A CONTRIBUTION TO THE BIOLOGY
OF *ASTRORHIZA LIMICOLA*
(FORAMINIFERA)

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(Text-figs. 1–5)

In the last few years the exceptionally large monothalamous arenaceous rhizo-pod, *Astrorhiza limicola* Sandahl, 1858, has been collected in appreciable numbers from the Blyth and Plymouth areas of British coastal waters. These collections of the living animals have enabled the authors, both independently and jointly, to make certain observations of the behaviour of the animal, and of the structure of the test, which have not been appreciated hitherto. With the exception of two early accounts of *A. limicola*, one by Bessels (1875) under the name *Haeckelina gigantea* and the other by Schultz (1915), very little appears to be known of the biology of any member of the family Astrorhizidae.

DISTRIBUTION

Astrorhiza limicola, the type species of the genus *Astrorhiza*, was first described from specimens collected off the Bolus coast, Skagerak (Sandahl, 1858) and recent faunistic accounts by Högland (1947) and Christiansen (1958) indicate that it is well established in the sandy-mud sediments in shallow water (12–58 m) of the Kattegat, Skagerak, the Gullmar and Oslo Fjords (Dröbak Sound). The numerous records of the animal in British coastal areas are all from sand, sandy-mud, or miry sediments at depths ranging from 20 to 130 m (Brady, 1884, 1887; Robertson, 1901; Heron–Allen and Earland, 1909; Stephen, 1923; Plymouth Marine Fauna, 1957). This apparently consistent occurrence in shallow waters, also noted by Cushman (1918) who lists early records from the North Atlantic coast of America, is upset by two old yet often neglected records, one by Carpenter & Wyville Thomson (1868) from a station due north of the Hebrides at 59° 36′ N. 7° 20′ W. and the other by Norman (*teste* Jeffreys, 1876) in the Davis Strait at 59° 10′ N. 50° 25′ W., where the depths are 970 and 3200 m, respectively. Although the specimens do not appear to be available for examination, the short descriptive accounts indicate that the records are justified, so that

the depth range of the species has to be extended beyond that which it is customary to acknowledge.

Apart from the North Atlantic, records from the Arctic north of the New Siberian Islands (Stschedrina, 1946) of *A. limicola* var. *arenifera* and *A. limicola* var. *sabulifera* are of interest, although in a recent private communication Mrs Stschedrina has informed one of us that she is revising her opinion about the systematic position of these forms. The only reports of *A. limicola* from the southern hemisphere are those from the east coast of Africa (Heron-Allen & Earland, 1915), the Antarctic (Heron-Allen & Earland, 1922) and South Georgia (Earland, 1934) all of which are based on either fragments or odd specimens. Re-examination of this material from the southern hemisphere has led to the conclusion that these records should be provisionally considered as doubtful.

QUANTITATIVE DATA AND THE NATURE OF THE ENVIRONMENT

The distribution of *A. limicola* has been most fully studied on the offshore grounds of the southern half of the Northumberland coast. All along this coast there is a strip of muddy sand from 8 to 10 miles wide at depths from 30 to 70 m running parallel to the coastline. Farther offshore the bottom falls off to depths of 80–100 m where the sediments are predominantly sandy silt. At a distance of 20–25 miles offshore the bottom rises once again to depths of 60–70 m and muddy sand sediments are again encountered. Broadly speaking the sediments can be regarded as being a broad area of muddy sand divided down the middle by a strip of sandy silt which corresponds to a tongue of deep water (80–100 m) running approximately north to south at a distance of about 15 miles offshore all along the southern half of the Northumberland coast. The inshore strip of muddy sand is itself divided approximately down the middle by a long tongue of almost clean sand over 20 miles in length and varying from 1 to 7 miles in width at depths of 40–60 m. The offshore area of muddy sand also has areas, like the inshore, which as a result of tidal scour are swept almost clean of fine sedimentary material. It is on these sandy areas both inshore and offshore that *A. limicola* is a constant and conspicuous constituent of the benthic fauna. The bottom in these areas is fine to medium sand (250–500 μ) with generally less than 10% silt (particles less than 62 μ) and less than 2% clay (particles less than 4 μ). It should be emphasized that these sandy areas are isolated patches or strips surrounded by muddy sand and that their fauna does not represent a discrete community of species, but rather a modification of the fauna found on the muddy sand surrounding them, which can be broadly described as belonging to the classical 'Echinocardium-filiformis' community of Petersen.

