Fld Stud. (1976), 4, 457–464

WOODLAND MOLLUSCA AROUND NETTLECOMBE, SOMERSET

By M. J. BISHOP*

University of Cambridge, Department of Zoology, Downing Street, Cambridge CB2 3EJ

Introduction

The terrestrial molluscs of Somerset were described by Swanton (1912), particularly the rich faunas on the Carboniferous limestone habitats of the Mendips. Hadden (1923) published an account of the Porlock and Minehead district. Bantock and Nobel (1973), Bantock (1974) and Bantock and Price (1975) have detailed the ecological genetics of *Cepaea hortensis* and *C. nemoralis* in the Brendon Hills, including the Nettlecombe valley.

The area around Nettlecombe Court (Fig. 1) is noteworthy not for any nationally rare Mollusca but for the diversity of habitats within it. This results from geological variety; Mesozoic rocks are exposed here for the last time as one travels west. It is the junction zone between 'lowland' calcareous southern Britain and the 'highland' acidic south-west peninsula. The Jurassic Lower Lias strata at the coast around Watchet give rise to calcareous soils. The Devonian strata of the Brendon Hills (though containing local calcareous bands) generally produce highly acidic soils which may show intense podsolization. Some Permian and Triassic strata also occur in the district.

Despite the south-western maritime setting, local temperatures vary markedly with changes in topography. The climate of the Brendon Hills, which rise to 450 m, differs considerably from the more equable coastal strip. In the Nettlecombe Valley, ground frost may occur in any month and a temperature inversion happens on 60 per cent of all nights (Ratsey, 1973).

This study illustrates something of the ecological diversity of the area in terms of the woodland mollusc faunas.

Methods

Seven sample sites, each of area 1000 m^2, were selected in August 1974 on the basis of their vegetation: each, within itself, was uniform, without obvious environmental or vegetational change.

Five samples were obtained from the top 50 mm of soil at each site, and their pH was determined electrometrically in 1 : 2·5 suspension (by volume) with distilled water.

A description of the vegetation was prepared for each site.

The mollusc fauna was sampled by sieving litter and top soil through a 10 mm sieve. Slugs and the larger snails were searched for under fallen logs, under stones and moss and in the crevices around the boles of trees. In the laboratory, the sieve samples were separated into three fractions by the use of 2·5 and 0·6 mm sieves. Each fraction was hand sorted twice under a magnifying glass and the live molluscs identified.

* Present address: Queensland Museum, Gregory Terrace, Fortitude Valley, Queensland, Australia, 4006.

