brush. The spermatozeugma moves forward by means of undulations of the plate's margin and lashing of the eupyrene spermatozoa.

As *Ianthina* has no powers of locomotion the sexes can only meet when accidentally drifted together and as, too, there are no copulatory organs the method of transference of spermatozoa poses a problem. Graham (1954), indeed, finds nothing in the reproductive physiology of *I. janthina* incompatible with a possibility of self-fertilization, while Ankel (1930) only obtained his spermatozeugmata by dissection. Our observation of the actual discharge of aggregates of these elaborate structures supports the view that they are an adaptation enabling spermatozoa to make the relatively long journeys between individuals of a shoal.

## Epizoic Animals

On a shell (2·1 cm high) of a living *Ianthina* picked up at Trevone there were growing four living specimens of *Lepas pectinata* Spengler. The capitulum of the largest barnacle was 1·3 cm long, of the smallest 1·1 cm. They were attached in a cluster close to the mouth of the shell beside the columella, and in the normal floating position of the snail the barnacles would be growing more or less upright, pressing perhaps against the base of the float, which was

not present when they were found. Over part of the capitulum of one barnacle there was growing a colony of the hydroid *Laomedea geniculata* (L.). Another colony of the same species of hydroid was growing on the shell of the *Ianthina* whose photograph is reproduced in Pl. I, fig. 1. Both colonies of the hydroid were kindly identified by Dr P. L. Kramp, who remarks that the species is particularly inclined to attach itself to floating objects.

Grateful thanks are due to the many who have made this paper possible and whose names are recorded in the text. In addition we should like to thank Professor A. Graham and Dr J. E. Morton for placing their knowledge of the Ianthinidae at our disposal. For our account of the winds we acknowledge our indebtedness to the Daily and Monthly Weather Reports of the Meteorological Office, London.

## Summary

1. During the exceptional westerly weather of August 1954 large numbers of *Ianthina janthina* (L.) were found on the north coasts of Cornwall and Devon, in what was almost certainly the largest stranding of this species on English shores for fifty years. The strandings are clearly correlated with periods of west to north winds.

