VARIATION IN SOME SHELL CHARACTERISTICS OF *CLAUSILIA BIDENTATA* (STRÖM, 1765) (GASTROPODA: PULMONATA: CLAUSILIIDAE)

A. A. WARDHAUGH

13 Captain Cook's Crescent, Marton, Middlesbrough.

Abstract *Variation in several shell features of five populations of* Clausilia bidentata *(Ström 1765) in north-east Yorkshire (VC 62), England, was recorded over a three year period. Mean shell height was found to differ significantly and consistently over the three years between population samples. Moreover, mean shell height rose in all five populations between the first and second year and then fell slightly in the third year, a pattern that may result from variation in weather conditions at a regional level. Shell height was found to vary proportionately more than shell breadth, thus taller shells were on average proportionately narrower and not simply bigger versions of the same conispiral. Greater shell height appears to be a result of both the development of additional whorls and increased pitch during growth. Overall, 4.79% (24/502) of shells had the parietal area of the lip attached to the adjacent whorl. The frequency of this minor variant showed neither any association with other factors investigated nor any consistent pattern in occurrence. The number of extralamellar denticles varied from none to (rarely) three and fluctuated between population samples and between years for each population with no evident pattern.*

Key words Clausilia bidentata, *shell*, *variation*, *England*

INTRODUCTION

During warmer months in Britain, the pulmonate snail *Clausilia bidentata* (Ström,1765) sometimes can be found in considerable numbers, for example crawling or at rest on the trunks of broadleaved trees, notably Beech (*Fagus sylvatica*) and Ash (*Fraxinus excelsior)*. It is a species that exhibits a good deal of variation in shell characteristics. Kerney & Cameron (1979) describe it thus: "9–12×2.3–2.7mm [height×breadth]… Columellar lamella weak, sometimes bifurcating feebly onto the lip; occasionally 1–2 rudimentary interlamellar folds (usually none)…finely and regularly ribbed (about 11 ribs per mm on penultimate whorl) with a delicate spiral striation visible under high magnification." An accompanying line drawing depicts a shell with about eleven whorls. Earlier, Ellis (1969; additional note, page 278) described it as 9.5 to 13mm in height and 2.5 to nearly 3.0mm in breadth. Casual observation reveals that adult *C. bidentata* can vary a good deal in height, in the number of whorls, the number of interlamellar folds, coarseness of transverse ribbing and extent of spiral striation. In addition, the shell lip in the parietal region is usually free from the whorl behind but is occasionally fused to it.

Boycott (1919) found that populations of *C. bidentata* from similar habitats in the same neighbourhood in north Wales generally differed in size; these were from stone walls about half a mile (one km) apart. In a subsequent study Boycott (1920) compared shell size of populations of *C. bidentata* from different areas within a Beech wood in Wiltshire, England. Shells from groups of trees within a few meters of one another did not usually differ significantly in mean height or breadth but shells from areas 50–300 yards apart (about 45–275m) sometimes did so. In addition, there was some evidence to suggest that size variation was a result of environmental differences between sites, samples from more sheltered areas being of larger mean size.

The present study arose from this background, the aim being to investigate variation within and between a series of populations of *C. bidentata* in north-east England, selected to be far enough apart to be genetically isolated but close enough together to be subject to similar regional variations in weather patterns. Thus for shell size in particular it was hoped that comparison over a number of years might indicate what factors influence variation. Also, the nature of size variation itself was to be investigated: are larger shells simply bigger versions of smaller ones i.e. proportionately greater in both height and breadth and with the same number of whorls? Or is size variation more complex: are larger shells proportionately taller relative to breadth and, if so, does the animal achieve this through the growth of

Contact author : tonyandmoirawardhaugh@btinternet.com

more shell whorls or by increased pitch during shell growth (i.e. taller but with the same number of whorls)?

Methods

Five sites were selected for study, all located in north-east Yorkshire (vice-county 62), England (Fig. 1, Table 1). Four sites were woodlands where snails were collected from tree trunks, few snails with fully formed shells being present in leaf litter at this season. The fifth site (Cattersty Dunes) was selected as a deliberate contrast; here snails were quite readily found at ground level. Samples of live snails with fully formed shells were collected from each locality once per year for three consecutive years (2012 to 2014), very largely during the months August to October, as opportunity permitted. From these samples the following data were recorded for all specimens.

- Shell height and breadth (as indicated by Kerney & Cameron, 1979).
- Number of whorls, counted as the number visible with the shell mouth facing the observer.
- Number of transverse ribs per mm, counted as the number within one mm on the last whorl immediately above the shell mouth.
- The attachment, or not, of the parietal region of the lip to the whorl behind it.
- The number of extralamellar denticles (= folds).

