
The Non-Marine Mollusca of the Interglacial Deposits at Bobbitshole, Ipswich

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THE NON-MARINE MOLLUSCA OF THE INTERGLACIAL DEPOSITS AT BOBBITSHOLE, IPSWICH

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[Plates 3 and 4]

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The non-marine Mollusca from the Eemian (Last) Interglacial deposits at Bobbitshole, Ipswich, are analyzed. The fauna is a local one of marsh and fresh-water species and contains very few species which appear to have been washed in from other environments. The more common Mollusca are arranged into groups of climatically tolerant, less tolerant and least tolerant species, and the percentage frequency of both species and groups is analyzed through the deposit. Tolerant species dominate in the lower part of the deposit, while the less and least tolerant groups become successively important higher up. A puzzling secondary maximum of tolerant species near the top of the deposit is discussed. The conclusions about local and climatic conditions reached from the Mollusca agree closely with those derived from the plants. It is concluded that the relative abundance of the different species of Mollusca, rather than the presence or absence of isolated specimens of certain species, is important in deducing the conditions under which they lived.

1. INTRODUCTION

The outstanding success achieved by pollen and seed analyses in the interpretation of interglacial deposits has naturally led to the hope that useful results might be obtained from a numerical analysis of the second most abundant group of interglacial fossils, land and fresh-water Mollusca. These have been the subject of research for a century or more, but few attempts have been made to analyze the frequency of species at different horizons in a deposit. Although a frequency diagram of Mollusca cannot be of such value as a pollen diagram, partly because of the larger size of sample required and partly because of the fact that molluscan faunas are subject to great local variation, even relatively coarse diagrams might be useful in deposits containing no pollen. Such work must be closely connected with botanical investigations in the first place, so that the value of the evidence provided by the Mollusca may be checked. The interglacial beds at Bobbitshole, which contain an extraordinary abundance of Mollusca, over 30 000 in about 3 m of 4 in. diameter core, provided a splendid opportunity to do this. These beds, which were deposited in a lake basin in a plateau formed of Gipping boulder clay and glacial sands

and gravels, have been demonstrated by West to belong to the first half of the Eemian (Last) Interglacial (see preceding paper).

2. THE NATURE OF THE MATERIAL

To enable as close a comparison as possible to be made with the pollen analysis, Mollusca were collected from the borehole cores of West's site no. 4 and from known horizons in open sections. The latter were fitted into the core succession, which forms the main part of the following analysis, on the basis of their pollen content. The divisions used

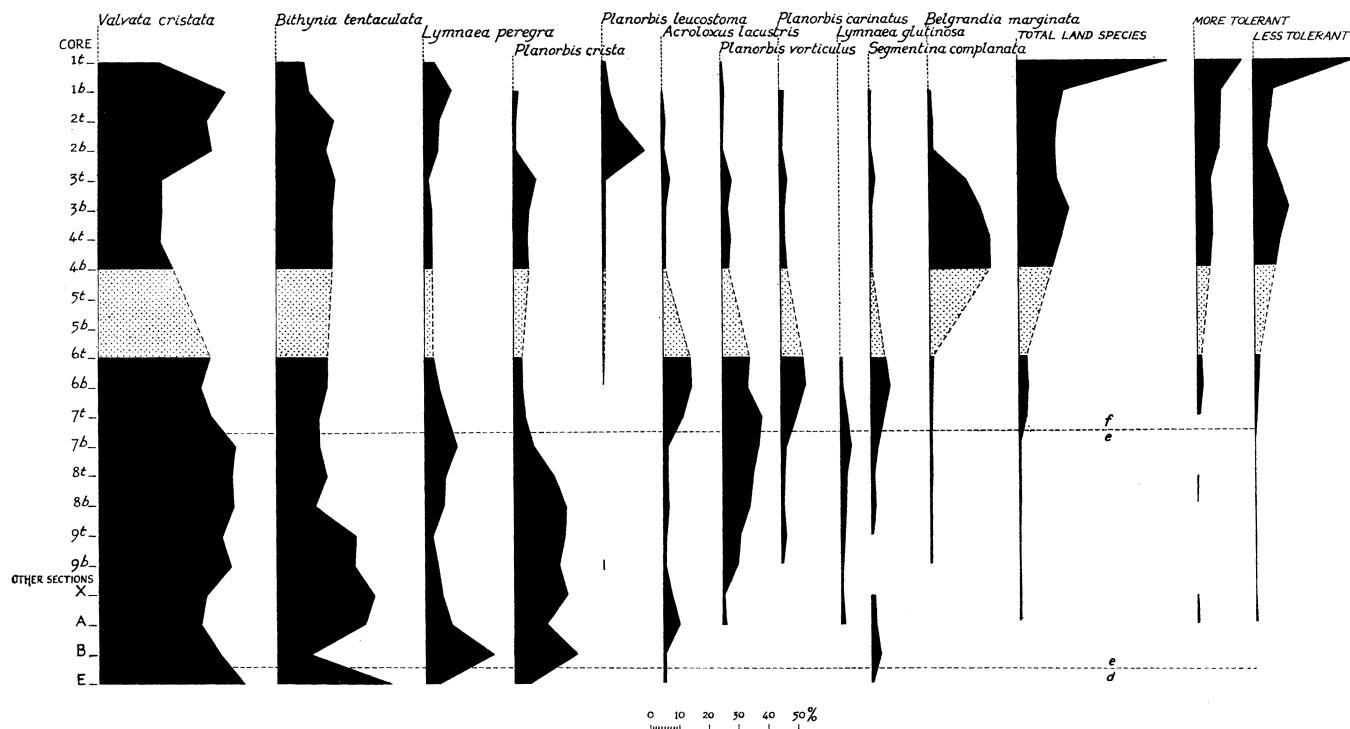


FIGURE 1. Percentage frequency diagram of selected species of Mollusca at Bobbitshole; the horizontal divisions are pollen zones.

were necessarily coarse compared with those used for the pollen analysis; intervals of about 20 to 30 cm were used for the open sections, while the core itself provided two samples from each of its nine divisions with the exception of core 5, which was not available owing to a mishap during its extraction. The notation of the samples used in table 1 and figures 1 and 2 is the same as that used in the preceding paper by West, except for sample X, which is not included in his account.

The material was washed down through a $\frac{1}{2}$ mm sieve to retain broken pieces of the smallest Mollusca and then sorted under a low-power binocular microscope in order that all recognizable fragments should be recovered. Normally only apical fragments were counted so that the same shell should not be included twice, but fragments containing the aperture of the genera *Carychium* and *Vertigo* were used, as these are necessary for their specific identification. Both the shells and the opercula of *Bithynia tentaculata* were counted separately and the highest figure, usually that for the opercula, recorded in the list (table 1). The numbers of *Pisidia* recorded in the same list refer to valves and should be halved to

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TABLE 1. DISTRIBUTION OF NON-MARINE MOLLUSCA AT BOBBITSHOLE

Land species are marked with asterisks.

