

THE TERRESTRIAL MOLLUSCA OF THE MALHAM AREA

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INTRODUCTION

THE most recent account of the molluscs of the Malham area is that of the late L. W. Stratton (1956), whose own work and survey of previous publications makes the area one of the best known malacologically in Britain. Since 1956, several field courses on molluscs have been run at Malham Tarn Field Centre both by Stratton and by ourselves. These visits have resulted in the investigation of more sites, and in the discovery of species new to the district.

Further, since 1956, taxonomic revision has resulted in the splitting of erstwhile single species into two or more new ones. This paper therefore presents a new account of the terrestrial molluscs, based on our own and on Stratton's unpublished notes. A recent account of the molluscan fauna of the Tarn itself is given in Holmes (1965), and the account of other freshwater habitats in Stratton (1956) cannot yet be usefully added to.

THE AREA

The map (Fig. 1) shows the area and localities sampled. One site from elsewhere is added to the localities shown—Colt Park Wood on the lower slopes of Ingleborough (Grid Reference S.D.775775). Accounts of the geology (O'Connor, 1964), climate (Manley, 1957), and vegetation (Sinker, 1960) give details of the area relevant to this study. The area is dominated geologically by Carboniferous Limestone, and, in consequence many of the soils are extremely calcareous. There are, however, areas of acidic rocks, and areas covered with acidic drift.

Climatically, the most important features affecting the mollusca are the very damp climate (average annual rainfall 57.4 in., and all monthly averages above 3 in.), and the coolness imposed by high altitude and northerly latitude (information from Manley, 1957; figures are for Malham Tarn House at 1,300 ft.; conditions in Gordale and Malham village, below the Middle Craven Fault, may be considerably milder and drier).

THE SAMPLES

We have included in this account all samples made on our field-courses coming from apparently stable habitats where an intensive search was made. Stratton left very complete accounts of all his visits and courses at the Field Centre. It is, however, not possible to use all his samples, for there are few indications of habitat, and in some cases he states specifically that the site was not sufficiently investigated. We have used records from Stratton's notes where it appears that the sample is complete, and where the habitat can be clearly ascertained. Where the same site has been sampled by both Stratton and ourselves, the results of both samples have been combined.

Samples have been made in most of the habitats characterized by Sinker (1960) for the area around Malham Tarn, and we have followed his classification of habitats with the addition of natural or semi-natural woodland, which does not occur in the area he studied.

Table 1. *Species composition of woodland faunas. Sites 1-3 are from old woodland, 4-9 are Stratton; T = evidence of trampling. Site 15 is from Malham Tarn House*

Species							
	1	2	3	4	5	6	7
<i>Carychium tridentatum</i>	+	+	+	+	+		
<i>Lymnaea truncatula</i>							
<i>Succinea putris</i>							
<i>Azeca goodalli</i>	+	+	+				
<i>Cochlicopa lubrica</i>	+	+	+				
<i>Cochlicopa lubricella</i>	+	+	+				
<i>Pyramidula rupestris</i>	+	+	+				
<i>Columella edentula</i>		+	+				
<i>Lauria cylindracea</i>	+	+	+				
<i>Acanthinula aculeata</i>		+	+				
<i>Ena obscura</i>	+	+	+				
<i>Clausilia bidentata</i>	+	+	+				
<i>Clausilia dubia</i>	+	+	+				
<i>Balea perversa</i>	+						
<i>Arianta arbustorum</i>	+	+	+				
<i>Cepaea hortensis</i>	+	+	+				
<i>Cepaea nemoralis</i>	+	+	+				
<i>Hygromia striolata</i>	+	+	+	+	+	+	
<i>Hygromia hispida</i>	+	+	+				
<i>Monacha granulata</i>	+						
<i>Punctum pygmaeum</i>	+			+			
<i>Discus rotundatus</i>	+	+	+	+	+	+	+
<i>Arion intermedius</i>	+	+	+				
<i>Arion circumscriptus</i>	{	{		+			
<i>Arion fasciatus</i>	+	+					
<i>Arion hortensis</i>	+		+	+	+	+	+
<i>Arion subfuscus</i>	+	+	+				
<i>Arion ater</i>	+	+	+		+	+	
<i>Euconulus fulvus</i>	+	+	+	+	+	+	
<i>Vitrea crystallina</i>	+	+	+			+	+
<i>Vitrea contracta</i>	+	+	+		+	+	
<i>Vitrea diaphana</i>		+	+				
<i>Oxychilus cellarius</i>	+	+	+	+	+	+	+
<i>Oxychilus alliarius</i>	+	+	+	+	+	+	+
<i>Oxychilus helveticus</i>	+	+				+	
<i>Retinella radiatula</i>		+	+				
<i>Retinella pura</i>	+	+	+			+	
<i>Retinella nitidula</i>	+	+	+		+	+	
<i>Vitrina pellucida</i>	+	+	+		+	+	+
<i>Limax maximus</i>		+					
<i>Lehmannia marginata</i>	+		+	+			
<i>Agriolimax reticulatus</i>	+	+	+	+	+	+	+
Total	34	34	33	11	12	14	7
pH	7.5+	7.5+	7.5+	5.5	6.0	6.5	5.0
Collector	SC	SC	SC	C	C	C	C