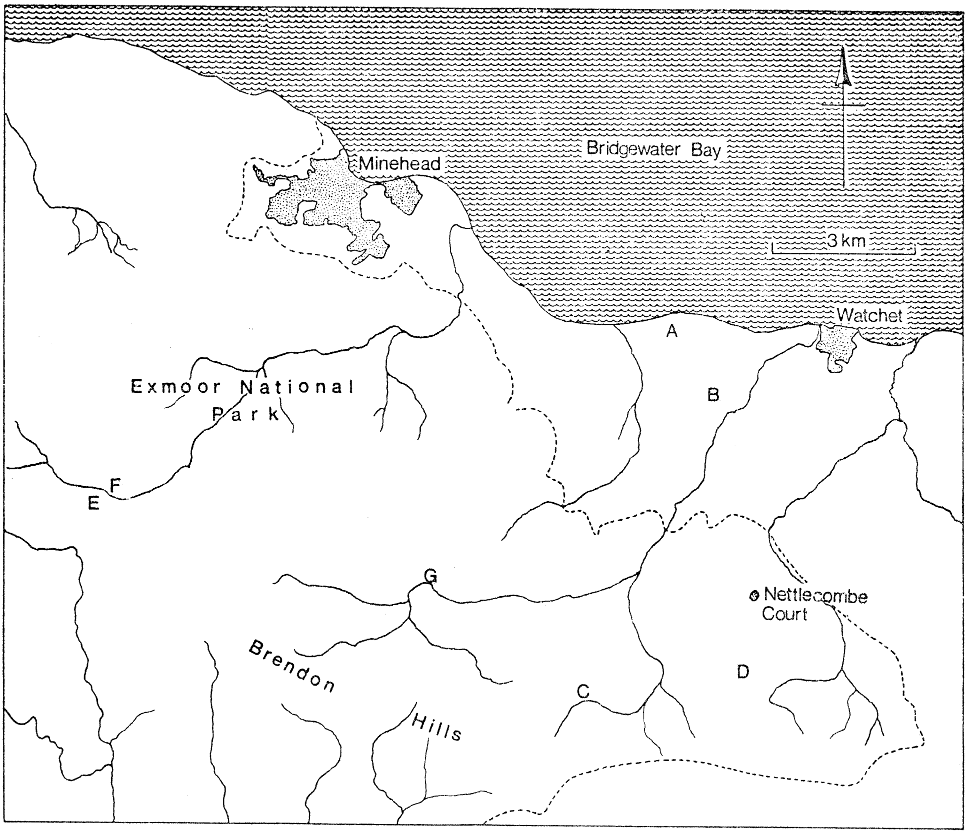

Fig. 1.
The area around Nettlecombe Court, locating the seven study sites.

Results

The Study Sites

Fig. 1 shows the location of the seven sites A-G. Most of the area is grazing land, with some arable, especially near the coast. The patches of deciduous woodland are all more or less altered, although in the steepest valleys often appearing semi-natural. There are also extensive areas of recent coniferous plantation.

Site A is east of Blue Anchor (British National Grid Reference 31/039435), 65 m above sea-level. The woodland of oak, ash, elm and sycamore, on a calcareous substrate derived from the Lower Lias limestones and mudstones, showed signs of recent disturbance.

Site B is east of Old Cleeve (31/048421), at a height of 80 m. The woodland of oak, ash, hawthorn, holly and sycamore is much disturbed, constituting little more than a shelter belt between the road and the arable fields. The underlying rock is Keuper Marl.

At site C, near Leigh Barton (31/022357), 215 m up, the undisturbed woodland of oak, ash, hazel, holly, hawthorn and sycamore is on the south facing slope of the deep Comberow valley on Middle or Upper Devonian sandstones and shales.

Site D is above the head of the Nettlecombe valley (31/054362) at a height of 315 m. The woodland is a recent uniform plantation of ash, pine, hazel and sycamore on Middle or Upper Devonian sandstones and shales.

Sites E and F are on the southwest and northeast of the Cutcombe valley, near North Hawkwell (E 21/918398, 250 m; F 21/923399, 180 m). Both looked well managed. At E, the woodland is of oak and birch and at F of oak, holly and hazel. The underlying rocks are Lower Devonian sandstone and shales.

At site G, in Slowley Wood, Luxborough (21/988380), at 200 m, the woodland of oak, holly, hazel and hawthorn, although situated in a region where much coniferous plantation has taken place, has a semi-natural appearance. The underlying rocks are Lower Devonian sandstones and shales.

Table 1 shows the soil pH at the seven sites, which can be divided into a base-rich series A-D, with a soil pH range of 5·5–7·4, and a base-poor series E-G, with a soil pH range of 4·7–4·8. The base-rich series can be sub-divided, A and B with free calcium carbonate and a soil pH range of 7·1–7·4, and C and D without free calcium carbonate and a pH range of 5·5–5·9.

Table 1. *Measurements of soil pH at the seven sites around Nettlecombe Court, Somerset*

	A	B	C	D	E	F	G
Mean (N=5)	7·4	7·1	5·9	5·5	4·8	4·8	4·7
Standard devn.	0·3	0·4	0·3	0·6	0·1	0·1	0·1

The Vegetation

The vascular vegetation of the seven sites is summarized in Table 2. The base-rich series A-D is characterized by ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), wood avens (*Geum urbanum*), nettle (*Urtica dioica*) and the grass *Brachypodium sylvaticum*. A and B are characterized by plants often found on limestone such as cuckoo pint (*Arum maculatum*) and stinking iris (*Iris foetidissima*), with spindle tree (*Euonymus europaeus*), dogwood (*Thelycrania sanguinea*) and stinking hellebore (*Helleborus foetidus*) at site B. C and D are characterized by enchanter's nightshade (*Circaea lutetiana*) and red campion (*Silene dioica*), with the golden-saxifrage *Chrysosplenium oppositifolium* at site D. The moister soil may be important at sites C and D.