Observations were made using a GX stereomicroscope (XTL3T101) fitted with a reticule eyepiece for making measurements. A sample of repeat measurements showed this to be accurate to at least ±0.05mm.

Snails were returned to the general localities where collected but not to the exact sites, this being done in order to prevent any possibility of the same individual being collected again in a subsequent year.

Figure 1 The localities from which *Clausilia bidentata* were collected. **A** Airy Holme Wood. **C** Cattersty dunes. **O** Oakrigg Wood. **R** Rievaulx Terrace. **Y** Yearby Wood.

Results

Shell height In total 502 shells were measured during the study (Table 2). For any one year, in many instances, the difference in mean height between any two sites is statistically significant (Table 3). Interestingly there is a pattern which remained consistent over the three years in that

Table 1 The localities from which Clausilia bidentata were collected.

Site Name	Grid Reference (Latitude & Longitude)	Habitat
Oakrigg Wood	NZ783167 (54.539, -0.792)	Ancient semi- natural woodland. From beech and ash trunks
Airy Holme Wood	NZ579113 (54.493, -1.107)	Ancient semi-natural woodland. From ash trunks and fallen branches
Yearby Wood	NZ602206 (54.576, -1.069)	Deciduous woodland edge. From ash and sycamore trunks.
Cattersty dunes	NZ709205 (54.574, -0.904)	Coastal sand dunes. From grass, horsetail and willow litter.
Rievaulx Terrace	SE579848 (54.255, -1.112)	Broadleaf plantation adjacent to ancient semi-natural woodland. Mostly from beech trunks.

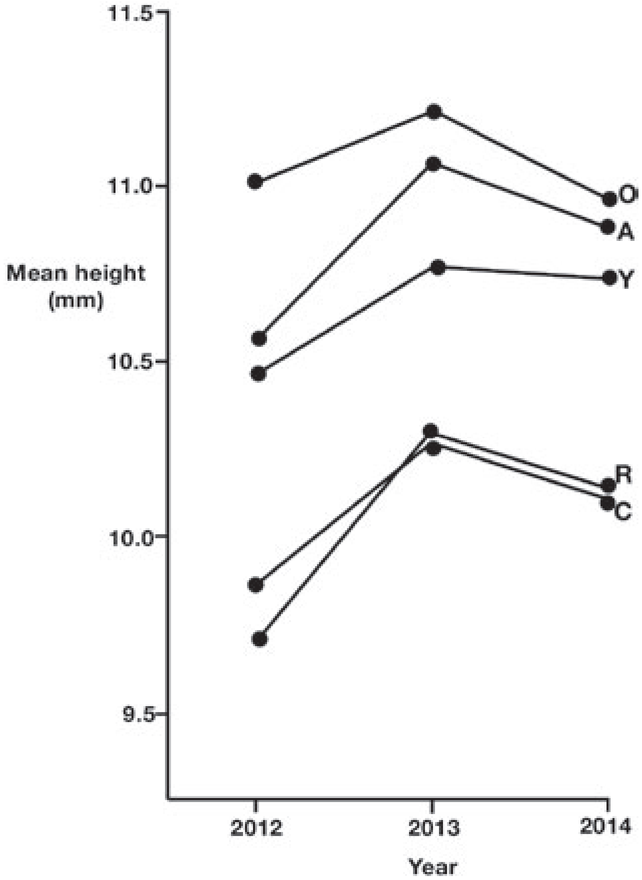

Figure 2 *Clausilia bidentata*: mean heights of shells 2012 to 2014. **A** Airy Holme Wood. **C** Cattersty dunes. **O** Oakrigg Wood. **R** Rievaulx Terrace. **Y** Yearby Wood.

shells from Oakrigg Wood were always greatest in mean height followed by those from Airy Holme Wood (although the difference was statistically significant only in 2012). Those from Rievaulx Terrace and Cattersty dunes were shortest, closely similar and in no year statistically significantly different from one another but always statistically significantly different from the other three sites in all three years. *C. bidentata* from Yearby Wood occupy an intermediate position with respect to mean shell height.

A further pattern (Fig. 2) is a consistent increase in mean height in all five populations between 2012 and 2013. This was statistically significant (unpaired two-tailed t tests) for Airy Holme Wood ($P < 0.01$), Cattersty Dunes ($P < 0.05$) and Rievaulx Terrace ($P < 0.001$). Between 2013 and 2014 there was a decrease in mean shell height in all five population samples (Table 2, Fig. 2) but in no case was this statistically significant. Nonetheless the extent to which changes over the three years were synchronous is striking.