Samples of land molluscs made to estimate densities of species are difficult to make, and take much time and effort to process. All the samples used here are qualitative only—being the results of searching by eye over the area concerned and by bringing back small quantities of soil and litter for examination in the laboratory—hand sorting with the aid of soil sieves. Consequently only presence and absence data for each species have been used for our results and discussion. Where the same sites were visited during our field courses in 1970 and 1971, very similar species-lists were obtained on each occasion, and it is clear that we are finding the great majority of species present. Measurements of pH were made colourimetrically on the top 1 cm. of soil in each woodland site.

from Tarn House Woods, 10-12 from plantations near the Tarn. A = recorded as acid by gardens and outhouses. S = Collected by Stratton. C = Collected by us

Sites							
8	9	10	11	12	13	14	15
+	+		+		+		
	+				+	+	
	+						+
		+					+
	+		+			+	+
+		+	+			+	+
+			+	+			+
{+}	{+}		+	{+}	{+}		+
+			+	+			+
+	+		+	+	{+}	{+}	+
	+		+				
+	+	+	+	+	+	+	+
+			+	+			+
			+				+
	+		+	+	+	+	+
	+	+	+				+
			+				+
			+				+
			+				+
			+				+
12	18	7	18	10	13	8	12
A	7·5+	T	6·5		A	A	—
S	S	S	SC	S	S	S	C

RESULTS

(1) General

The appendix lists the species of land mollusc found in the Malham area, with the last date on which each has been found. Since the publication of Stratton's (1956) list, the following additions have been made: *Vallonia costata* and *V. excentrica*, both from site 39, and *Agriolimax agrestis*. This last is the second record of the species in England, the other find being in Norfolk, but it has been found several times in Scotland (Ellis, 1967).

Since 1956, a revision of slug species in the genus *Arion* (Ellis, 1969) has led to the splitting of *Arion circumscriptus* into three species, of which two, *A. circumscriptus*