Fifty-six stations were sampled with a Van Veen grab throughout the extent of the sandy area with *A. limicola* occurring in 82% of the hauls at an

average density of 53 specimens per square metre, the greatest density being 240 individuals per square metre. The animals found commonly in this association are listed in Table 1.

TABLE 1. OTHER ANIMALS FOUND ASSOCIATED WITH *A. LIMICOLA* WITH THEIR AVERAGE NUMBERS PER SQUARE METRE FOR FIFTY-SIX HAULS

	No. per m²		No. per m²
Astrorhiza limicola	53	*Dentalium entalis*	4
Amphiura filiformis	47	*Echinocyamus pusillus*	4
Nephthys spp.	13	*Venus striatula*	3
		Ampelisca brevicornis	2
Owenia fusiformis	5	*A. macrocephala*	1
Echinocardium flavescens	4	*Phaxas pellucidus*	2
E. cordatum	1	*Sthenelais limicola*	2
Goniada maculata	4	*Astropecten irregularis*	2
Dosinia lupinus	4	*Abra prismatica*	1

Quantitative data are sparse for other areas but two records are worth noting. Stephen (1923) reports the rhizopod from a grab haul taken at a depth of 101 m off the Butt of Lewis where ten specimens were obtained in 0·1 m², together with *Echinocardium flavescens, Dentalium entalis, Ophiura affinis, Abra prismatica* and *Mactra elliptica*. Secondly, an association similar to that found off Northumberland has been described by Caspers (1950) from off the Heligoland coast. Here *Astrorhiza limicola* reached a maximum density, in one haul, of sixty-seven individuals in 0·1 m² but this high density appears to be confined to a very small area. Figures given by Caspers (1950) for the particle size analysis of the bottom sediment also appear to be very similar to the Northumberland sediments and consist mainly of sand fractions from 125 to 500 μ at a depth of 22–25 m. The associated animals off Heligoland are *Amphiura filiformis, Owenia fusiformis, Nephthys* spp., *Venus striatula, Spisula solida, Cochlodesma praetenue, Echinocyamus pusillus* and *Phoronis mulleri*. In both the Northumberland and Heligoland areas the ecological conditions appear to be very similar and both are isolated sandy areas more or less surrounded by a typical 'Amphiura' community. Thorson (1957) suggested that the Heligoland association, in which *Astrorhiza limicola* is dominant, may be regarded as a 'Foraminifera' community, whereas we are of the opinion that this association should be regarded as a variation or faciation of the 'Amphiura' community (Thorson, 1957) where it is in a state of transition to a 'Venus' community. This transition is never completed off the Northumberland coast, since the sediments rapidly become more muddy again as deeper water is approached and the characteristic associations of a true 'Venus' community are never found to be sufficiently significant to dominate the population.

Dense populations of *A. limicola* always appear to be associated with stable areas of fine to medium sand, with only small amounts of silt and clay, containing a relatively rich interstitial fauna. Such areas seem to lie intermediate,