| SAMPLE POLLEN ZONE | H | G | F | E | B | A | X | 9b | 9t | 8b | 8t | 7b | 7t | 6b | 6t | 5b | 5t | 4b | 4t | 3b | 3t | 2b | 2t | 1b | 1t | TOTAL | |
|---|-----------|------------|-----------|------------|------------|------------|-------------|------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|----|----|-------------|-------------|-------------|-------------|------------|-------------|------------|------------|---------------|----|
| | b | c | d | d | e | e | e | e | e | e | e | e | f | f | f | f | f | f | f | f | f | f | f | f | f | | |
| <i>Valvata cristata</i> Müller | | 4 | 18 | 119 | 161 | 241 | 1019 | 179 | 484 | 1028 | 884 | 935 | 2004 | 1170 | 1258 | | | 721 | 720 | 702 | 288 | 253 | 160 | 182 | 47 | 12577 | |
| <i>Valvata macrostoma</i> Mörch | | | | | | | | | | | | | | | | | | 8 | 6 | 2 | 4 | | | | | 20 | |
| <i>Valvata piscinalis</i> (Müller) | | | 1 | | | | | 3 | 2 | 2 | 2 | | | | | 1 | | 29 | 37 | 33 | 21 | 3 | 5 | 9 | | 148 | |
| <i>Belgrandia marginata</i> (Michaud) | | | | | | | | 1 | 5 | 5 | 9 | 2 | 17 | 15 | 33 | | | 575 | 706 | 565 | 164 | 10 | 6 | 3 | | 2116 | |
| <i>Bithynia tentaculata</i> (Linné) | 9 | 35 | 10 | 94 | 45 | 207 | 937 | 105 | 308 | 297 | 332 | 292 | 741 | 587 | 572 | | | 526 | 660 | 605 | 271 | 113 | 86 | 4.7 | 22 | 6901 | |
| * <i>Carychium minimum</i> Müller | 1 | 1 | | | | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 11 | 12 | 26 | | | 102 | 189 | 218 | 72 | 14 | 9 | 18 | 38 | 719 | |
| * <i>Carychium tridentatum</i> (Risso) | | | | | | | | | | | | | | | | | | 2 | 1 | 1 | | | | | | 4 | |
| <i>Lymnaea truncatula</i> (Müller) | | | | | | | | 3 | 1 | | | | 15 | 14 | 14 | | | 4.6 | 63 | 91 | 50 | 16 | 14 | 13 | 13 | 353 | |
| <i>Lymnaea palustris</i> (Müller) | | | | | | | | | 5 | | | 2 | 24 | 21 | 23 | | | 22 | 16 | 15 | 5 | 20 | 10 | 6 | 3 | 172 | |
| <i>Lymnaea stagnalis</i> (Linné) | | | | | | | | | | | | | 1 | | | | | | | | | | | | | 1 | |
| <i>Lymnaea auricularia</i> (Linné) | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | |
| <i>Lymnaea peregra</i> (Müller) | | | 11 | 88 | 64 | 161 | 17 | 27 | 139 | 126 | 210 | 403 | 150 | 79 | | | 58 | 74 | 68 | 18 | 29 | 22 | 37 | 8 | 1789 | | |
| <i>Lymnaea glutinosa</i> (Müller) | | | | | | 8 | 11 | 3 | 14 | 42 | 39 | 71 | 110 | 21 | 14 | | | | | | | | | | | 333 | |
| <i>Aplexa hypnorum</i> (Linné) | | | | | | | | | | | | | | 1 | | | | | 3 | | | | | | | 4 | |
| <i>Physa fontinalis</i> (Linné) | | | | | | | | | | | | | | 1 | | | | | | | | 1 | 1 | | | 3 | |
| <i>Planorbis carinatus</i> Müller | | | | | | | | 2 | 18 | 19 | 22 | 32 | 280 | 273 | 259 | | | 55 | 54 | 50 | 28 | 3 | 4 | 5 | | 1104 | |
| <i>Planorbis vorticulus</i> Tröschel | | 1 | | | | 9 | 6 | 20 | 70 | 212 | 199 | 245 | 701 | 287 | 313 | | | 67 | 114 | 64 | 50 | 1 | 3 | 5 | 1 | 2368 | |
| <i>Planorbis vortex</i> (Linné) | | | | | | | | | | | | | | | | | | | | | | 3 | 2 | | | 5 | |
| <i>Planorbis leucostoma</i> Millef | | | | | | | | | 1 | | | | | 1 | 1 | | | 13 | 21 | 17 | 9 | 94 | 25 | 9 | 3 | 194 | |
| <i>Planorbis laevis</i> Alder | | | | | 1 | | 3 | | | | | | | 2 | 1 | | | 7 | 34 | 24 | 6 | | 1 | | | 79 | |
| <i>Planorbis albus</i> Müller | | | | | | | | | | | | | | | | | | 4 | | | | | | | | 4 | |
| <i>Planorbis crista</i> (Linné) | | 1 | 2 | 14 | 80 | 73 | 509 | 61 | 199 | 393 | 263 | 132 | 189 | 78 | 77 | | | 137 | 151 | 165 | 102 | 3 | 2 | 7 | | 2638 | |
| <i>Segmentina complanata</i> (Linné) | | | | 2 | 12 | 13 | 41 | | 7 | 41 | 27 | 47 | 225 | 218 | 165 | | | 22 | 29 | 25 | 26 | 2 | 1 | 1 | | 904 | |
| <i>Segmentina nitida</i> (Müller) | | | | | | | | | | | | | | 3 | 10 | 7 | | | | | | | | | | 20 | |
| <i>Acroloxus lacustris</i> (Linné) | | | 1 | 2 | 3 | 40 | 81 | 4 | 10 | 46 | 34 | 33 | 337 | 323 | 305 | | | 40 | 45 | 45 | 32 | 5 | 6 | 1 | | 1393 | |
| * <i>Succinea oblonga</i> Draparnaud | | | | | | | | | | | | | | | | | | 4 | 3 | 6 | 1 | 3 | 1 | | 5 | 23 | |
| * <i>Succinea putris</i> (Linné) | | | | | | 1 | 1 | | 2 | 1 | | 17 | 25 | 17 | | | 10 | 34 | 10 | 5 | 8 | 8 | 5 | 1 | | 145 | |
| * <i>Succinea pfeifferi</i> Rossmässler | | | | | | | | | | 1 | | | | | | | | 3 | 3 | 2 | | | | | 1 | 10 | |
| * <i>Cochlicopa lubrica</i> (Müller) | | 1 | | | | | | | | | | | 2 | 2 | | | | 16 | 13 | 16 | 6 | 1 | 2 | 1 | 1 | 61 | |
| * <i>Vertigo antivertigo</i> (Draparnaud) | | | | | | 2 | 1 | | 1 | 2 | | 18 | 28 | 22 | | | | 33 | 52 | 63 | 24 | 18 | 7 | 12 | 16 | 299 | |
| * <i>Vertigo mouliinsiana</i> (Dupuy) | | | | | | | | | | | | 15 | 12 | 5 | | | | 17 | 15 | 28 | 8 | 3 | 2 | 2 | 5 | 112 | |
| * <i>Vertigo angustior</i> Jeffreys | | | | | | | | | | | | | 2 | 1 | | | | 12 | 10 | 10 | 2 | 1 | 2 | 2 | 2 | 42 | |
| * <i>Pupilla muscorum</i> (Linné) | | | | | | | | | | | | | | | | | | | | 1 | | | 1 | 1 | | 3 | |
| * <i>Acanthinula aculeata</i> (Müller) | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | |
| * <i>Acanthinula lamellata</i> (Jeffreys) | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | | | 2 | |
| * <i>Vallonia costata</i> (Müller) | | | | | | 1 | | | | | | | | | 3 | | | | 1 | 2 | | | 1 | 1 | | 9 | |
| * <i>Vallonia pulchella</i> (Müller) | | | 1 | | | | | 1 | | | | | | | | | | | 5 | 2 | 1 | | 2 | 5 | | 17 | |
| * <i>V. pulchella</i> var. <i>enniensis</i> (Gredler) | | | | | | 1 | | | | | | 9 | 17 | 13 | | | | 54 | 78 | 105 | 27 | 10 | 12 | 7 | 33 | 366 | |
| * <i>Helix p. nemoralis</i> Linné | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | |
| * <i>Hygromia hispida</i> (Linné) | | | | | | | | | | | | | | | | | | | 2 | 3 | 4 | 1 | 2 | 2 | 4 | 1 | 19 |
| * <i>Punctum pygmaeum</i> (Draparnaud) | | 1 | | | | | | | | | | | | | 1 | | | | | 2 | | | | | | 4 | |
| * <i>Euconulus fulvus</i> (Müller) | | | | | | | | | | | | | | 1 | 1 | | | | 7 | 5 | 8 | 4 | | | 3 | 29 | |
| * <i>Vitrea contracta</i> (Westerlund) | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | |
| * <i>Retinella radiatula</i> (Alder) | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | |
| * <i>Retinella pura</i> (Alder) | | | | | | | | | | | | | | | | | | | | | 1 | | | | | 1 | |
| * <i>Zonitoides nitidus</i> (Müller) | | 1 | | | | | | | 1 | | | | 5 | 5 | 8 | | | 13 | 29 | 38 | 15 | 7 | 8 | 4 | 5 | 139 | |
| * <i>Agriolimax p. agrestis</i> (Linné) | | | | | | | | | | 2 | 1 | | 5 | 6 | 6 | | | 32 | 28 | 22 | 7 | 11 | 2 | 4 | 3 | 129 | |
| * <i>Agriolimax p. reticulatus</i> (Müller) | | | | | | | 1 | | | 3 | | | | 1 | | | | 10 | 17 | 2 | 3 | 3 | 2 | | | 42 | |
| * <i>Agriolimax p. caruanae</i> Pollonera | | | | | | | | | | | | | | 2 | | | | | 2 | 4 | 5 | | 1 | 1 | 1 | 16 | |
| * <i>Agriolimax p. laevis</i> (Müller) | | | | | | | | | | | | | | | | | | | 4 | 1 | 1 | | | | | 6 | |
| <i>Sphaerium corneum</i> (Linné) | | | 1 | | 1 | 5 | 4 | 1 | 8 | 6 | 15 | 10 | 29 | 28 | 27 | | | 6 | 6 | 9 | 3 | 2 | | 1 | 1 | 163 | |
| <i>Pisidium amnicum</i> (Müller) | | | | | | | | | | | | | | 2 | | | | 10 | 15 | 9 | 2 | | | | | 38 | |
| <i>Pisidium casertanum</i> (Poli) | | | | | | | 2 | | | | | | | | 1 | | | 12 | 18 | 23 | 7 | 4 | | 3 | | 70 | |
| <i>Pisidium personatum</i> Malm | | | | | | | | | | | | | 1 | | | | | 5 | 14 | 16 | 4 | 1 | | | 5 | 46 | |
| <i>Pisidium obtusale</i> (Lamarck) | | | | | 2 | 1 | | | | | | | 16 | 24 | 17 | | | 54 | 68 | 52 | 14 | 11 | 16 | 18 | 7 | 300 | |
| <i>Pisidium milium</i> Held | | | | 1 | 2 | 8 | 5 | | | 3 | 3 | 1 | 25 | 54 | 37 | | | 12 | 17 | 21 | 18 | 2 | 1 | | | 210 | |
| <i>Pisidium subtruncatum</i> Malm | | | | | | 7 | 11 | | | 1 | 1 | 2 | 2 | 8 | 4 | 6 | | 14 | 45 | 19 | 13 | | | | | 137 | |
| <i>Pisidium henslowianum</i> (Sheppard) | | | | | | | 3 | | | | | | | | | | | | | 3 | | | | | | 6 | |
| <i>Pisidium nitidum</i> Jenyns | | | | 1 | | 16 | 19 | 6 | 2 | 11 | | | 12 | 41 | 17 | 16 | | 27 | 58 | 52 | 39 | 4 | 11 | 7 | 2 | 341 | |
| <i>Pisidium pulchellum</i> Jenyns | | | | | | | 2 | | | | | | | | | | | 1 | 3 | | | | | | | 6 | |
| TOTAL | 10 | 4.4 | 34 | 245 | 393 | 699 | 2821 | 403 | 1167 | 2257 | 1961 | 2027 | 5254 | 3413 | 3328 | | | 2790 | 3480 | 3218 | 1353 | 661 | 4.37 | 423 | 227 | 3664.5 | |