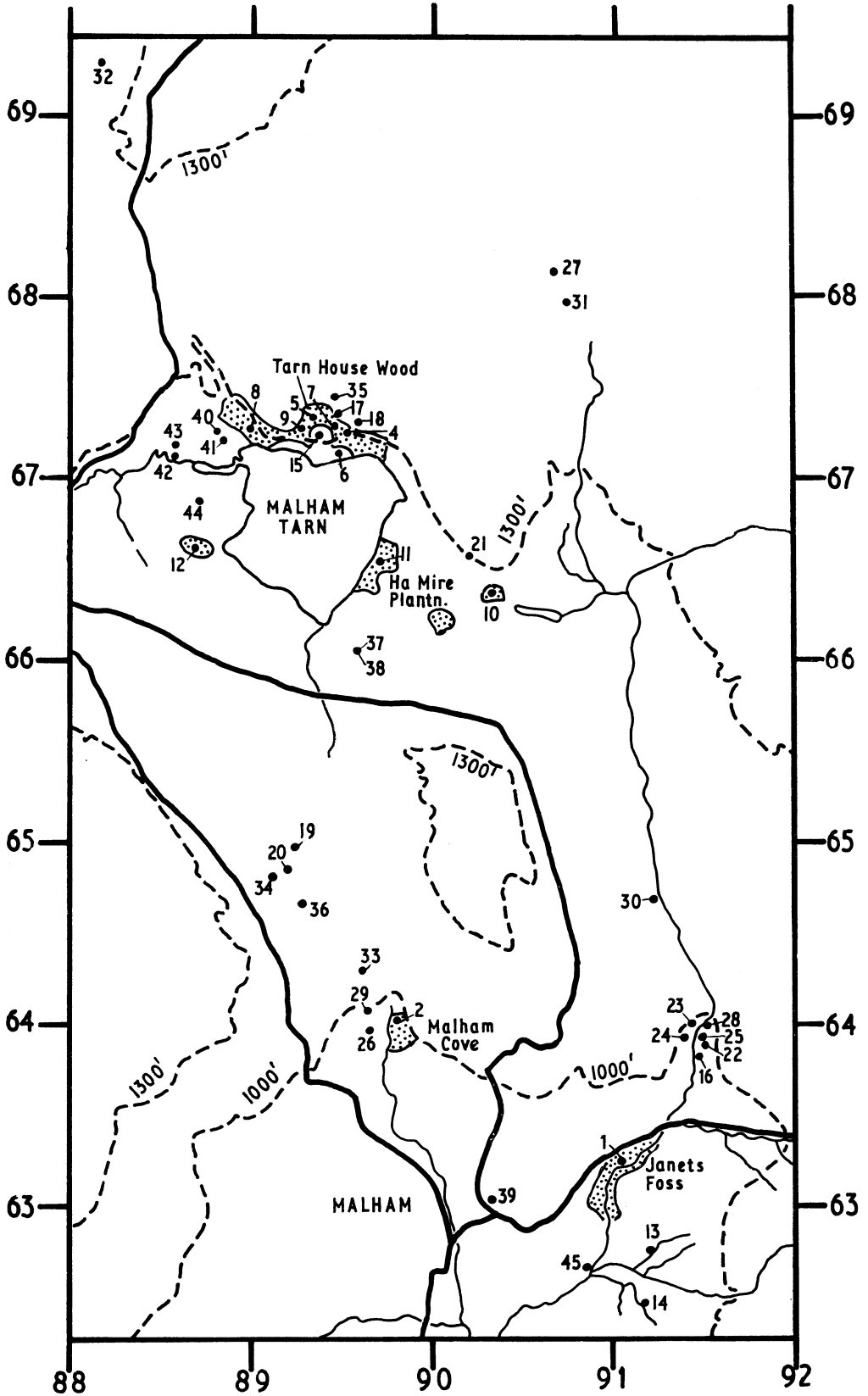


FIG. 1.

A map of the Malham area, with the sample sites marked. Roads, rivers and the 1000 ft. and 1300 ft. contours are shown. The Ordnance Survey 1 km. grid is shown in the margins.

s.s., and *A. fasciatus* have been confirmed for the area. Similarly, the species *Vitrea crystallina*, as recognized by Stratton, in fact comprises two species, *V. crystallina* s.s. and *Vitrea contracta* (Kuiper, 1964), and both occur at Malham. A further species, *V. diaphana*, has recently been discovered, for the first time in Britain, at sites close to Malham (Kerney and Fogan, 1969), and inspection of Stratton's samples revealed its occurrence in Tarn House Wood. It has since been found in other sites in the Malham area.

2. Distribution of species by habitat

(a) Woodlands.

Table 1 shows the species composition of 14 woodland samples, all but one of which lie within the area of Fig. 1. There is considerable variation in species composition between sites, with the richest having nearly five times as many species as the poorest.

Sites 1, 2, and 3, conspicuously the richest, are all in natural or semi-natural woodland. Colt Park Wood (3) is an open ash *Fraxinus excelsior* wood growing on large limestone pavements. The wood at the base of Malham Cove (2) is likewise an open ashwood, on talus slopes with many large limestone boulders. The wood below Janet's Foss (1) is different, being a mixed deciduous wood on slopes below a low scar, running down to Gordale Beck. There is more soil and ground cover, with dog's mercury *Mercurialis perennis* and wild garlic *Allium ursinum* being common. There are, however, small cliffs and exposed boulders. The soils of all three are highly calcareous (pH 7.5+).

All other woods sampled are plantations. Sites 4-9 are all from Tarn House Wood, which is the largest and most heterogeneous of these. The richest of these sites has six species not found in the others—it is the only plantation site with an alkaline soil. Sites 10-12 are from other plantations near the Tarn; Great Close Plantation (10) shows signs of extensive trampling by cattle. The last two sites, 13 and 14, are from ashwoods on much more acid soil overlying Bowland Shales.

(b) Screes, limestone grassland, limestone pavements and drift grassland.