in bottom conditions, between the muddy sand areas, with slow bottom currents allowing quantities of silt and clay to accumulate, and clean sand areas with relatively strong bottom currents and probably less interstitial stability. In the few areas which have been quantitatively studied the intermediate bottom conditions are confirmed by a fauna, occurring with *A. limicola*, which is generally in the nature of a mixed community.
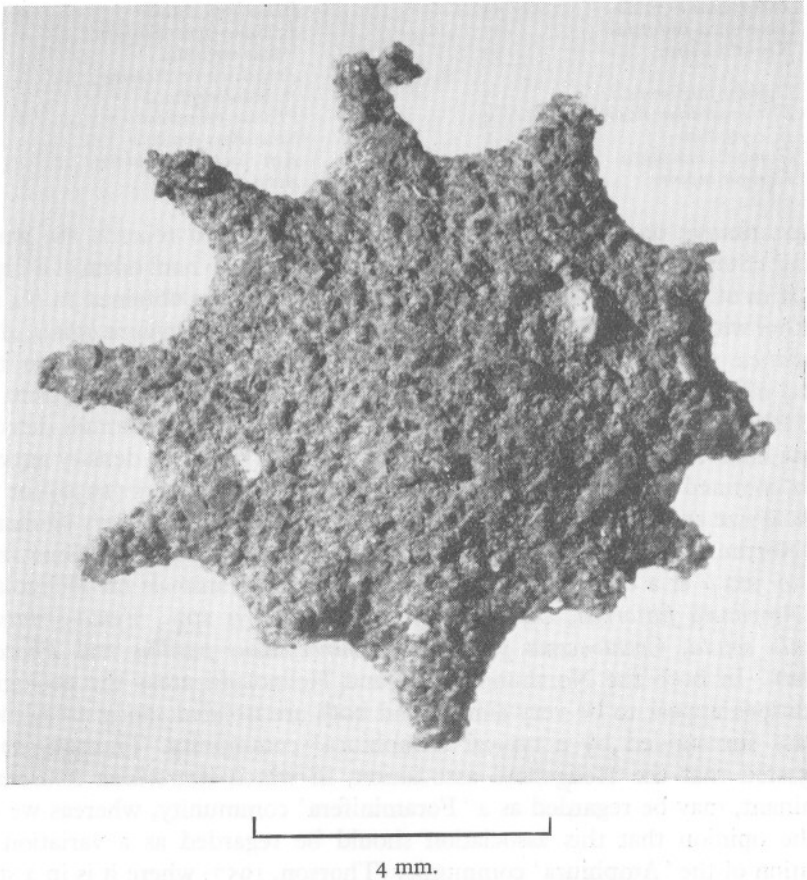

4 mm.

Fig. 1. A typical *Astrorhiza limicola* collected from the Northumberland coast.

STRUCTURE OF THE TEST

Individuals of *A. limicola* are surrounded by a well-defined stellate test built up of extraneous material from the bottom sediments on which they lie (Figs. 1, 2). In addition to this foreign material there is an organic cement, secreted by the animal, causing the sand grains to cohere and ensuring the stability and form of the arenaceous test.

The extraneous constituents

In the Northumberland specimens the tests are constructed for the most part from inorganic material in which quartz grains predominate, although other materials, such as shell fragments and small echinoderm spines, are often incorporated. Although quantitative sampling has shown that the rhizopods occur in the largest numbers on the clean, comparatively silt free, sands, they can be collected in small numbers over a wide range of bottom conditions from fine silty sand to clean coarse sand. Individuals collected from these different areas show obvious superficial differences in external appearance suggesting that the material utilized in test building is obtained in a non-selective manner. Furthermore, in laboratory experiments *A. limicola* will readily utilize such materials as powdered glass and 'Perspex' shavings to effect a repair of a damaged test.

A large sample of individuals collected from several different types of sea bottom was treated with sodium hypochlorite solution resulting in the destruction of the organic matter and leaving a dispersed sample of the inorganic constituents of the test. Particle size analysis of this material showed that a complete range of particles was present from somewhat over 1000 μ down to slightly under 30 μ. Several other samples of *Astrorhiza* were similarly analysed along with analyses of the bottom sediment from which they were collected. It was found that for any particular locality the material in the test and the material from the bottom sediment produced an almost exact correspondence in analysis figures, indicating, that with the exception of the coarsest material and fine gravels, the animal incorporates the bottom sediment material into its test in almost exactly the same proportions as it is found in the sediment samples.