obtain the frequency of individuals. *Pisidia* are, however, so fragile and juveniles so difficult to identify that the number of valves is probably a fair measure of the frequency of the species. In spite of these precautions there may still be some misrepresentation of the frequency of the various species due to two causes: some species are more readily crushed and destroyed than others, while some are much more readily recognizable from fragments than others. Although this may lead to the recording of wrong frequencies, the relative frequency at different horizons should still be representative of actual conditions.

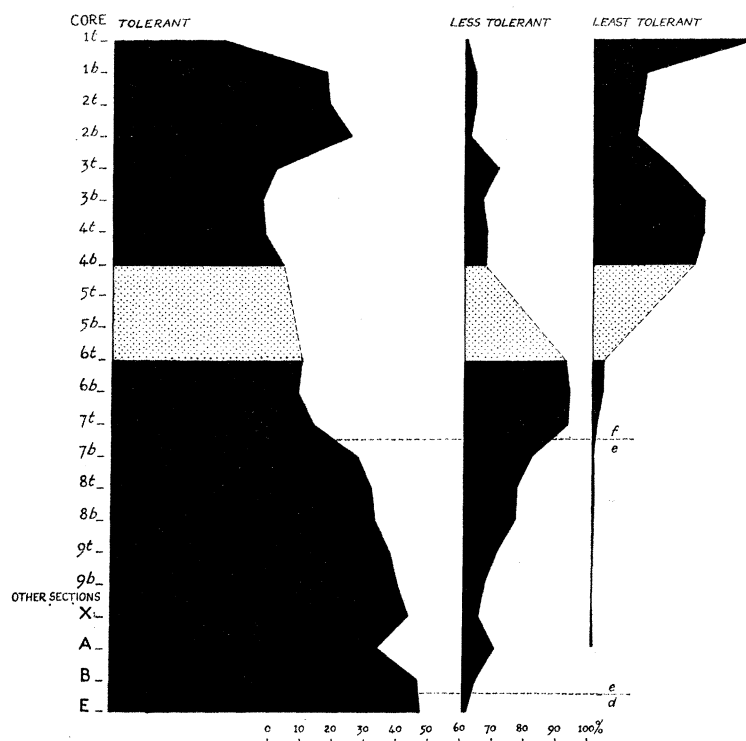
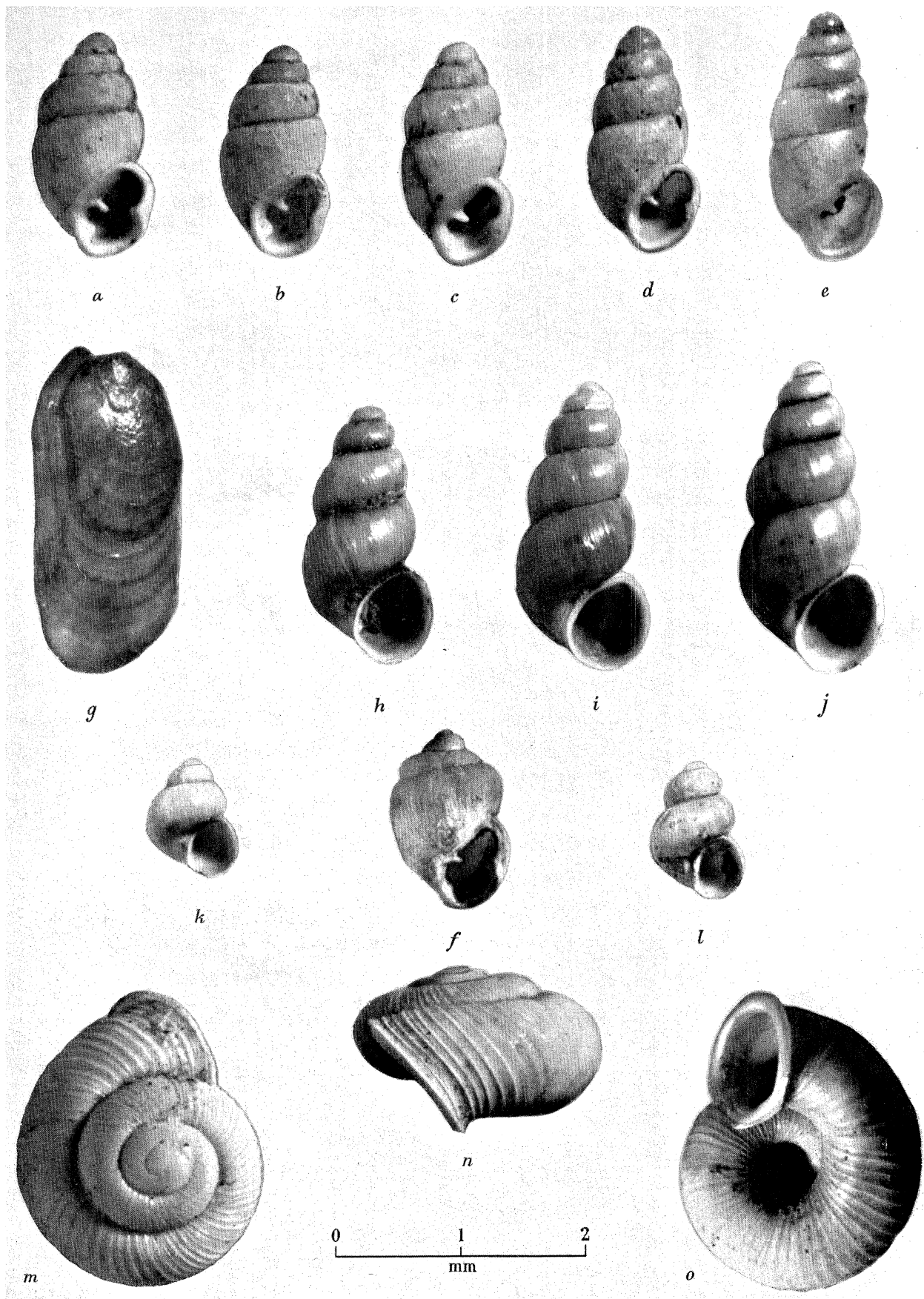