Table 2 shows the species composition of samples from these habitats. There is little consistent difference between samples from screes and limestone grassland, and they are considered together. All the grassland sites, with the possible exception of site 26, are on steep rocky slopes presenting conditions similar to those on screes. If sites 21 and 27 are omitted (they may be undercollected), there is a considerable similarity between the faunas of the sites, reflecting, perhaps, the greater uniformity in soil conditions and past history than that between woodland sites. Sites with differing aspects are represented here, but aspect does not appear to influence species composition.

Limestone pavements, as a whole, have poorer faunas than grassland-scree. Most of them are subject to heavy grazing or recreational pressure; it may be significant that one of the two richest sites (35, Highfolds Scar) is protected from grazing, and in consequence has more luxuriant vegetation. The faunas of the pavements seem to be impoverished versions of those on screes and grassland. Only two species are found in pavements and not in the others, and both are found in one site only.

Little work has been done on drift grassland. Sites 37 and 38 represent the results of Stratton's investigation of one area of drift. The presence (37) or absence (38) of calcareous erratics evidently has a profound effect on the fauna.

Table 2. *Species composition of open habitat faunas. Sites 16-25 = Scree, 26-29 = Limestone*

	16	17	18	19	20	21
<i>Carychium tridentatum</i>			+			
<i>Azeca goodalli</i>				+		
<i>Cochlicopa lubrica</i>		+	+	+		
<i>Cochlicopa lubricella</i>	+		+	+	+	
<i>Pyramidula rupestris</i>	+	+	+	+	+	+
<i>Columella edentula</i>		+				
<i>Vertigo pygmaea</i>						
<i>Pupilla muscorum</i>						
<i>Lauria cylindracea</i>	+	+	+	+	+	
<i>Acanthinula aculeata</i>						
<i>Vallonia pulchella</i>						
<i>Vallonia excentrica</i>						
<i>Vallonia costata</i>						
<i>Ena obscura</i>	+			+		
<i>Clausilia bidentata</i>	+	+	+	+	+	
<i>Clausilia dubia</i>	+	+	+	+	+	+
<i>Balea perversa</i>	+					
<i>Cecilioides acicula</i>		+				
<i>Helicigona lapicida</i>						
<i>Arianta arbustorum</i>	+			+		
<i>Cepaea hortensis</i>	+					
<i>Cepaea nemoralis</i>	+	+	+	+		
<i>Hygromia striolata</i>	+		+	+	+	
<i>Hygromia hispida</i>			+	+		+
<i>Monacha granulata</i>						
<i>Punctum pygmaeum</i>						
<i>Discus rotundatus</i>	+	+	+	+	+	+
<i>Arion intermedius</i>				+		
<i>Arion circumscriptus</i>						
<i>Arion hortensis</i>						
<i>Arion subfuscus</i>				+		
<i>Arion ater</i>			+	+	+	
<i>Euconulus fulvus</i>						
<i>Vitrea crystallina</i>	+	*		*		*
<i>Vitrea contracta</i>			+		+	
<i>Vitrea diaphana</i>			+			
<i>Oxychilus cellarius</i>	+	+	+		+	+
<i>Oxychilus alliarius</i>	+	+		+		
<i>Oxychilus helveticus</i>					+	
<i>Retinella radiatula</i>	+	+		+	+	
<i>Retinella pura</i>	+		+		+	
<i>Retinella nitidula</i>	+	+	+	+	+	+
<i>Vitrina pellucida</i>				+		
<i>Lehmannia marginata</i>				+		
<i>Agriolimax reticulatus</i>				+		
Total	18	14	17	23	14	7
Collector	C	S	C	S	C	S

* = aggregate species, collected before 1959.

(c) Man-made environments.

Included here are such habitats as walls, gardens and roadside verges. Few such sites have been intensively investigated, and they are necessarily a very varied collection. One species list for a grassy and rocky roadside (39) is included in Table 2, and another, for the gardens and outhouses of the Field Centre, is in Table 1 (15). Site 39 is exceptionally rich for an open roadside verge, and two species, *Vallonia costata* and *Pupilla muscorum*, have been recorded only for this site in the district. Site 15 has a fauna clearly derivative from that of Tarn House Wood, which nearly surrounds it; only *Limax maximus* is present in it but not in the wood. Other man-

Grassland, 30-36 = Limestone pavements, 37-38 = Drift Grassland (37 with erratics,

22	23	24	25	26	27	28	29	30
+		+			+			
+	+	+	+	+	+	+	+	
+	+	+	+		+	+	+	+
							+	
+	+	+	+	+		+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+		+	+	+	+
+			+	+				
+	+	+	+	+	+	+	+	+
	+		+					
+	+	+	*		*	+		*
+	+	+	+	+	+	+	+	+
+		+	+			+		+
+	+	+	+	+		+		+
+	+	+	+	+		+	+	+
			+					
			+					
20	17	16	20	12	9	16	15	10
C	C	C	S	S	S	C	C	S

continued overleaf

made sites have been investigated only casually, but Stratton (1955) discusses the influence of walls on the distribution of certain species.