Specimens obtained from Plymouth had tests constructed of rather coarse sand and shell particles indicating that the bottom on which they lie is probably of shelly-gravel and coarse sand. The superficial difference between these specimens and those from the muddier areas of Northumberland is very marked, again suggesting that the nature of the material incorporated into the test appears to have little significance.

The organic cement

Microscopic examination and manipulation of a portion of the test wall shows this interstitial substance to have the consistency of a rigid gel, whereas after fixation in alcohol and in dried specimens, it is very contracted, giving the impression that little organic cement is present.

The cement has an affinity for basic dyes; it stains when immersed in a 0·01 % aqueous solution of toluidine blue, exhibiting γ-metachromasia when examined in water (Pearse, 1953) and reacts positively with Schiff's reagent

after prior oxidation with periodic acid (Hotchkiss, 1948). Attempts to demonstrate the presence of certain amino acids, and thereby protein, by the Millon and Sakaguchi reactions, have not been successful, although a positive result was obtained after the coupled tetrazonium reaction procedure for tyrosine, tryptophane or histidine (Pearse, 1953). From these results it appears that the cement is a protein-carbohydrate material with part at least being an acid mucopolysaccharide. Little more of any significance can be said about the chemical composition of the cement in the absence of a full analysis. It can, however, be referred to as 'tectin' (Hyman, 1940), although it must be emphasized that this term implies no precise chemical composition beyond the fact that the substance is composed of protein and carbohydrate in combination, that is, a type of glycoprotein. As there are many different forms of glycoproteins so there will be many different tectins.
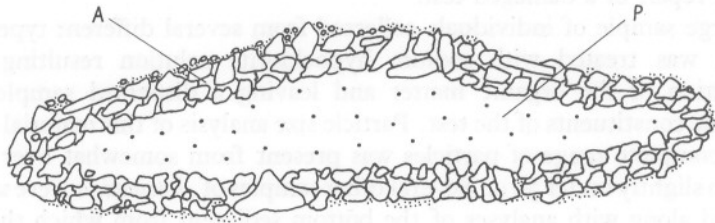

Fig. 2. A diagrammatic transverse section of *Astrorhiza limicola*. *A*, arenaceous wall; *P*, protoplasm.

The 'inner chitinous lining' of the test

The term 'chitinous' has often been used in foraminiferal work as an adjective of convenience to describe any of a variety of organic structures, including a thin lining to the interior of the test wall in *A. limicola* (Cushman, 1948). No worker, to the authors' knowledge, has demonstrated chitin in any part of the test of *A. limicola*, or indeed in any arenaceous foraminifer, and as no organic residue has been found after boiling in caustic potash there is no reason to suppose that chitin is present.

The inner organic layer of the test, just referred to, has some taxonomic significance, for Stschedrina (1946) notes that *A. limicola* var. *arenifera* differs from the typical *A. limicola* in having a more fragile and thin test and in the absence of an 'inner chitinous lining'. It must be pointed out that to the authors' knowledge the inner lining to the test of *A. limicola* has never been described or figured, and the question arises, does one exist at all? The following observations are relevant to this problem.

None of the living specimens from Blyth and Plymouth which have been examined possessed a recognizable inner organic lining to the test, nor was there an excessively large amount of organic cement on the internal surface