2. With the *Ianthina* there were often stranded many living *Velella*.

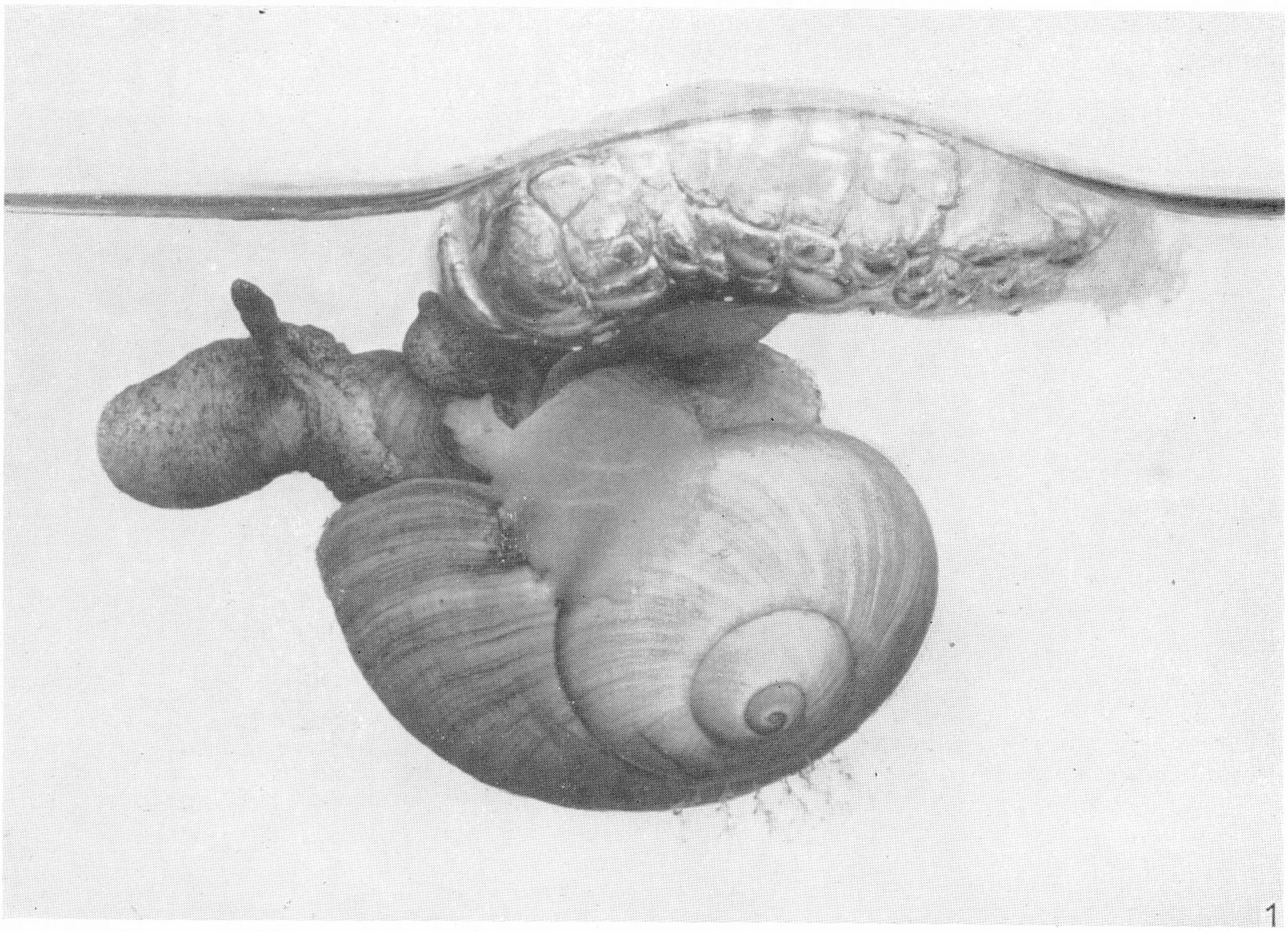
3. A sufficiently large number of unbroken shells were obtained to allow of some investigation into the relationship between width and height. It was found that while there is considerable variation at any one height the width is relatively less in older shells than in young ones. In the past these varied shapes have led to many different species being described. The results in the main confirm Laursen's conclusions (1953); when his careful drawings of different shell types were measured, it was seen that their ratios were in general agreement with those of the 1954 specimens.

4. Earlier accounts of float-building were confirmed from observations of healthy specimens obtained in 1954; a few new details were added.

5. The epipodium as observed in life is described and its function discussed.

6. Some notes on the feeding habits of this species, made by Mr Peter David on board *Discovery II*, are reproduced by permission. He makes the interesting suggestion that the purple dye of *Ianthina* can anaesthetize its main prey, *Velella*.

7. Shedding of larvae and sperms was observed in living specimens. In both sexes the genital products, organized in packets, were shot out of the mouth of the shell on the morphologically left side, that which is not covered by the epipodium. Our observations support the view that the elaborate organization of the sperms into compound structures is an adaptation enabling them to travel from males to females floating well apart.