(d) Wetlands.

There are many kinds of wetland in the area. Table 3 lists the faunas of those sampled. Most sites are from Malham Tarn Moss; two (40 and 41) from the central area of the fen (in Poor Fen of Sinker (1960)); two (42 and 43) from Marsh-Meadows dominated by Meadowsweet *Filipendula ulmaria*, and one (44) from the main body of the raised bog. This last, like most areas of acid peat, has very few species.

38 without). 39 = Grassy roadside verges

31	32	33	34	35	36	37	38	39
		+						+
	+							+
+	+	+	+	+	+	+		+
		+	+					+
+	+							+
		+						+
	+							+
+	+	+		+				+
		+	+					+
	+							+
+	+	+	+	+	+			+
						+		
						+		
						+		
						+		
+	*	+		+	+		+	+
		+						+
	+		+	+				+
	+					+		+
	+	+	+	+	+	+		+
	+					+		+
9	15	11	10	14	10	12	2	27
S	S	C	C	C	C	S	S	SC

Of the many areas of calcareous marsh in the areas, only the cattle-trampled area between Ha Mire Plantation and the northeast corner of the Tarn has been investigated in detail. Molluscs are not abundant, and, with the exception of *Lymnaea truncatula*, are mostly restricted to stones, and pieces of timber which provide some protection from trampling. It is here that the very rare *Agriolimax agrestis* occurs.

There are many collections from small marshy sites all over the area, usually with only two or three species recorded from each. The last column of Table 3 shows the number of times each species recorded has been found in 12 such sites. *Lymnaea truncatula* and *Succinea pfeifferi* are nearly universal; all others are merely occasional

Table 3. *Species composition of Wetland faunas. Laterally * = aggregate species. M = combined occurrences in 12 calcareous marsh sites. Species marked X are Freshwater species*

	40	41	42	43	44	45	M
<i>Carychium minimum</i>		+	+	+		+	
<i>Carychium tridentatum</i>	+		+	+			
<i>Lymnaea truncatula</i>	+	+		+		+	10
* <i>Lymnaea palustris</i>	+	+	+				
* <i>Planorbis leucostoma</i>	+	+					
* <i>Planorbis contortus</i>		+					
<i>Succinea putris</i>						+	2
<i>Succinea pfeifferi</i>	+	+	+	+		+	9
<i>Cochlicopa lubrica</i>		+	+			+	
<i>Vertigo antivertigo</i>	+	+					
<i>Vertigo substriata</i>	+	+					
<i>Arianta arbustorum</i>						+	
<i>Hygromia hispida</i>						+	1
<i>Monacha granulata</i>						+	
<i>Punctum pygmaeum</i>	+	+					
<i>Arion hortensis</i>		+				+	
<i>Arion subfuscus</i>			+				
<i>Arion ater</i>	+				+		1
<i>Euconulus fulvus</i>		+	+	+			3
<i>Vitrea crystallina</i>	*		+	+		*	1
<i>Vitrea contracta</i>			+	+			
<i>Oxychilus alliarius</i>		+					2
<i>Retinella radiatula</i>	+	+	+	+			2
<i>Agriolimax agrestis</i>							1
<i>Agriolimax laevis</i>	+	+	+	+			2
* <i>Lymnaea pereger</i>							5
<i>Retinella nitidula</i>							1
Total	12	15	11	9	1	10	13
Collectors	S	C	C	C	S	S	SC

with the exception of *Lymnaea pereger* which is an aquatic species confined to open water within the marshes.

The last individual site (45) in Table 3 is from a reed-bed on the banks of Gordale Beck. It is included as an example of a transitional habitat between wetland and the merely damp, with such species as *Arianta arbustorum*, *Hygromia hispida* and *Monacha granulata* as well as the typical wetland fauna.

DISCUSSION

The Malham area is one of the richest upland areas for terrestrial molluscs in Britain. Fifty-seven species (excluding *Lymnaea truncatula*) have been recorded, although two of these, *Vertigo pusilla* and *Abida secale* have not been confirmed since the late nineteenth century. The list must be nearly complete, and includes about half the total British fauna. This richness is due to the unusual combination of calcareous soils, damp climate, and minimal recent disturbance. The cool upland climate and northerly latitude account for many of the absences from the list.