Shell breadth There was little variation in mean shell breadth between population samples in any one year (Table 4). In addition there was no consistent pattern of broadest to narrowest between populations during the three years as was the case for mean shell height. However there was a slight increase in mean shell breadth between 2012 and 2013 for all populations except Cattersty dunes and a slight decrease for all between 2013 and 2014. On an individual basis none of these year to year differences is statistically significant but the overall pattern of increase then decrease follows that for mean shell height (Table 2).

Height and breadth variation compared Considering the data set as a whole (all localities all years) mean shell height varied more that mean shell breadth. Height range of the 502 shells measured was 8.6 to 12.8mm (hence the tallest was 48.8% taller than the shortest) whilst breadth range was 2.3 to 2.8mm (broadest 21.7% broader than the narrowest). Further, for each of the 15 samples, comparison of the mean/standard deviation for

Table 2 *Clausilia bidentata*: mean height of shells /mm ±S.D. [range] (sample size)

Year	Oakrigg Wood	Airy Holme Wood	Yearby Wood	Cattersty Dunes	Rievaulx Terrace
2012	**11.01**±0.624 [10.2–12.0] (13)	**10.56**±0.593 [9.6–11.8] (31)	**10.47**±0.588 [9.1–11.4] (30)	**9.89**±0.522 [9.1–10.7] (21)	**9.70**±0.608 [8.6–10.9] (25)
2013	**11.22**±0.744 [9.7–12.5] (17)	**11.07**±0.601 [10.0–12.5] (29)	**10.78**±0.693 [9.4–12.3] (35)	**10.27**±0.593 [9.3–12.3] (36)	**10.28**±0.513 [9.2–11.4] (29)
2014	**10.96**±0.572 [10.0–12.7] (59)	**10.90**±0.629 [9.6–12.8] (49)	**10.74**±0.488 [9.9–11.9] (50)	**10.11**±0.590 [8.8–11.5] (44)	**10.14**±0.644 [8.7–11.7] (34)

Table 3 *Clausilia bidentata*: Height comparisons between populations.
Values of P for unpaired two-tailed t tests. n.s.=not significant.
(Data normally distributed i.e. variances not significantly different [by f test] other than those marked * for which P adjusted accordingly).

		Rievaulx	Cattersty	Yearby	Airy Holme
2012	**Oakrigg**	< 0.0001	< 0.0001	< 0.01	< 0.05
	Airy Holme	< 0.0001	< 0.0001	n.s.	
	Yearby	< 0.0001	< 0.001		
	Cattersty	n.s.			
2013	**Oakrigg**	< 0.0001*	< 0.0001	< 0.05	n.s
	Airy Holme	< 0.0001	< 0.0001	n.s.	
	Yearby	< 0.01	< 0.01		
	Cattersty	n.s.			
2014	**Oakrigg**	< 0.0001	< 0.0001	< 0.05	n.s.
	Airy Holme	< 0.0001	< 0.0001	n.s.	
	Yearby	< 0.0001*	< 0.0001		
	Cattersty	n.s.			

Table 4 *Clausilia bidentata*: mean breadth of shells /mm ±S.D. [range]

Year	Oakrigg Wood	Airy Holme Wood	Yearby Wood	Cattersty Dunes	Rievaulx
2012	**2.58**±0.099 [2.4–2.7]	**2.57**±0.114 [2.3–2.8]	**2.54**±0.067 [2.4–2.7]	**2.58**±0.133 [2.3–2.7]	**2.48**±0.118 [2.3–2.7]
2013	**2.62**±0.081 [2.5–2.8]	**2.62**±0.099 [2.5–2.8]	**2.57**±0.076 [2.4–2.7]	**2.56**±0.113 [2.3–2.8]	**2.60**±0.118 [2.3–2.8]
2014	**2.55**±0.088 [2.4–2.8]	**2.58**±0.091 [2.4–2.8]	**2.54**±0.088 [2.3–2.7]	**2.52**±0.070 [2.4–2.7]	**2.54**±0.112 [2.3–2.7]

Table 5 *Clausilia bidentata*: height/breadth of shells ±S.D. [range]