which could have been mistaken for a distinct inner layer. In alcohol-preserved and particularly dried specimens, however, the protoplasm has invariably changed colour from the normal cream to a dark red-brown and with the resultant dehydration the shrivelled protoplasm has assumed positions, especially in the radiating arms, which give the impression of a brown organic lining. It is quite likely that this abnormal state may account for some of the categorical statements of the presence of an inner lining, especially when it is noted that many faunistic accounts of Foraminifera have been based on dry collections.
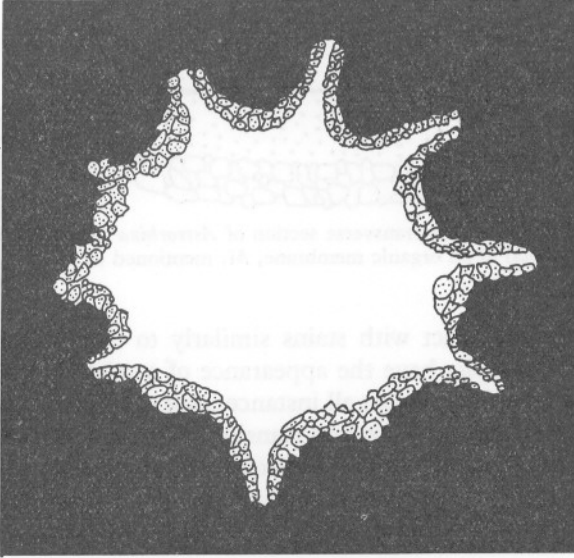

Fig. 3. A diagrammatic top view of *Astrorhiza limicola* after the roof has been removed to reveal the internal creamy protoplasm.

Another way in which the 'inner lining' character may have become established in the literature is through the examination of specimens which have at some time been damaged and have subsequently undergone repair. Although no examples of this sort have been collected by us, certain laboratory experiments of a damage and repair nature have been carried out, and the results may have some bearing on the problem. If, for example, the roof of a test is removed leaving the creamy protoplasm exposed (Fig. 3) and this damaged animal is left in a container without sand grains it will always secrete a membrane (Fig. 4), usually within 12 h. This organic membrane is approximately 10 μ thick, separate from and independent of the protoplasm which has secreted it, and completely covers that part of the test which has been damaged. If a

damaged animal such as this is now placed in a container with sand grains
these are manoeuvred by the pseudopodia on to the membrane and cemented
to it until the wall appears normal. In this case *A. limicola* does have an inner
organic lining to the test, but only to that part which has been repaired.
When animals are placed among sand grains immediately after being damaged
they usually repair their tests by incorporating the sand grains on the exposed
surface without the secretion of a definite foundation membrane. There is,
however, no precise procedure which can be said to take place in every case.
If the animal is squeezed out of the test and left naked in a container free of
sand grains it soon secretes a membranous test, completely surrounding the
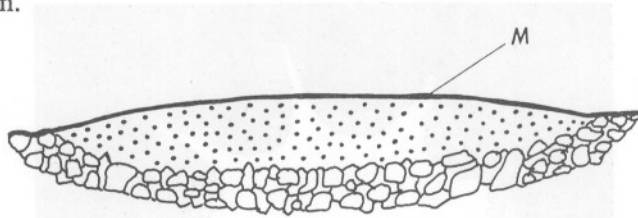protoplasm.

Fig. 4. A diagrammatic transverse section of *Astrorhiza limicola* to show the
position of an organic membrane, *M*, mentioned in the text.

These membranes react with stains similarly to the cement of the test
wall. They are isotropic, have the appearance of a relatively strong protein-
aceous structure, and, in almost all instances, are clear and transparent when
newly formed, becoming brown and translucent after a few days.

It is concluded that normally *A. limicola* does not possess a distinct lining
of organic material on the interior wall of the test, although under certain
rather unusual conditions an organic membrane is secreted.