The base-poor sites E to G are characterized by bilberry (*Vaccinium myrtillus*). F was a floristically poor site. Wavy hair-grass (*Deschampsia flexosa*) and cow-wheat (*Melampyrum pratense*) characterized sites E and G, with golden rod (*Solidago virgaurea*), foxglove (*Digitalis purpurea*), tormentil (*Potentilla erecta*) and woodrush (*Luzula sylvatica*) at site E.

Table 2 contrasts the floral composition of the sites. For example, Site G does not have many species in common with Site A. To express this mathematically, a table of similarities was constructed for each pair of sites in terms of distances such that the least similar sites were placed farthest apart. It would need axes in seven dimensions fully to represent these distances, but an adequate representation in fewer dimensions was obtained when new unrelated axes were calculated and the sites plotted as in Fig. 2 (upper). The technique used was principal co-ordinates analysis (Blackith and Reyment, 1971) and the new axes represent the more important directions of variation in the vegetation. The site principal co-ordinate scores on the most im-

Table 2. *Vegetation of the seven sites around Nettlecombe Court, Somerset*

	A	B	C	D	E	F	G
TREES AND SHRUBS							
Acer campestre L.	.	.	+	.	.	.	.
A. pseudoplatanus L.	+	+	+	+	.	.	.
Betula pendula Roth	.	.	.	.	+	.	.
Corylus avellana L.	.	.	+	+	.	+	+
Crataegus monogyna Jacq.	.	+	+	.	.	.	+
Euonymus europaeus L.	.	+	.	.	.	.	.
Fraxinus exelsior L.	+	+	+	+	.	.	.
Hedera helix L.	+	+	+	.	+	+	+
Ilex aquifolium L.	.	+	+	.	.	+	+
Lonicera periclymenum L.	.	.	.	.	.	+	+
Pinus sylvestris L.	.	.	.	+	.	.	.
Quercus robur L.	+	.	.	.	.	.	.
Q. petraea (Mattuschka) Liebl.	.	+	+	.	+	+	+
Rhododendron ponticum L.	.	.	.	.	+	.	.
Rosa canina agg.	+	+	.	.	.	.	.
Rubus fruticosus L. agg.	+	+	+	+	+	+	+
Sorbus aucuparia L.	.	.	.	.	.	.	+
Tamus communis L.	.	+	.	.	.	.	.
Thelycrania sanguinea (L). Fourr.	.	+	.	.	.	.	.
Ulmus sp.	+	+	.	.	.	.	.
Vaccinium myrtillus L.	.	.	.	.	+	+	+
PTERIDOPHYTES							
Dryopteris dilatata (Hoffm.) Gray	.	+	+	+	+	.	+
D. filix-mas (L.) Schott	+	.	+	.	.	.	.
Phyllitis scolopendrium (L.) Newm.	+	+	+	.	.	.	+
Polypodium vulgare L.	.	.	.	.	+	+	+
Pteridium aquilinum (L.) Kuhn	.	.	+	.	+	+	.
GRASSES							
Brachypodium sylvaticum (Huds.) Beauv.	+	+	+	+	.	.	.
Deschampsia flexuosa (L.) Trin.	.	.	.	.	+	.	+
OTHER MONOCOTYLEDONS							
Arum maculatum L.	+	+	.	.	.	.	.
Iris foetidissima L.	+	+	.	.	.	.	.
Luzula sylvatica (Huds.) Gaud.	.	.	.	.	+	.	.
DICOTYLEDON HERBS							
Ajuga reptans L.	.	.	.	+	.	.	.
Anemone nemorosa L.	.	.	.	+	.	.	.
Arctium nemorosum Lejeune	.	.	.	+	.	.	.
Ballota nigra L.	.	.	+	.	.	.	.
Chaerophyllum tementulum L.	.	+	.	.	.	.	.
Chrysosplenium oppositifolium L.	.	.	.	+	.	.	.
Circaea lutetiana L.	.	.	+	+	.	.	.
Digitalis purpurea L.	.	.	.	.	+	.	.
Filipendula ulmaria (L.) Maxim	+	.	+	.	.	.	.
Galium odoratum (L.) Scop.	.	+	.	.	.	.	.
Geranium robertianum L.	+	+	+	+	.	.	.
Geum urbanum L.	+	+	+	+	.	.	.
Helleborus foetidus L.	.	+	.	.	.	.	.
Heracleum spondylium L.	.	.	+	.	.	.	.
Lathyrus sylvestris L.	.	+	.	.	.	.	.
Lysimachia nemorum L.	.	.	.	+	.	.	.
Melampyrum pratense L.	.	.	.	.	+	.	+
Mercurialis perennis L.	.	.	+	.	.	.	.
Oxalis acetosella L.	.	.	.	+	+	.	+
Potentilla erecta (L.) Raüsch	.	.	.	.	+	.	.
Primula vulgaris Huds.	+	+	+	+	.	.	.
Rumex conglomeratus Murr.	+	+	.	+	.	.	.
Sanicula europaea L.	.	+	.	.	.	.	.
Silene dioica (L.) Clairv.	.	.	+	+	.	.	.
Solidago virgaurea L.	.	.	.	.	+	.	.
Urtica dioica L.	+	+	+	+	.	.	.
Viola spp.	+	+	+	+	.	.	.