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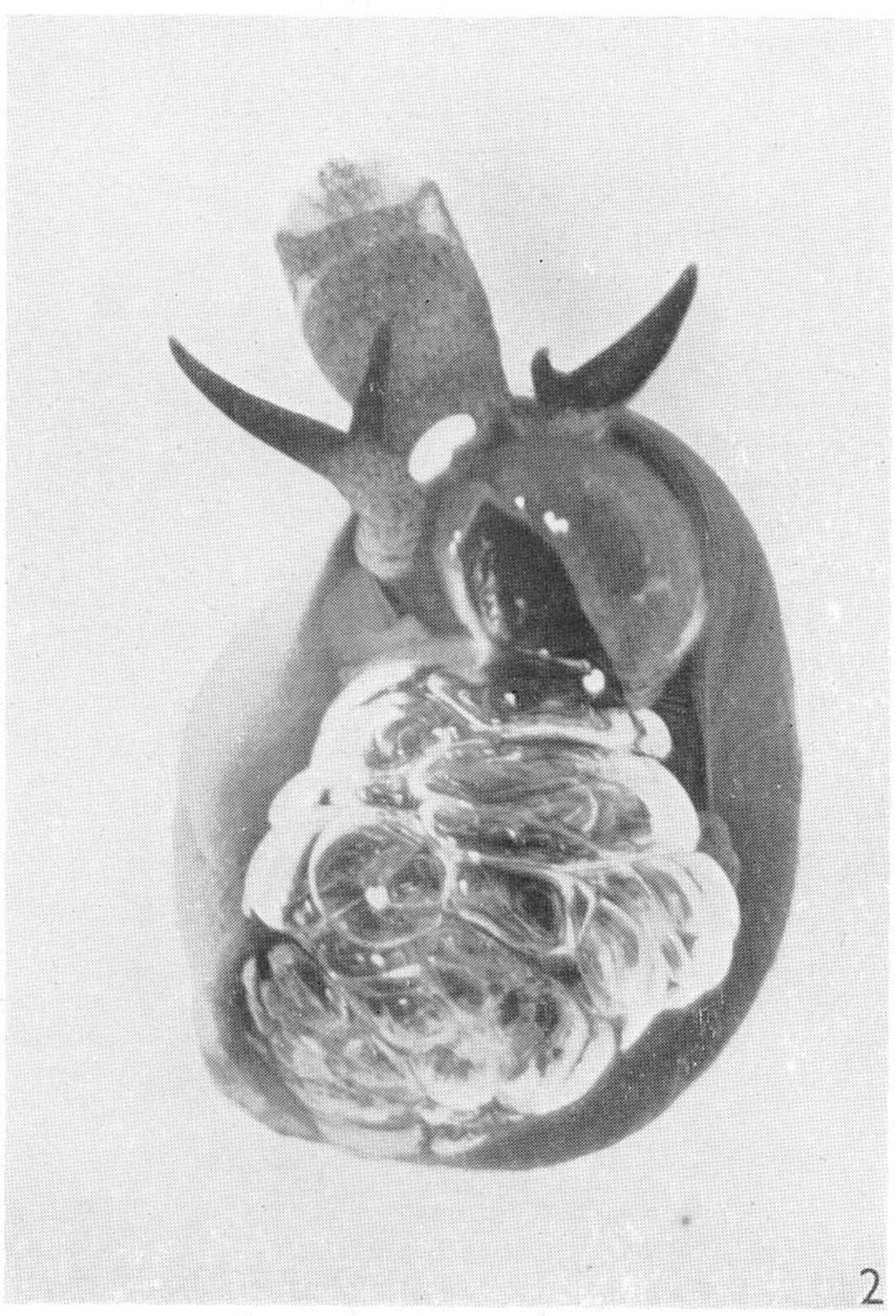