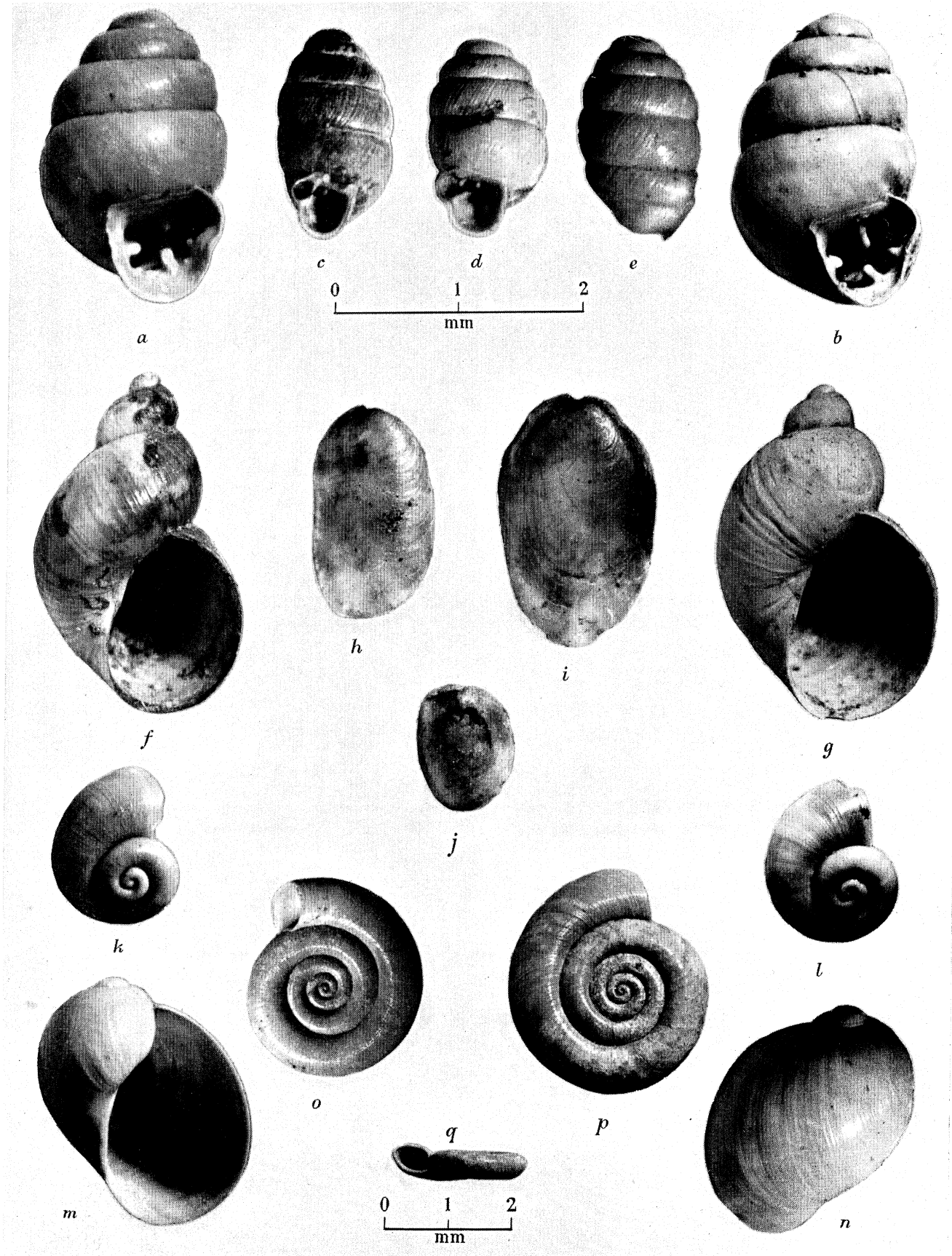
FIGURE 2. Percentage frequency diagram of three main groups of Mollusca at Bobbitshole; the horizontal divisions are pollen zones.

An analysis of a core, involving the determination of many broken and juvenile forms, is of necessity attended by doubts concerning the correct identification of some species. Some genera, such as *Valvata*, *Lymnaea* and *Succinea*, are subject to considerable variation, and some of the species resemble each other so closely that apical fragments cannot be separated with certainty. This difficulty applies to the two *Valvata* species, *piscinalis* and *macrostoma*, the latter being recorded with some doubt. There does, however, appear to be

DESCRIPTION OF PLATE 3

- | | |
|--|---|
| a. <i>Carychium minimum</i> Müller. | h. <i>Belgrandia marginata</i> (Michaud). |
| b. <i>Carychium minimum</i> Müller. | i. <i>Belgrandia marginata</i> (Michaud). |
| c. <i>Carychium minimum</i> Müller. | j. <i>Belgrandia marginata</i> (Michaud). |
| d. <i>Carychium minimum</i> Müller. | k. <i>Belgrandia marginata</i> (Michaud). Juvenile. |
| e. <i>Carychium tridentatum</i> (Risso). | l. <i>Belgrandia marginata</i> (Michaud). Juvenile. |
| f. <i>Carychium minimum</i> Müller. Deformed specimen. | m. <i>Vallonia pulchella</i> var. <i>enniensis</i> (Gredler). |
| g. <i>Agriolimax</i> cf. <i>caruanae</i> Pollonera. | n. <i>Vallonia pulchella</i> var. <i>enniensis</i> (Gredler). |
| | o. <i>Vallonia pulchella</i> var. <i>enniensis</i> (Gredler). |





a division in the broken and juvenile material, some of which is probably referable to *macrostoma* (plate 4, figures *k* and *l*), which has been recorded in an earlier list (Davis 1955). A similar difficulty attends the separation of *Planorbis planorbis* and *P. carinatus*, only the latter being recorded, as all half-grown or fully grown specimens were of that species. Similarly, all the fully grown *Cochlicopa* were *lubrica*, and the apical fragments seemed to be the same species and not *lubricella*. The single specimen of *Helix* is again an apical fragment and could be either *nemoralis* or *hortensis*, but only the former has been recorded by Davis.