Year	Oakrigg Wood	Airy Holme Wood	Yearby Wood	Cattersty Dunes	Rievaulx Terrace
2012	**4.26**±0.231 [3.81–4.48]	**4.12**±0.201 [3.73–4.46]	**4.12**±0.215 [3.64–4.48]	**3.87**±0.194 [3.41–4.26]	**3.91**±0.316 [3.38–4.60]
2013	**4.29**±0.294 [3.73–4.81]	**4.22**±0.217 [3.78–4.60]	**4.21**±0.250 [3.76–4.92]	**4.02**±0.212 [3.65–4.73]	**3.96**±0.262 [3.50–4.43]
2014	**4.30**±0.244 [3.89–4.92]	**4.23**±0.208 [3.78–4.92]	**4.23**±0.230 [3.85–4.72]	**4.01**±0.231 [3.54–4.48]	**4.00**±0.233 [3.54–4.52]

height and for breadth reveals a good deal more variation in the former. To take two data sets as examples, in 2014 for Oakrigg Wood the figures are 19.16 for height and 28.98 for breadth. For Cattersty dunes for the same year they are 17.14 and 36.0 respectively. It follows inevitably from this that samples of shells of greater mean height (e.g. those from Oakrigg Wood) are of proportionately greater height relative to breadth. This pattern holds true across the whole data set when mean height/breadth is compared (Table 5. Compare with Table 2). This pattern became evident after the first year of the study and therefore it was decided that in subsequent years the number of whorls would be counted in order to assess whether taller shells were composed of more whorls.

Number of whorls Counted as described earlier, number of whorls varied from nine to twelve (Table 6). Samples of shells of greater mean height (Oakrigg Wood and Airy Holme Wood) have proportionately more shells with eleven whorls (and hardly any shells with nine whorls) compared with samples of shells from Cattersty dunes and Rievaulx Terrace (lesser mean height, proportionately fewer eleven whorled and more nine whorled shells). Shell samples from Yearby Wood were again intermediate in this respect. The overall pattern was the same in both 2013 and 2014. Fig. 3 serves to demonstrate this, where the percentage of each sample with eleven whorls is plotted against mean height of the sample from that locality.

This indicates quite simply that snails with shells of greater height achieve this, at least in part, as a result of developing more whorls. Nonetheless this does not preclude the possibility that increased pitch may also contribute to greater shell height. However, further analysis becomes

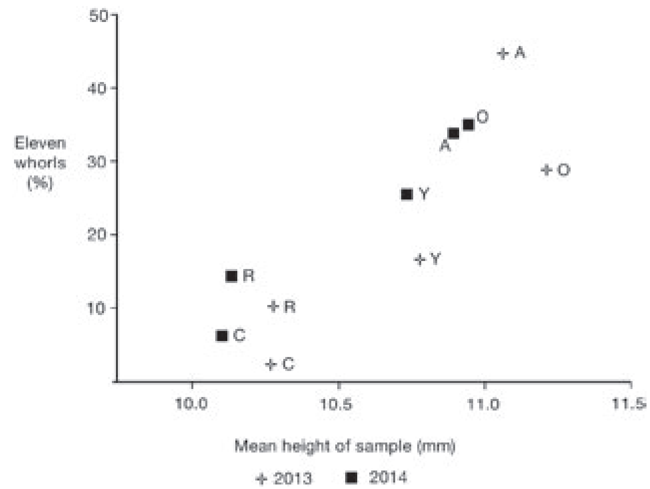

Figure 3 *Clausilia bidentata*: percentage of samples with eleven whorls. **A** Airy Holme Wood. **C** Cattersty dunes. **O** Oakrigg Wood. **R** Rievaulx Terrace. **Y** Yearby Wood.

complex for a number of reasons. Firstly, a large homogenous data set would be needed but combining the present 15 data sets on mean shell height and whorl number would not be reliable owing to statistically significant variation in the former between population samples and between years for any particular locality. Secondly, shells approximate to conispirals and not to simple

Table 6 *Clausilia bidentata*: mean height for each whorl-number class of shells /mm ±S.D. (sample size)

Year	Site	Whorl Number			
		9	10	11	12
2013	**Oakrigg**	**9.70** (1)	**10.96**±0.66 (11)	**12.08**±0.369 (5)	
	Airy Holme		**10.72**±0.368 (16)	**11.50**±0.555 (13)	
	Yearby	**9.47**±0.504 (3)	**10.65**±0.449 (26)	**11.87**±0.314 (6)	
	Cattersty	**9.77**±0.364 (13)	**10.47**±0.342 (22)	**12.30** (1)	
	Rievaulx		**10.19**±0.454 (26)	**11.07**±0.230 (3)	
2014	**Oakrigg**		**10.66**±0.358 (38)	**11.50**±0.486 (21)	
	Airy Holme	**10.00** (1)	**10.62**±0.449 (30)	**11.34**±0.441 (17)	**12.80** (1)
	Yearby	**10.10** (1)	**10.57**±0.384 (36)	**11.25**±0.361 (13)	
	Cattersty	**9.47**±0.329 (14)	**10.34**±0.348 (27)	**11.07**±0.513 (3)	
	Rievaulx	**9.37**±0.426 (6)	**10.13**±0.388 (23)	**11.16**±0.409 (5)	