The presence of iron in the test

The ferruginous nature of *A. limicola* is demonstrated when the sand grains
and organic cement are coloured blue after immersion in acidified potassium
ferrocyanide (equal parts 2% hydrochloric acid and 2% potassium ferro-
cyanide). This production of the Prussian blue compound is the end product
of a specific reaction and chemical test for ferric iron. The presence of iron in
the tests of a number of other arenaceous forms has been commented upon
by Vinogradov (1953) and a question of some interest is whether the source
of the iron is directly from the immediate environment or whether it is being
secreted by the animal. The same problem is discussed by Hedley (1960)
in relation to *Gromia oviformis*, a rhizopod with an organic test, where it does
appear that the animal is secreting iron in some form which, in part at least, is
deposited in the test wall. As far as the arenaceous foraminifera are concerned
Vinogradov (1953) summarizes the available data and infers that there is an

active physiological process whereby iron is 'precipitated' by the animals. One of us is currently investigating a number of arenaceous forms with this problem in mind, so that at this stage only those observations on *A. limicola* will be discussed: (*a*) Tests for iron in the protoplasm, using 6μ paraffin sections, have failed to reveal any structures which are iron positive. (*b*) Freshly secreted membranes of damaged animals are iron negative. (*c*) If *A. limicola* is placed in a dish containing sand grains from the sediment in which it was living at the time of collection, but which have been treated with concentrated hydrochloric acid to remove the iron and then thoroughly washed, any subsequent addition to the test, either sand grains or organic cement, is iron negative.

The foregoing observations suggest that the ferruginous nature of the test wall is the result of the iron already present on the sand grains of the sediment which are incorporated into the test by the animal. Consequently at this stage there is no evidence of the animal secreting iron.
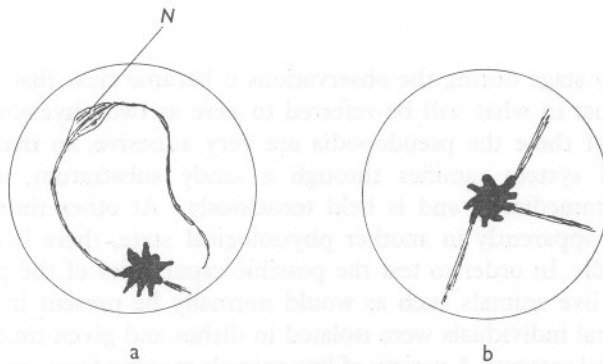

Fig. 5. Drawings showing the extent of two pseudopodial systems as they were seen when individuals were isolated in plastic dishes in the laboratory. The black circles represent the edges of the dishes and the nodule, N, is noted in the text (natural size).

BEHAVIOUR

The presence of epizoic growths of hydroids, ascidians and other arenaceous foraminifera on the upper surface of many tests of *Astrorhiza* shows that the animal normally lives on the sand surface and does not burrow. This was confirmed by observation of living material in the laboratory. When freshly collected animals are isolated in dishes with a sand substratum, they move in a more or less elliptical path for considerable distances. Schultz (1915) noted a distance of 25 cm covered in 24 h and speeds of this order have been confirmed on several occasions. The distance and route covered by isolated animals can be easily observed, since a furrow is left in the sand as a result of the leading edge of the test being preceded by a raised mound or

'bow-wave' of sand. When movement ceases this mound of sand may cause the test to appear buried to a very small extent. After a period of roaming about the dish, often lasting 24 hr, the animal settles and proceeds to develop an extensive pseudopodial system.

The pseudopodia ramify both over the sand surface and through the interstitial spaces to a depth of about 2–3 mm below the surface. Naturally they are more readily observed in dishes without a sand substratum and in such cases it is apparent that the pseudopodia occasionally have relatively large masses of protoplasm, forming nodules, along their length. Two typical pseudopodial arrangements are presented in Fig. 5a, b. Bessels (1875) drew a group of *Astrorhiza* showing seven specimens connected together to form a network, but we have not observed any actual union of different pseudopodial systems or of tests belonging to two or more individuals. Nevertheless a sediment inhabited by a number of *A. limicola* must be regarded as being very extensively ramified by their pseudopodia which may extend to distances of more than 6–7 cm from the central protoplasmic mass of each individual.