For the slug genus, *Agriolimax*, the difficulty lies not in the broken nature of the material, but in the variability of these degenerate shells and in our limited knowledge of this variability. The shells have been examined by Mr Hugh Watson, and it is agreed that they are all *Agriolimax* and that all British species are represented, although there must be some doubt about the exact numbers assigned to each. Typical forms of the species found at Bobbitshole are illustrated in plate 3, figure *g*, and in plate 4, figures *h*, *i* and *j*.

3. THE FAUNA

A comprehensive list of species from this deposit has already been published (Davis 1955). The present list, although intended mainly to illustrate distribution, nevertheless contains sixty species, some of which are not included in the earlier list, while more from the latter have not been found during this investigation. Combining the two lists a total of approximately eighty species of land and fresh-water Mollusca is now known from the deposit. Only a few other Pleistocene deposits in Britain are as rich in species: they are—West Runton, Norfolk; Swanscombe; Clacton; Stutton, Suffolk; Barnwell Abbey, Cambridge; Nazeing, north London; and Broughton, Brigg, Lincolnshire.

Approximately half the recorded species are fresh-water species, but the number of specimens of these is much greater than that of the land species. Only two extinct species are listed in table 1: they are *Belgrandia marginata* (plate 3, figures *h-l*) and *Vallonia pulchella* var. *enniensis* (plate 3, figures *m-o*). To these may be added *Limax* cf. *modioliformis*, recorded by Davis. This is a low proportion, as approximately 15% of the total species recorded from British deposits assigned to the Eemian (Last) Interglacial are now extinct in Britain.

The deposit is characterized by the abundance of a number of local and rather rare species. Of these, *Belgrandia marginata* (plate 3, figures *h-l*), now extinct in Britain but found in a few localities in southern France, probably occurs in greater numbers than in any other British Pleistocene deposit. *Planorbis vorticulus* (plate 4, figures *o-q*) and

DESCRIPTION OF PLATE 4

- | | |
|---|--|
| a. <i>Vertigo moulinsiana</i> (Dupuy). | j. <i>Agriolimax</i> cf. <i>laevis</i> (Müller). |
| b. <i>Vertigo moulinsiana</i> (Dupuy). | k. <i>Valvata</i> cf. <i>macrostoma</i> Mörch. Juvenile. |
| c. <i>Vertigo angustior</i> Jeffreys. | l. <i>Valvata</i> cf. <i>macrostoma</i> Mörch. Juvenile. |
| d. <i>Vertigo angustior</i> Jeffreys. | m. <i>Lymnaea glutinosa</i> (Müller). Juvenile. |
| e. <i>Vertigo angustior</i> Jeffreys. | n. <i>Lymnaea glutinosa</i> (Müller). Juvenile. |
| f. <i>Succinea oblonga</i> Draparnaud. | o. <i>Planorbis vorticulus</i> Troschel. |
| g. <i>Succinea oblonga</i> Draparnaud. | p. <i>Planorbis vorticulus</i> Troschel. |
| h. <i>Agriolimax</i> cf. <i>agrestis</i> (Linné). | q. <i>Planorbis vorticulus</i> Troschel. |
| i. <i>Agriolimax</i> cf. <i>reticulatus</i> (Müller). | |

Valvata macrostoma (plate 4, figures *k* and *l*) are rare and local in their present distribution in the British Isles (Ellis 1951), although the former is very abundant at Bobbitshole and both appear to have been more widespread in the Pleistocene than at present. *Lymnaea glutinosa* (plate 4, figures *m* and *n*) is another species of the same type, although its Pleistocene records may not be all correct due to confusion with inflated and short-spined forms of *L. peregra*, as appears to have occurred at Hoxne, Suffolk (Sparks in West 1956). Both *Vertigo moulinsiana* (plate 4, figures *a* and *b*) and *V. angustior* (plate 4, figures *c–e*) are fairly rare species both fossil and living. The most interesting record is that of the slug species, *Agriolimax caruanae*, which was originally described from Malta and later found in a few localities in Britain. There is some doubt whether it was introduced into Britain from Malta or into Malta from Britain or some other locality (Quick 1949). Recently, however, shells greatly resembling those of *A. caruanae* have been found in two Post-Glacial deposits (Hayward 1954). The figures given by Hayward and Quick show shells very similar to the Bobbitshole specimens (plate 3, figure *g*), and Mr Watson agrees with this determination. It seems likely, therefore, that *A. caruanae* may well be native in Britain, for shells indistinguishable from it have now been found in both Post-Glacial and Eemian (Last) Interglacial deposits. It cannot be recorded with absolute certainty, because *A. agrestis* has a similar but less elongated shell with a concave right border (plate 4, figure *h*) and the degree of variability of this species is not sufficiently well known.

4. LOCAL CONDITIONS INDICATED BY THE MOLLUSCA

The majority of the fresh-water species indicate quiet but not stagnant water, although there is some slight variation in the actual conditions preferred (Boycott 1936). Some species, such as *Planorbis carinatus* and *Bithynia tentaculata*, either prefer quietly moving water or are often found in such conditions. Others, such as *Valvata cristata* and *Lymnaea stagnalis*, like a combination of mud and moving water, while *Acroloxus lacustris* is a typical inhabitant of quiet water with a muddy bottom and plenty of water plants on which it lives. With these are allied some catholic species, such as *Lymnaea peregra* and *Planorbis crista*, and a few which are definitely tolerant of poor conditions, e.g. *Aplexa hypnorum*, *Planorbis leucostoma*, *Pisidium personatum* and *P. obtusale*. The apparent exception is *Belgrandia marginata*, which in the few localities where it is known prefers springs (Germain 1930). But, if the general picture of quietly moving water, comparable with parts of the Fens and Norfolk Broads to-day, is correct, the water may well have been clear enough for *B. marginata* in places, especially if there were local springs, and muddy enough for the species tolerant of poor conditions in others.

The majority of the land species are undoubtedly local, because all those occurring in great numbers are marsh dwellers. The three species of *Succinea* and the three species of *Vertigo* found in the deposit, together with *Agriolimax laevis* and *Zonitoides nitidus*, are all listed by Boycott (1934) as obligatory hygrophiles. A second group, including *Agriolimax agrestis*, *Retinella radiatula*, *Euconulus fulvus*, *Punctum pygmaeum*, *Hygromia hispida*, *Cochlicopa lubrica* and *Carychium minimum*, are stated by Boycott to be common in the same type of marshy situation. To these may be added *Vallonia pulchella*—Boycott lists *excentrica*, but this is surely a misprint for it is well known that *excentrica* prefers drier localities than *pulchella*—and its variety, *enniensis*. The latter, which may be a distinct species (Sparks

1953), is said to occupy very marshy places (Plate 1950) and was first described from saturated mossy areas in the Tyrol (Gredler 1856). Its distribution in the Pleistocene deposits of Britain largely confirms this. *Vitrea contracta* is often found in marshy places, while *Agriolimax reticulatus* and *Helix nemoralis*, although ubiquitous species, are also often found in marshes.

Some of the species are either included by Boycott (1934) as 'woodland' species or are often found in the leaf litter of woods or beneath the bark of decaying logs. In this group are *Carychium tridentatum* (Morton 1954), *Acanthinula lamellata*, *A. aculeata*, *Retinella pura* and four species from Davis's list, *Clausilia bidentata*, *Cochlodina laminata*, *Discus rotundatus* and *Helicodonta obvoluta*. It is noteworthy that all these species occur in small numbers and only in the upper part of the section, where the litter from a mixed oak forest would be more to their liking than that from the birch and pine forests below.

A third miscellaneous group, represented by very few specimens, includes two xerophiles, *Pupilla muscorum* and *Truncatellina cylindrica*, the latter recorded by Davis (1955); *Pomatias elegans*, also recorded by Davis, which prefers friable calcareous soil; *Vallonia costata*, which prefers drier places than *V. pulchella* and its variety *enniensis*; and *Agriolimax caruanae*, which has been found living in Britain mainly in gardens, parks and cultivated land (Quick 1949).