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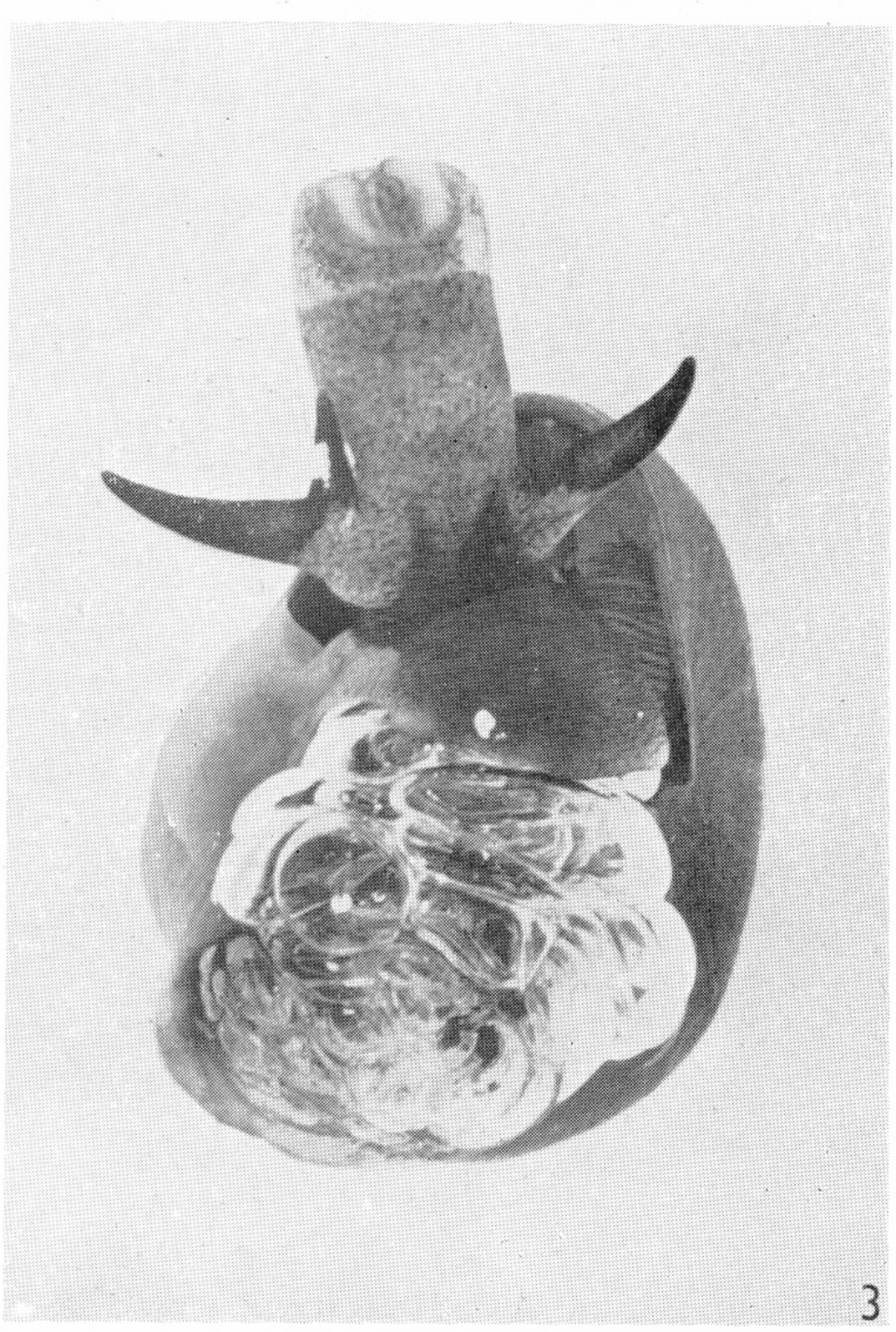

3

(*Facing p.* 304)

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## EXPLANATION OF PLATE I

(Black and white photographs from Kodachrome originals, taken by electronic flash. Reproduced about twice natural size.)

Fig. 1. Lateral view of a living *Ianthina janthina* L. floating against the side of a cylindrical vessel: the meniscus is arched where the float contacts the glass. The snout and tentacles are not quite fully extended. The colourless translucent epipodium of the right side and its serrated border are well shown. The propodium in its contracted state is seen at rest against the proximal (anterior) end of the float. The distal extremity of the float is disintegrating and losing air. A hydroid is growing on the shell.

Figs. 2, 3. Views from above of another specimen adding a bubble to its float. In Fig. 2 the edges of the expanded hood-shaped propodium are contracting together to enclose a bubble of air. Within the hood is visible the dark epithelium, which secretes a coat of mucus around the bubble. In Fig. 3 the propodium is pressing the bubble against the base of the float and cementing it into position. In these photographs the snout and tentacles are fully extended. The irregular white patches are highlights where wet, and therefore shiny, rounded parts just break the surface film. In this view only the top of the bubble float, which is entirely above water, is visible. The epipodium of the right side (left side of each picture) is seen wrapping around the shell surface. Gill lamellae within the mantle cavity are glimpsed through the shell mouth, especially in Fig. 3. It is through this open portion of the shell mouth, on the left side of the snail, that the genital products were shed (see page 303).