Feeding

At an early stage during the observations it became clear that the pseudopodia can exist in what will be referred to here as two physiological states. In the first of these the pseudopodia are very adhesive, so that, when the pseudopodial system ramifies through a sandy substratum, any particle sticks to it immediately and is held tenaciously. At other times, with the pseudopodia apparently in another physiological state, there is no adhesive property at all. In order to test the possible capabilities of the pseudopodia for catching live animals such as would normally be present in the natural habitat, several individuals were isolated in dishes and given time to develop a pseudopodial system. A variety of live animals ranging from small copepods and amphipods to nematodes and small echinoderms were then introduced. Although these animals were in a healthy state and moving briskly, they were firmly held whenever they came in contact with the adhesive pseudopodia. *A. limicola* proved itself quite capable of holding and eventually immobilizing such animals as fully grown cumaceans (*Diastylis laevis*), caprellids up to 2–3 cm in length and small recently metamorphosed *Echinocardium flavescens* as well as a variety of small crustacea. Similar experiments were carried out in dishes with a sandy substratum into which actively swimming *Artemia* were introduced. Whenever an *Artemia* landed on the bottom at a point where the pseudopodia were exposed it was firmly held. In all these experiments the captured animals struggled for long periods, invariably in vain, gradually becoming weaker and eventually dying. On examination after a period of 1–2 days nothing remained of a caught animal other than a clean cuticle.

There is no evidence that a toxin is secreted by *Astrorhiza* to kill the animals after they have been caught by the pseudopodia. Observations of the

process tend rather to support the opinion that the prey gradually dies through exhaustion and perhaps suffocation as a result of being firmly held by the pseudopodia. As no process of ingestion has been observed it is implicit that there is some process of extracellular digestion such as is said to occur in the case of *Elphidium crispum* (Jepps, 1942).

From the information obtained from laboratory feeding experiments there would seem to be strong evidence that *Astrorhiza limicola* is an active, mobile predator of the interstitial sand fauna and of the smaller faunal elements associated with the sediment surface. Schultz (1915) suggested that it feeds on small protozoans and flagellates, and from sections we have seen that diatoms are ingested. It seems likely that just as the animal is non-selective in test building it is also not very selective in feeding. If, as seems probable, interstitial organisms constitute the main food supply, the interstitial microfauna of those areas where *A. limicola* occur in large numbers must be profoundly affected.

SUMMARY

A general account, based on literature records, is given of the distribution of *Astrorhiza limicola* in addition to a more detailed account of its distribution and ecology off the Northumberland coast. The animal is seen to be non-selective of the materials used for test construction and an account of the test structure considers the significance of its ferruginous nature, the organic cement component secreted by the animal, and an 'inner chitinous lining' often reported in the literature.

Laboratory observations of living animals indicate that *A. limicola* may be regarded as a mobile predator of interstitial sand metazoans.

REFERENCES

BESSELS, E., 1875. *Haeckelina gigantea*. Ein Protist aus der Gruppe der Monothalamien. *Jena Z. Naturw.*, Bd. 9, pp. 265–79.

BRADY, H. B., 1884. Report on the Foraminifera dredged by H.M.S. 'Challenger' during the years 1873–1876. *'Challenger' Rep.*, Vol. 9, pp. 800.

—— 1887. A synopsis of the British Recent Foraminifera. *J. R. micr. Soc.*, 1887. Part 6, pp. 872–927.

CARPENTER, W. B. & WYVILLE THOMSON, C., 1868. Preliminary report of dredging operations in the seas to the north of the British Islands. *Proc. roy. Soc.*, Vol. 17, pp. 168–200.

CASPERS, H., 1950. Die Lebensgemeinschaft der Helgoländer Austernbank. *Wiss. Meeresunters.*, Abt. Helgoland, Bd. 3, pp. 119–69.

CHRISTIANSEN, B., 1958. The foraminifer fauna in the Dröbak Sound in the Oslo Fjord (Norway). *Nytt Mag. Zool.*, Vol. 6, pp. 5–91.