Nevertheless, the number of land snails not characteristic of marshes is very small indeed, and it may be concluded that the fauna is almost entirely a local one such as might be found in a marshy locality with quiet but not completely stagnant water. The number of species from different habitats is far smaller than it usually is in Pleistocene deposits, many of which have been laid down by rivers of some size. This is probably due to the smallness of the area draining into Bobbitshole.

5. VARIATIONS IN MOLLUSCA THROUGH THE DEPOSIT

With the large numbers of shells available from most horizons it was found possible to express various species as percentages of the total fauna at the various levels and to plot a diagram comparable with a pollen diagram (figure 1). As far as is known this has not been possible for any previously described deposits, although the list for Nazeing (Allison, Godwin & Warren 1952) does give percentage frequencies of the species at different levels.

Most Mollusca will tolerate a wide range of climatic conditions, so that it is not usually possible to state that any particular species must represent a certain type of climate. It is far safer to consider the total composition of the fauna, especially the relative abundance of the more and less tolerant species. Accordingly, three groups of species have been formed, based upon the present known ranges of the species and on their Pleistocene distribution. The latter must be considered, for, with some snails, it conflicts with their present distribution, the best example being *Discus ruderratus*, usually considered as an Arctic-Alpine species to-day but characteristic of interglacial and warm Post-Glacial deposits as a fossil. The ranges quoted below are based principally on Ellis (1926, 1951), Geyer (1927), Ehrmann (1933) and Hubendick (1947).

The first group includes five species, *Valvata cristata*, *Bithynia tentaculata*, *Lymnaea peregra*, *Planorbis crista* and *P. leucostoma*, which are all very tolerant. All have wide ranges, usually being found up to and even beyond the Arctic Circle in Scandinavia and some in Iceland and Greenland. *Planorbis crista* and *Valvata cristata* do not seem to extend as far north as the

others in Sweden and Finland, but are found in latitude 65°N, while the latter is found near Archangel (Ložek 1955). All have wide distributions in Pleistocene deposits.

The second group also includes five species: *Acroloxus lacustris*, *Planorbis vorticulus*, *P. carinatus*, *Segmentina complanata* and *Lymnaea glutinosa*. These do not extend quite as far north as those in the first group, the first two reaching Denmark and south Scandinavia, the third and fourth 63°N in Finland, while the last is mainly a lowland species but is said to be found well to the north in Finland. Its inclusion in this group is, therefore, somewhat doubtful, although the curve of its distribution corresponds fairly closely with those of the other members of the group (figure 1).

The final group includes less tolerant species. *Belgrandia marginata*, which is known living from a few localities in the Pyrenees and southern Alps (Germain 1930) but occurs in the Pleistocene in northern France (Breuil 1952), Germany (Geyer 1927) and Britain, is definitely a southern species. The total percentage of land species is plotted, because land snails are probably more sensitive indicators of climate than fresh-water Mollusca, as the range of temperature on land is much greater than in water. The land snails are also split into more and less tolerant groups. In the latter are included both species of *Carychium*, *Vertigo moulinsiana*, *V. angustior*, *Vallonia pulchella* var. *enniensis*, *Retinella pura*, *Agriolimax caruanae*, both species of *Acanthinula*, *Helix nemoralis* and *Vitrea contracta*. The first five are the only species present in sufficient numbers to affect the distribution to any extent. Their northern limits are as follows: *Carychium* reaches 63°N in Sweden and 65°N in Finland, but is only common in Pleistocene deposits indicating mild conditions; *Vertigo moulinsiana* reaches Denmark and Lithuania but not Scandinavia proper; *Vallonia pulchella* var. *enniensis* is mainly south European and Balkan in its distribution; *Vertigo angustior* reaches Jämtland (about 63°N) in Sweden. Jämtland, however, is an area where Silurian limestone and calcareous drift are important and is, furthermore, more oceanic in its climate than much of Sweden, due to the presence of low passes at little above 2000 ft. to the west (Zimmermann 1933). For both reasons one would expect more southern species of Mollusca to extend well north here, especially as limestones lead to favourable micro-climates. The remaining species included in the less tolerant group of land snails all appear to reach their northern limits in southern Sweden and southern Finland, although *Helix nemoralis* also extends to Jämtland.

The remaining species of land snails range much farther north, usually beyond 65°, with the possible exception of *Succinea oblonga*, concerning the distribution of which there appears to be some doubt (Geyer 1927).

Certain of the Bobbitshole species are not included in any of these groups, some because they are so rare there and others, mainly the *Pisidia*, because their identification is so difficult that their ranges are not accurately known.

The individual species and groups of land species discussed above are plotted separately in figure 1 and as the three main groups of tolerant, less tolerant and least tolerant species in figure 2.

It is clear from the diagrams that there are systematic variations through the Bobbitshole deposit. Species included in the tolerant group dominate at the bottom, but decrease upwards except for a secondary maximum in core 2 (figure 2), which will be discussed below. Those in the less tolerant group increase upwards to a maximum in cores 7 and 6,

while the least tolerant group achieves its maximum in the upper part of the deposit, with the exception of a regression in core 2 corresponding with the secondary maximum of the tolerant group. The question to be decided is whether these variations are due to the slowly changing climatic conditions of the interglacial or to changes in the local environment. Difficulties arise because those Mollusca which are least exacting in their choice of environment often show the greatest capacity for rapid distribution (Hubendick 1947).

From the lowest level at which Mollusca are recorded up to core 4 the changes appear to be too regular to be attributed to environmental changes, with the possible exception of the increase in land species from core 7 top. The increasing importance of the less tolerant fresh-water species and later of the southern fresh-water species, *Belgrandia marginata*, points probably to a steady improvement in the climate. But even at the bottom there are species which one would not expect under really cold conditions. In samples H and G *Carychium minimum* occurs; these samples are from the junction of pollen zones *b* and *c* and from zone *c*, which are zones of park-tundra with birch and birch forest respectively. The presence of *C. minimum* at these levels is comparable with West's records of thermophilous plants from the same zones and supports his conclusion that the climate was probably not really cold. In the next two samples, representing pollen zone *d* and the base of zone *e*, *Planorbis vorticulus*, *Segmentina complanata* and *Acroloxus lacustris* all appear during the period when the immigration of thermophilous trees is marked, although the dominant trees are still birch and pine.

Nevertheless, the fauna below core 7 is dominated by tolerant fresh-water species of Mollusca. Less tolerant species appear in very small numbers, but do not become important until the improvement of climatic conditions higher in the section. Even some of the least tolerant species were introduced very early, but do not increase greatly until high in the section. This can be clearly seen in several examples: *Planorbis vorticulus*, introduced in zone *d* (birch-pine forest), does not become important until zone *e* (pine-oak forest); *Acroloxus lacustris*, also introduced in zone *d*, does not reach its maximum until zone *f* (mixed oak forest); *Carychium minimum*, introduced in zone *b* or *c* (park-tundra or birch forest), only becomes important in zone *f*; and *Belgrandia marginata*, introduced in the lower half of zone *e*, reaches its maximum in zone *f*.

Even at the lowest levels there are no exotic northern forms, but only a fauna dominated by the more tolerant of ordinary British species. In this respect the Bobbitshole beds are exactly comparable with the earlier Hoxne Interglacial, where at about the same level the same type of fauna was found (Sparks in West 1956).