The influence of soil pH and disturbance on the distribution of mollusca

The association of rich mollusc faunas with soils of high pH is well known (Atkins and Lebour, 1923; Boycott, 1934), and it is clear from recent studies that it is the availability of Calcium rather than alkalinity as such which is important (Wareborn, 1969). In the Malham area, alkaline soils are derived almost entirely from limestone.

At first sight, there is a pronounced association between number of species and soil pH in woods (Fig. 2). The association is partly spurious, for three of the four sites with pH 7.5+ are from the undisturbed, natural woodlands, while all the rest are from plantations. Eleven species from the woodland list occur only in the four

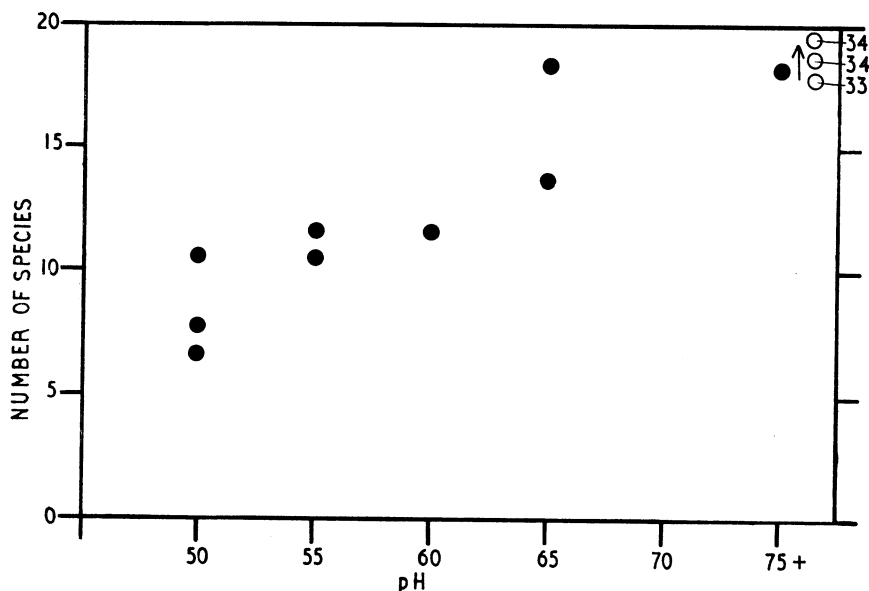


FIG. 2.
Variation in number of species with soil pH for woodland sites. ● = plantation sites, ○ = old woodland sites. The trend for association between high species number and high pH within the plantation sites is significant (Spearman's $\rho = 0.9417$, $P < 0.01$).

alkaline sites; six of these are restricted to the natural woodlands, so that lack of disturbance (and low altitude) could be important factors influencing their distribution. Further, species in this group such as *Pyramidula rupestris* and *Clausilia dubia* are restricted to rocks and *Lauria cylindracea* is frequently associated with them. Rocks are usually abundant at the surface in alkaline sites, but are rarer or absent in acid ones. Other species, such as *Cochlicopa lubrica* and *C. lubricella*, are much more frequent in the alkaline sites than the acid, although they are relatively tolerant of low pH (Boycott, 1934). There remains, however, a trend for association between faunal richness and high pH within the plantations alone.

There are many fewer sites from acid soils in other habitats. The very poor faunas of erratic-free drift and from the raised bog are typical of upland acid sites.

The enriching effect of calcareous soils can be seen by comparing the Malham area with the area around Dale, Pembrokeshire (Stratton, 1964) which, like Malham, has a damp climate, but has almost entirely acid soils. Only 35 species of terrestrial mollusc occur there.

Comparison of faunas from different habitats

It is well known that many species of land mollusc have very broad ranges of habitat in Britain (Boycott, 1934). Descriptions of habitat-range based on observations from all over Britain may, however, be misleading, because profound changes

in habitats occupied by some species occur over short distances (5–10 km.) in the presence of large climatic gradients (Cameron, 1970; Cameron and Palles-Clark, 1971).

Most land molluscs are polyphagous; snails in particular are usually detrital feeders. Differences in the plant compositions of different habitats are therefore of importance mainly in the variations in cover and microclimate so produced (Boycott, 1934), woods providing damper and more sheltered sites than open habitats. In southern England, the contrast between the faunas of woods and those of chalk or limestone grassland is marked, with few species occurring frequently in both (Boycott, 1934).