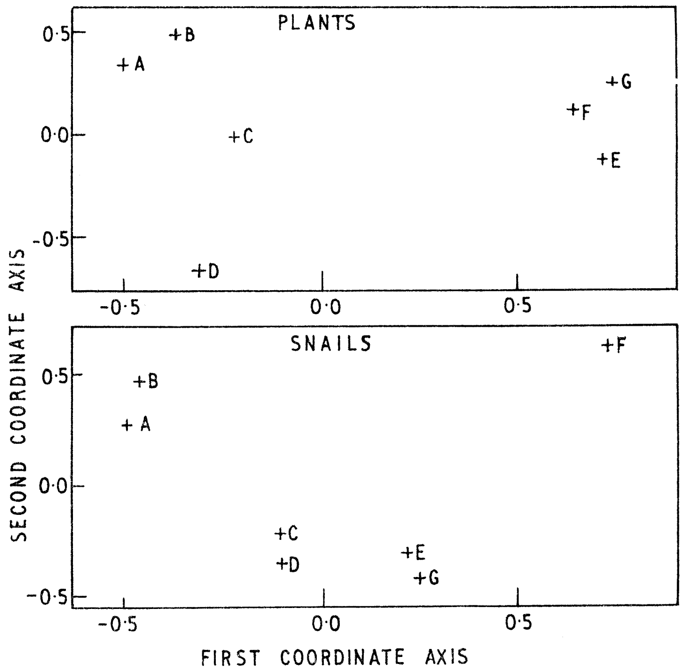

FIG. 2.

The position of the seven study sites on axes representing the most important independent directions of variation between sites for plant species (upper) and snail species (lower). The more similar sites are closer together on the diagrams. Note a correspondence in the patterns of site similarities for plants and snails.

portant direction of variation (axis 1) were significantly correlated with site pH values (Pearson's product-moment correlation coefficient $r = -0{\cdot}87$, probability $p = 0{\cdot}01$).

The Snail Fauna

The presence or absence of the sites of 43 species of snails is presented in Table 3. *Aegopinella pura, Discus rotundatus* and *Oxychilus alliarius* are common in woodland all over Britain.

The snail fauna of the base-rich series is characterized by *Acanthinula aculeata* and *Arion circumscriptus,* with *Carychium tridentatum* and *Helix aspersa* at sites A, B and C. Sites A and B have *Cochlodina laminata, Oxychilus helveticus* and *Vitrea contracta,* with the calcicoles *Pomatias elegans* at site A and *Helicigona lapicida* at site B. The presence of *Arion ater rufus* and *Trichia striolata* at site B supports the suggestion of excessive human interference. Sites C and D have *Carychium minimum* and *Deroceras reticulatum,* with *Arianta arbustorum* at site C. The presence of *C. minimum* at these sites is in line with the higher moisture status indicated by the flora.

No snail species uniquely characterized the base-poor series E-G. *Arion subfuscus* and *Zonitoides excavatus* were at sites E and G and *Columella aspera* at site G.

From the list of snails (Table 3), the major directions of variation in snail fauna were extracted, as for vegetation. The ordination of the sites on the first two axes is shown in Fig. 2 (lower). Again there was a highly significant correlation between the scores for each site on axis 1 and pH ($r = -0{\cdot}88$, $P < 0{\cdot}01$).