Up to core 7 bottom, there is a regular increase in the less tolerant group and virtually no increase in the least tolerant group (figure 2), but in core 7 both groups increase more rapidly, while the tolerant group suffers a sharp fall. At the same level or immediately above, several of the least tolerant species appear for the first time, namely, *Segmentina nitida*, *Vertigo moulinsiana* and *V. angustior*, while the real introduction of *Vallonia pulchella* var. *enniensis* occurs, although a single specimen has been found lower down (table 1). These changes correspond with two vegetational changes: the first is the rapid increase of hazel marking the beginning of zone *f*, and the second is the change from open water to reed-swamp. The latter change may be partly responsible for the increase in land species, but not for the increase of *Belgrandia marginata* above this level. In fact, as far as the peak

in the *B. marginata* curve in core 4, the changes in Mollusca are likely to be related mainly to general climatic change. Core 4 represents a climate as warm, if not warmer, than that prevailing to-day, if one may judge from the abundance of *B. marginata* and *Vallonia pulchella* var. *enniensis*. This agrees with the climatic conclusions reached by West (see preceding paper) from the botanical evidence.

Above this level the regular pattern of changes is spoiled. Core 3 shows the decrease of *Belgrandia marginata* followed by a decrease in the total of land species and by a large increase in the tolerant group, especially marked in *Valvata cristata* and *Planorbis leucostoma* (figures 1 and 2).

The question naturally arises whether these changes were caused by a deterioration in the climate or by a marked change in local conditions. It can be seen from the lower parts of the diagrams that minor changes in local conditions do not appear to have affected the clarity of the general sequence, but a major and more permanent change might have an appreciable effect. Unfortunately, from about this level the pollen appears to have been subjected to weathering and little remains in the uppermost levels. The weathering, which took place along cracks in the material, does not appear to have affected the Mollusca selectively, though there is a considerable variation in the degree of corrosion of individual specimens.

In favour of the hypothesis that these changes were caused by local conditions may be cited the fact that the material contains much more clay and silt from core 3 upwards. In addition, the reed-swamp has already changed to marsh (see preceding paper). In all probability *Belgrandia marginata* cannot tolerate muddy and silty conditions, because it and other closely related species and genera live in clear spring water (Germain 1930). The two tolerant species which increase most at this same level, *Valvata cristata* and *Planorbis leucostoma*, are both tolerant of mud, especially the latter, which can stand muddy ponds subject to periodic drying (Boycott 1936).

Local change, however, cannot account for the fall in the land species, unless it is assumed that the extent of the water was increased as well. Further, when the land species are split into the more and less tolerant groups, it is seen that the tolerant species are hardly affected in their rate of increase, while the less tolerant species decrease quite strikingly (figure 1).

It is quite clear, however, from the uppermost level that the climatic optimum of the interglacial has not been passed. Between cores 2 and 1 the percentage of the tolerant group again decreases strikingly and a corresponding increase in the least tolerant group occurs. Further, it is the less tolerant of the land species which show the most marked increase (figure 1). The large increase in the number of land species must also be interpreted as indicating a marked drying up of the area. Unfortunately, the succession ends here, so that the second half of the interglacial with its deteriorating climate is not represented.

6. CONCLUSIONS

The regular changes in the molluscan diagram leads to the hope that it may prove possible to treat other deposits in a similar way. The distribution of Mollusca is controlled very much by local conditions, so that all deposits must not be expected to show exactly the same graphs. It may be necessary in other deposits to choose other species, depending

upon their frequency, although it should be possible to place these in the major groups of species used here. If this is so, one would expect to see regular changes comparable with those at Bobbitshole, provided that the succession is all obtained at one place. Composite sections, based on a number of exposures, may yield a peculiar graph due to differences in local environment, even though they may provide a perfectly satisfactory pollen diagram. If future work confirms the value of molluscan diagrams of this type, we may be provided with another method of assessing the position of deposits in an interglacial period. The method is, however, less refined than pollen technique due to the size of the samples required, and it will probably not be nearly as useful in distinguishing between deposits of different interglacials. The practicability of approximate zoning by means of the Mollusca was tested on samples from unknown levels, kindly supplied by Mr H. E. P. Spencer of the Ipswich Museum. Those which came in the range covered by the diagrams (figures 1 and 2) were zoned to within 20 cm, as checked by pollen analyses.

The changes in the Bobbitshole succession involve species which are almost all living to-day in Britain. In the lower and bleaker parts of the interglacial the species are essentially the most tolerant of our native snails and principally fresh-water forms, while less tolerant species are introduced into the succession and gradually assume a more important part in the fauna as the climate improves. The changes are secular, the faunas at different levels differing in degree rather than in type. The overall composition of the fauna is significant, isolated specimens of southern species being found quite early in the interglacial. In this connexion, it would be particularly interesting to have a molluscan diagram of a deposit containing *Corbicula fluminalis* to see more precisely what the presence of this southern species means.

My thanks are due to Mr Hugh Watson for his examination of difficult specimens and to Dr R. G. West for providing the samples for this analysis.

APPENDIX. NOTES ON CERTAIN SPECIES

Succinea oblonga. Although the proportion of the total height occupied by the aperture and the depth and obliquity of the suture are variable (plate 4, figures *f* and *g*), the shells all appear to belong to this species and not to the very similar *Catinella arenaria*, which prefers a different environment and is found in Pleistocene deposits of a different type.

Carychium minimum. The variation in form of this species at Bobbitshole (plate 3, figures *a-d*) covers almost the range illustrated by Watson & Verdcourt (1953, plate 9, figures 1-4), but even the most elongated is quite distinct from *C. tridentatum* (plate 3, figure *e*), which here appears in a form as elongated as any of those figured by the same authors (Watson & Verdcourt 1953, plate 9, figures 5-9). The identifications were confirmed by breaking the last whorl of some specimens to examine the parietal fold, which showed the distinctive characteristics stressed by these authors. A peculiar deformed specimen of *C. minimum* (plate 3, figure *f*) is of interest, because such deformities seem to be very rare in this genus.

Belgrandia marginata. Elongation is also apparent in some adult specimens of this species (plate 3, figures *h-j*). A similar tendency towards elongated and even scalariform specimens has been observed in German Pleistocene deposits (Geyer 1927).

Vertigo moulinsiana. Some variation is apparent between the size of the aperture and the whole shell (plate 4, figures *a* and *b*).

Vertigo angustior. The specimens range from a slender form with a compressed aperture (plate 4, figure *c*) to a more inflated form with a wider aperture (plate 4, figure *d*). The arrangement of denticles and strong striation serve to separate it immediately from *pusilla*, the other sinistral species of *Vertigo*. Even without cleaning the aperture, the marked external groove on the last whorl (plate 4, figure *e*), corresponding with the strong palatal denticle within, clearly distinguishes it from *pusilla*.

Hygromia hispida. Most of the specimens from the core were broken, but some seemed more like *H. liberta*, both being recorded by Davis (1955). However, as there is doubt whether *liberta* is a good species and, if it is, whether it should be called *liberta*, and as *hispida* is very variable, all the specimens are recorded as *hispida*.

Six species recorded from Bobbitshole appear to be not previously known from deposits belonging to and suspected to belong to the Eemian (Last) Interglacial in Britain. They are *Pomatias elegans*, *Cochlodina laminata* and *Limax* cf. *modioliformis*, recorded by Davis (1955) and *Vitrea contracta*, *Retinella pura* and *Agriolimax caruanae*. All but *Vitrea contracta* and *Agriolimax caruanae* appear to be known from earlier deposits.