CUSHMAN, J. A., 1918. The Foraminifera of the Atlantic Ocean. Part 1. Astrorhizidae. *Bull. U.S. nat. Mus.*, No. 104, 111 pp.

—— 1948. *Foraminifera, their Classification and Economic use.* 605 pp. Cambridge, Massachusetts: Harvard University Press.

EARLAND, A., 1934. Foraminifera. Part 3. The Falklands sector of the Antarctic (excluding south Georgia). '*Discovery*' *Rep.*, Vol. 10, pp. 1–208.

HEDLEY, R. H., 1960. The iron-containing shell of *Gromia oviformis* (Rhizopoda). *Quart. J. micr. Sci.* (in the Press.)

HERON-ALLEN, E. & EARLAND, A., 1909. On a new species of *Technitella* from the North Sea. *J. Queckett micr. Cl.*, Vol. 10, pp. 403–12.

—— 1915. The Foraminifera of the Kerimba Archipelago (Portuguese East Africa). *Trans. zool. Soc. Lond.*, Vol. 20, pp. 363–766.

—— 1922. Protozoa. Part 2. Foraminifera. *British Antarctic* ('*Terra Nova*') *Expedition, 1910.* Nat. Hist. Rep., Zoology., Vol. 6, pp. 25–268.

HÖGLAND, H., 1947. Foraminifera in the Gullmar Fjord and the Skagerak. *Zool. Bidr. Uppsala*, Vol. 26, pp. 1–328.

HOTCHKISS, R. D., 1948. A microchemical reaction resulting in the staining of poly-saccharide structures in fixed tissue preparations. *Arch. Biochem.*, Vol. 16, pp. 131.

HYMAN, L. H., 1940. *The Invertebrates*: *Protozoa through Ctenophora*. 726 pp. New York and London: McGraw-Hill.

JEFFREYS, J. G., 1876. Preliminary report of the biological results of a cruise in H.M.S. 'Valorous' to Davis Strait in 1875. *Proc. roy. Soc.*, Vol. 25, pp. 177–230.

JEPPS, M. W., 1942. Studies on *Polystomella* Lamarck (Foraminifera). *J. mar. biol. Ass. U.K.*, Vol. 25, pp. 607–66.

MARINE BIOLOGICAL ASSOCIATION., 1957. Plymouth Marine Fauna.

PEARSE, A. G. E., 1953. *Histochemistry, theoretical and applied*. 530 pp. London: Churchill.

ROBERTSON, D., 1901. List of Foraminifera. In *Fauna, Flora and Geology of the Clyde Area*. Local Committee for the meeting of the British Association, Glasgow, 1901. pp. 376–83.

SANDAHL, O., 1858. Två nya former af Rhizopder. *Kongl. svenska VetenskAkad. Handl.*, Vol. 14, pp. 299–301.

SCHULTZ, E., 1915. Die Hyle des Lebens. 1. Beobachtungen und Experimente an *Astrorhiza limicola*. *Arch. EntwMech. Org.*, Bd. 41, pp. 215–36.

STEPHEN, A. C., 1923. Preliminary survey of the Scottish waters of the North Sea by the Petersen Grab. *Sci. Invest. Bd Fish. Scot.*, 1922, No. 3, 21 pp.

STSCHEDRINA, Z. G., 1946. New species of Foraminifera from the Arctic Ocean. *Northern Sea Route Board Drifting Expedition on the Icebreaker 'G. Sedov'.* Vol. 3, pp. 138–48. Leningrad: Arctic Institute. (Russian with English summary.)

THORSON, G., 1957. Bottom communities. In Hedgpeth, J. W. (Ed.) *Treatise on Marine Ecology and Paleoecology*, Vol. 1, *Ecology*. Geol. Soc. America, Mem. 67, pp. 461–534.

VINOGRADOV, A. P., 1953. The elementary chemical composition of marine organisms. *Mem. Sears Fdn. mar. Res.*, No. 2, pp. 1–647.