Table 3. *Occurrence of Mollusca at the seven sites in woodland around Nettlecombe Court, Somerset.*

	A	B	C	D	E	F	G
Acanthinula aculeata (Müll.)	+	+	+	+	.	.	.
Aegopinella nitidula (Drap.)	+	+	+	+	+	.	.
A. pura (Alder)	+	+	+	+	+	+	+
Arianta arbustorum (L.)	.	.	+	.	.	.	.
Arion ater (L.) *ater*	+	.	.	.	.	.	.
A. ater rufus	.	+	.	.	.	.	.
A. circumscriptus Johnston	+	+	+	+	.	.	.
A. hortensis Férussac	.	.	+	+	.	.	+
A. intermedius Normand	.	+	+	+	+	+	+
A. lusitanicus Mabille	.	.	+	.	+	+	.
A. subfuscus (Drap.)	.	.	.	.	+	.	+
Balea perversa (L.)	.	+	.	.	.	.	.
Carychium minimum Müll.	.	.	+	+	.	.	.
C. tridentatum (Risso)	+	+	+	.	.	.	.
Cepaea hortensis (Müll.)	+	+	+	+	.	.	+
C. nemoralis (L.)	+	+	.	.	+	.	+
Clausilia bidentata (Ström)	+	+	+	+	+	.	+
Cochlicopa lubrica (Müll.)	+	+	+	+	+	.	.
C. lubricella (Porro)	+	.	.	.	.	.	.
Cochlodina laminata (Montagu)	+	+	.	.	.	.	.
Columella aspera Waldén	.	.	.	.	.	.	+
C. edentula (Drap.)	+	.	.	.	.	.	.
Deroceras reticulatum (Müll.)	.	.	+	+	.	.	.
Discus rotundatus (Müll.)	+	+	+	+	+	+	+
Ena obscura (Müll.)	.	+	.	.	.	.	.
Euconulus fulvus (Müll.)	.	.	.	+	+	.	+
Helicigona lapicida (L.)	.	+	.	.	.	.	.
Helix aspersa Müll.	+	+	+	.	.	.	.
Lehmannia marginata (Müll.)	.	.	+	+	.	.	+
Limax cinereoniger Wolf	.	.	+	+	+	+	+
Nesovitrea hammonis (Ström)	+	.	.	.	.	.	.
Oxychilus alliarius (Miller)	+	+	+	+	+	+	+
O. cellarius (Müll.)	+	.	+	+	+	.	+
O. helveticus (Blum)	+	+	.	.	.	.	.
Pomatias elegans (Müll.)	+	.	.	.	.	.	.
Punctum pygmaeum (Drap.)	.	+	.	+	.	.	.
Trichia hispida (L.)	+	.	+	+	+	.	.
T. striolata (C. Pfeiffer)	.	+	.	.	.	.	.
Vitrea contracta (Westerlund)	+	+	.	.	.	.	.
V. crystallina (Müll.)	+	.	+	+	+	.	+
Vitrina pellucida (Müll.)	+	+	.	+	+	.	+
Zenobiella subrufescens (Miller)	.	.	+	.	+	.	.
Zonitoides excavatus (Alder)	.	.	.	.	+	.	+

Examination of the first axis scores for plants and snails showed a highly significant correlation between the two ($r=0\cdot89$, $P<0\cdot01$), indicating that the major directions of variation over the seven sites correspond.

Almost 70 % of the information about both flora and snail fauna is summarized in the first three axes. Tests of statistical significance show that vegetation and snail fauna vary in much the same way over the seven sites and that soil pH is highly correlated with both (Fig. 3).

Discussion

Earlier studies of woodland Mollusca should be compared with caution as they are often from sites of unspecified area and vegetation.

The results presented here are directly comparable with those of Cameron (1973), being drawn from a similar area (*ca.* 1000 m^2) of relatively uniform vegetation. The fall-off in numbers of snail species with increasing acidity is more marked in the

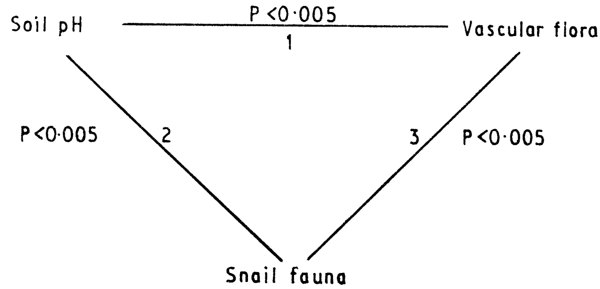

FIG. 3.