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a



b



c



d



e



g



h



i



j



k



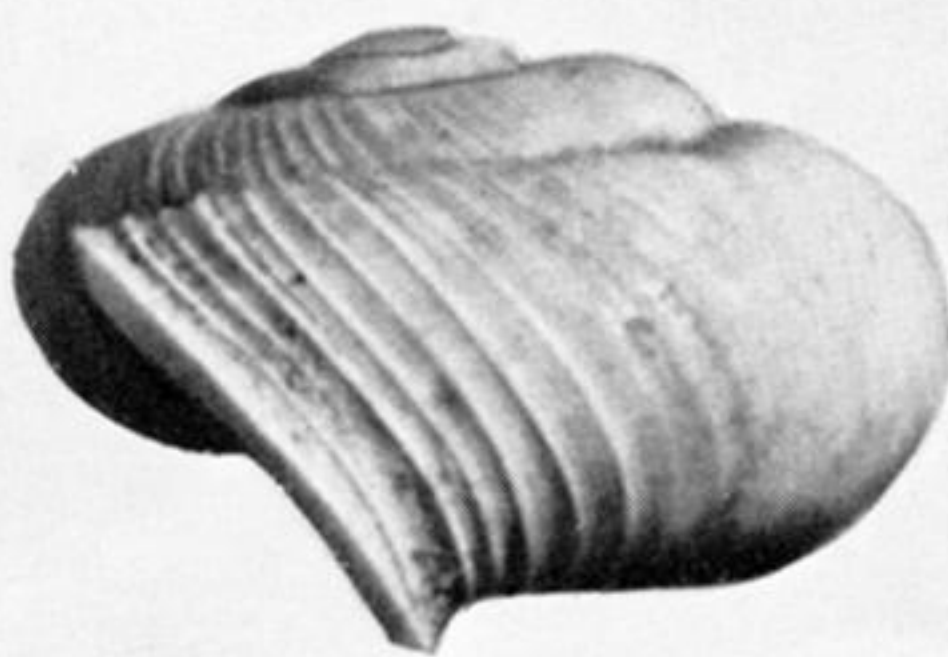
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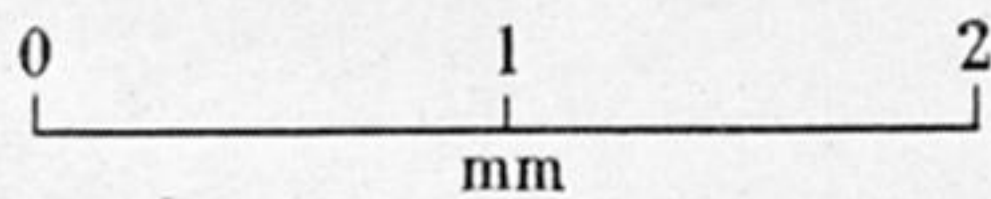
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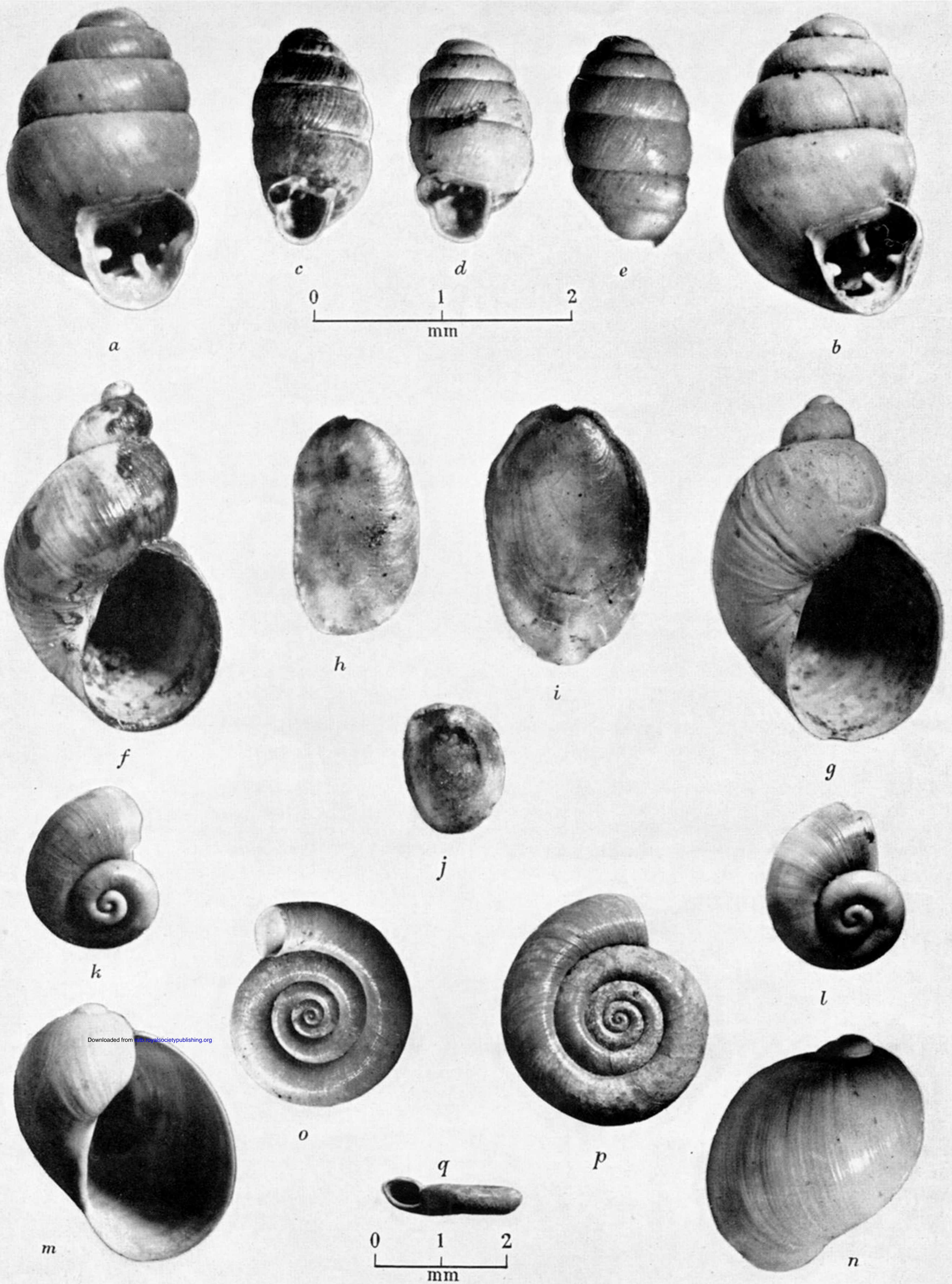
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DESCRIPTION OF PLATE 3

- a. *Carychium minimum* Müller.
- b. *Carychium minimum* Müller.
- c. *Carychium minimum* Müller.
- d. *Carychium minimum* Müller.
- e. *Carychium tridentatum* (Risso).
- f. *Carychium minimum* Müller. Deformed specimen.
- g. *Agriolimax* cf. *caruanae* Pollonera.

- h. *Belgrandia marginata* (Michaud).
- i. *Belgrandia marginata* (Michaud).
- j. *Belgrandia marginata* (Michaud).
- k. *Belgrandia marginata* (Michaud). Juvenile.
- l. *Belgrandia marginata* (Michaud). Juvenile.
- m. *Vallonia pulchella* var. *enniensis* (Gredler).
- n. *Vallonia pulchella* var. *enniensis* (Gredler).
- o. *Vallonia pulchella* var. *enniensis* (Gredler).



DESCRIPTION OF PLATE 4

- a. *Vertigo moulinsiana* (Dupuy).
 b. *Vertigo moulinsiana* (Dupuy).
 c. *Vertigo angustior* Jeffreys.
 d. *Vertigo angustior* Jeffreys.
 e. *Vertigo angustior* Jeffreys.
 f. *Succinea oblonga* Draparnaud.
 g. *Succinea oblonga* Draparnaud.
 h. *Agriolimax* cf. *agrestis* (Linné).
 i. *Agriolimax* cf. *reticulatus* (Müller).

- j. *Agriolimax* cf. *laevis* (Müller).
 k. *Valvata* cf. *macrostoma* Mörch. Juvenile.
 l. *Valvata* cf. *macrostoma* Mörch. Juvenile.
 m. *Lymnaea glutinosa* (Müller). Juvenile.
 n. *Lymnaea glutinosa* (Müller). Juvenile.
 o. *Planorbis vorticulus* Troschel.
 p. *Planorbis vorticulus* Troschel.
 q. *Planorbis vorticulus* Troschel.