The situation at Malham is very different. Forty-one species are recorded from the “grassland” habitats at Malham, and 42 from woods. Thirty-six species, the vast majority, are common to both lists. This similarity in faunas might be due to the occasional occurrence of a species in one habitat, when it is much more frequent in the other. We can examine this by considering those species which occur in at least half the sites in one habitat or the other (Table 4). Considering only these relatively common species does seem to increase the degree of difference between these two habitats. The differences are misleading, however, as an indication of the effect of shelter. All the species in the grassland list of Table 4 occur abundantly in the three ancient woodlands, and their absence from, or rarity in, the other woodland sites is likely to be due to disturbance or low pH (see above). On the other hand, most species frequent in woods, but not grassland, are certainly more characteristic of woods than grassland in the rest of Britain (Boycott, 1934).

Table 4. *Species occurring in at least half the sites from one habitat*

	Woods	Open habitats
Carychium tridentatum	+	
Cochlicopa lubricella	A	+
Pyramidula rupestris	A	+
Lauria cylindracea	A	+
Ena obscura	A	+
Clausilia bidentata	A	+
Clausilia dubia	A	+
Cepaea nemoralis	A	+
Hygromia striolata	+	+
Hygromia hispida	A	+
Discus rotundatus	+	+
Arion circumscriptus*	+	+
Arion hortensis	+	
Arion ater	+	
Euconulus fulvus	+	
Vitrea crystallina*	+	+
Oxychilus cellarius	+	+
Oxychilus alliarius	+	+
Retinella pura	+	
Retinella nitidula	+	+
Agriolimax reticulatus	+	

+ = present in more than half the sites in that habitat.
 A = present in all three natural woodland sites.
 * = aggregate species.

The difference between Malham and warmer, drier areas to the south is not due to the composition of woodland faunas. The faunas of the natural woods at Malham are amongst the richest recorded in Britain, but they are not very different from those

of other old calcareous woodlands with rocky ground (e.g. Whitcombe Wood in the Cotswolds, Boycott, 1934).

The contrast in grassland faunas, however, is extreme. Southern grassland faunas are dominated by xerophile species such as *Helicella* spp., *Vertigo pygmaea*, *Vallonia costata* and *V. excentrica* and *Pupilla muscorum* although other species often occur (Boycott, 1934; Evans, 1968; Chappell, Ainsworth, Cameron and Redfern, 1971). These species are rare or absent at Malham: *Helicella itala* is known only from two sites, and has not been found since 1958; *P. muscorum* and *V. costata* are known only from the roadside bank near Malham village, probably the warmest and driest site investigated; *V. excentrica* and *V. pygmaea* also occur here and in one or two other sites.

The Malham grassland faunas, indeed, are dominated by species regarded as typical of woodland elsewhere, and many of these species are used as indicators of woodland or "cover" in archeological and geological studies (Evans, 1968; Sparks, 1960). The exceptionally damp and cloudy climate of the Malham area seems the most probable explanation of this phenomenon; similar effects can be seen in Derbyshire (Cameron, 1970). The phenomenon reinforces the view of Boycott that differences in habitat between molluscs are related mainly to shelter rather than food. It should be added that some species found in Malham grasslands are rock-dwellers, and their absence from some southern sites is due to the absence of rocks rather than to dryness.

By contrast, the faunas of wetland sites at Malham are distinct from the others. Only 23 species of terrestrial mollusc occur in them; six of these occur nowhere else, and two more (*Succinea putris* and *Lymnaea truncatula*) occur in only one other site (almost certainly from the banks of a stream within it). All these eight are typical inhabitants of wet places in any part of Britain (Boycott, 1934; Watson and Verdcourt, 1953; Ellis, 1967). All the other species in the list, with the possible exceptions of *Carychium tridentatum* and *Vitrea contracta*, are also frequently found in wet places. The only oddity is the absence of *Zonitoides nitidus*, a common wetland species in most of Britain. The presence of standing water and waterlogged soil clearly reduces the dependence of the fauna on cover and climate.

SUMMARY

1. An account is given of the terrestrial mollusca of the Malham area, and their distribution in various habitats.
2. Within woodlands, soil pH and disturbance appear to be the main factors affecting the molluscs. Old woods with calcareous soils have exceptionally rich faunas.
3. There are few consistent differences in faunas between screes, limestone grasslands and pavements, except that the last have rather poor faunas where subject to grazing.
4. The faunas of open habitats other than wetlands are very similar to those of woods, which is atypical. They are very unlike the faunas of similar habitats in southern England, and this is probably due to the cool damp climate at Malham.
5. The faunas of wetlands are distinctive, and very similar to those of wetlands elsewhere.
6. The combination of calcareous soils, damp climate and minimal disturbance make Malham one of the richest upland areas for molluscs in Britain.