Correlations between soil pH and the principal coordinate scores on the first three axes for plants and snails.
1. Square of the multiple correlation coefficient (Draper and Smith, 1966) $R^2=0\cdot988$; F test $F=85\cdot3$, degrees of freedom $\nu=3$, probability $P<0\cdot005$.
2. $R^2=0\cdot983$; $F=58\cdot5$, $\nu=3$, $P<0\cdot005$.
3. First canonical correlation (Blackith and Reyment, 1971) $R_{C1}=0\cdot999$; Wilk's lambda $\lambda=0\cdot00029$, chi-square $\chi^2=28\cdot5$. $\nu=9$, $P<0\cdot005$.

woods on the South Downs, probably because of the drier climate. The much more acid Somerset woods maintain moderate numbers of snail species.

The garden snail (*Helix aspersa*), introduced in the first century AD (Evans, 1972), seems to have firmly established itself as a species of woodland in southern Britain. The idea that the slug *Limax cinereoniger* is an indicator of original forest (Boycott, 1934) is not true: it is common in woodland, including modern plantation (Site D), in the Nettlecombe district. *Arion lusitanicus* apparently often replaces *A. ater* in woodland in this part of Somerset; dissection is necessary for confirmation of the identification (Ellis, 1965).

Boycott (1934) considered that the local distribution of land snails in Britain could be primarily related to moisture, shelter and the availability of calcium. The omnivorous habit of the majority of land snails led Boycott to reject food as a factor affecting their distribution. He also largely dismissed inter-specific competition as a factor controlling their abundance. If Boycott's ideas are accepted, the associations of species of snails living together at one place do not result from the competitive interactions in a snail 'community'. The associations must instead be produced by particular habitats being either optimal or marginal for the species involved. Woodland snail faunas would be expected to be products of the physico-chemical and structural conditions in the habitat. A relationship with vegetation would be expected only in so far as the vegetation itself was controlled by the physico-chemical conditions and might produce the required structural features.

Soil pH, vegetation and snail fauna are so inexorably linked in the sites studied that it is not possible to sort out the causal relationships. Vegetation was as efficient as soil pH in explaining the variation in the snail fauna between sites, so that further examination of the relationship between snail fauna and vegetation would be profitable, while determining the effect of physico-chemical factors on both.

SUMMARY

(1) The area around Nettlecombe Court, Somerset, shows extreme ecological diversity, resulting primarily from the great topographical and geological variety.

(2) The local woodland habitats vary from alkaline to highly acidic.

(3) The snail fauna of these woodlands follows similar directions of variation as the vegetation, with a direct relationship to soil pH.

Acknowledgements

I wish to thank Mr. J. H. Crothers for his hospitality at Nettlecombe Court and Mr. J. W. Rodford for drawing the figures.

References

Bantock, C. R. (1974). Experimental evidence for non-visual selection in *Cepaea nemoralis*. *Heredity*, **33**, 409–412.

Bantock, C. R. and Noble, K. (1973). Variation with altitude and habitat in *Cepaea hortensis* (Müll.). *Zool. J. Linn. Soc.*, **53**, 237–252.

Bantock, C. R., and Price, D. J. (1975). Marginal populations of *Cepaea nemoralis* (L.) on the Brendon Hills, England. 1. Ecology and ecogenetics. *Evolution*, in press.

Blackith, R. E., and Reyment, R. A. (1971). *Multivariate morphometrics*. 412 pp. London: Academic Press.

Boycott, A. E. (1934). The habitats of land Mollusca in Britain. *J. Ecol.*, **22**, 1–38.

Cameron, R. A. D. (1973). Some woodland mollusc faunas from southern England. *Malacologia*, **14**, 355–370.

Draper, N. R., and Smith, H. (1966). *Applied regression analysis*. 407 pp. New York: Wiley.

Ellis, A. E. (1965). *Arion lusitanicus* Mabille in Devon. *J. Conch., Lond.*, **25**, 345–347.

Evans, J. G. (1972). *Land snails in archaeology*. 436 pp. London: Seminar Press.

Hadden, N. G. (1923). Additions to the Mollusca of Somerset. *J. Conch., Lond.*, **17**, 71–77.

Ratsey, S. (1973). The climate at and around Nettlecombe Court, Somerset. *Fld. Stud.*, **3**, 741–762.

Swanton, E. W. (1912). *Mollusca of Somerset*. Somerset. archaeol. nat. Hist. Soc.