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APPENDIX

A list of all the species of terrestrial mollusc found at Malham, with last date of finding.

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|----------------------------------------------|----------------------------------------------|
| <i>Carychium minimum</i> (Müller) 1971 | <i>Cepaea nemoralis</i> (L.) 1971 |
| <i>Carychium tridentatum</i> (Risso) 1971 | <i>Hygromia striolata</i> (C. Pfeiffer) 1971 |
| <i>Lymnaea truncatula</i> (Müller) 1971 | * <i>Hygromia hispida</i> (L.) 1971 |
| <i>Succinea putris</i> (L.) 1955 | <i>Monacha granulata</i> (Alder) 1971 |
| <i>Succinea pfeifferi</i> (Rossmassler) 1971 | <i>Helicella itala</i> (L.) 1958 |
| <i>Azeca goodalli</i> (Ferussac) 1971 | <i>Punctum pygmaeum</i> (Drap.) 1971 |
| <i>Cochlicopa lubrica</i> (Müller) 1971 | <i>Discus rotundatus</i> (Müller) 1971 |
| <i>Cochlicopa lubricella</i> (Stabile) 1971 | <i>Arion intermedius</i> (Normand) 1971 |
| <i>Pyramidula rupestris</i> (Drap.) 1971 | <i>Arion circumscriptus</i> (Johnston) 1971 |
| <i>Columella edentula</i> (Drap.) 1971 | <i>Arion fasciatus</i> (Nilsson) 1971 |
| <i>Vertigo pusilla</i> (Müller) 1882 | <i>Arion hortensis</i> (Ferussac) 1971 |
| <i>Vertigo antivertigo</i> (Drap.) 1971 | <i>Arion subfuscus</i> (Drap.) 1971 |
| <i>Vertigo substriata</i> (Jeffreys) 1970 | <i>Arion ater</i> (L.) 1971 |
| <i>Vertigo pygmaea</i> (Drap.) 1971 | <i>Euconulus fulvus</i> (Müller) 1971 |
| <i>Pupilla muscorum</i> (L.) 1971 | <i>Vitrea crystallina</i> (Müller) 1971 |
| <i>Lauria cylindracea</i> (da Costa) 1971 | <i>Vitrea contracta</i> (Westerlund) 1971 |
| <i>Abida secale</i> (Drap.) 1871 | <i>Vitrea diaphana</i> (Studer) 1971 |
| <i>Acanthinula aculeata</i> (Müller) 1955 | <i>Oxychilus cellarius</i> (Müller) 1971 |
| <i>Vallonia pulchella</i> (Müller) 1971 | <i>Oxychilus alliarius</i> (Müller) 1971 |
| <i>Vallonia excentrica</i> (Sterki) 1971 | <i>Oxychilus helveticus</i> (Blum) 1971 |
| <i>Vallonia costata</i> (Müller) 1971 | <i>Retinella radiatula</i> (Alder) 1971 |
| <i>Ena obscura</i> (Müller) 1971 | <i>Retinella pura</i> (Alder) 1971 |
| <i>Clausilia bidentata</i> (Strom) 1971 | <i>Retinella nitidula</i> (Drap.) 1971 |
| <i>Clausilia dubia</i> (Drap.) 1971 | <i>Vitrina pellucida</i> (Müller) 1971 |
| <i>Balea perversa</i> (L.) 1971 | <i>Limax maximus</i> (L.) 1966 |
| <i>Ceciloides acicula</i> (Müller) 1955 | <i>Lehmannia marginata</i> (Müller) 1971 |
| <i>Helicigona lapicida</i> (L.) 1970 | <i>Agriolimax agrestis</i> (L.) 1971 |
| <i>Arianta arbustorum</i> (L.) 1971 | <i>Agriolimax reticulatus</i> (Müller) 1971 |
| <i>Cepaea hortensis</i> (Müller) 1971 | <i>Agriolimax laevis</i> (Müller) 1971 |

*Some authors, including Stratton, recognize a further species, *Hygromia liberta*, which is to be found at Malham. We are doubtful of its specific status and have treated records of it as *H. hispida*.

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