helices so any increase in whorl number relative to length would be non-linear. Thirdly, this conispiral does not necessarily develop at a constant pitch during its growth i.e. it may depart from a strictly logarithmic conispiral. See e.g. Vermeij (1993) for further detail on shell geometry. Nonetheless some further analysis of the present data is possible without any amalgamation. Table 6 shows the mean heights for each whorl number. There are two patterns consistent across the two years. Firstly, as indicated above, greater whorl number is associated with greater mean height. Secondly, for a particular whorl number, shells vary in mean height between samples. Due to differences in whorl number across all samples there is enough data to analyze this pattern only for those shells with ten whorls. There is a statistically significant difference in mean height of ten-whorled shells between the two extreme samples, Oakrigg Wood and Rievaulx Terrace, in both 2013 and 2014 (unpaired two-tailed t test, $t=4.88$ and 5.45 respectively, $P < 0.0001$in both instances). This indicates that greater shell height is in part a result of greater pitch in the development of the shell as a conispiral. Hence the data show that both increased whorl number and increased pitch contribute to greater shell height.

Transverse ribs The number of transverse ribs per mm was recorded in 2012 only (Table 7). There is no evident pattern in the data nor any apparent correlation with any other feature investigated (e.g. ribs do not appear to be more tightly packed in shorter shells). For the data set as a whole (n=119) number of ribs varied from 9 to 18 per mm. The difference between the two samples exhibiting extremes (Yearby Wood 11.43 per mm and Rievaulx Terrace 12.72 per mm) is statistically significant (unpaired two-tailed t test, variances unequal, $t=2.90$, $P < 0.01$).

Lip attachment Frequency of the attachment of the parietal area of the lip to the adjacent whorl (Table 8) showed no obvious pattern nor any correlation with any other feature investigated e.g. shells with an attached lip do not appear to be shorter than those with an unattached lip. Overall, 24/502 (4.79%) had an attached lip. In shells with an unattached lip the subjective impression was that variation in the size of the space between the lip and adjacent whorl was continuous.

Extralamellar denticles The number of extralamellar denticles often showed considerable fluctuation between samples for any one year and between years for any one locality (Table 9). The presence of two extralamellar denticles was not uncommon: 8.1% n=382.

Discusssion

For shell height, breadth, number of ribs per mm and number of extralamellar denticles, data from the present study concur closely with information provided by Kerney & Cameron (1979); see introduction. These authors state that the number of ribs per mm is about eleven. In the

Table 7 *Clausilia bidentata*: number of transverse ribs per mm ±S.D. [range]

Oakrigg Wood	Airy Holme Wood	Yearby Wood	Cattersty dunes	Rievaulx Terrace
12.69±2.213 [10–18]	**11.68**±1.514 [9–15]	**11.43**±1.906 [9–17]	**12.00**±1.521 [9–15]	**12.72**±1.370 [10–16]

Table 8 *Clausilia bidentata*: number of individuals with the parietal area of the shell lip attached to the adjacent whorl (%).

Year	Oakrigg Wood	Airy Holme Wood	Yearby Wood	Cattersty Dunes	Rievaulx Terrace
2012	1/13 (8)	4/31 (13)	1/30 (3)	0/21 (0)	1/25 (4)
2013	2/17 (12)	1/29 (3)	6/35 (17)	2/36 (6)	2/29 (7)
2014	2/59 (3)	0/49 (0)	1/50 (2)	1/45 (2)	0/34 (0)

Table 9 Number of interlamellar denticles.

		Number of denticles				
Year	**Site**	**0**	**1**	**2**	**3**	**Total**
2013	**Oakrigg**	5	11	1	0	17
	Airy Holme	24	5	0	0	29
	Yearby	20	11	4	0	35
	Cattersty	28	5	3	0	36
	Rievaulx	17	10	1	1	29
2014	**Oakrigg**	37	16	6	0	59
	Airy Holme	39	9	1	0	49
	Yearby	19	20	11	0	50
	Cattersty	27	13	4	0	44
	Rievaulx	28	6	0	0	34
Total		244	106	31	1	382
(%)		(63.9)	(27.7)	(8.1)	(0.3)	

current investigation this feature was found to be quite variable ranging from nine to eighteen per mm. Number of whorls varied from nine to eleven with just one shell having twelve; Kerney & Cameron (1979) do not provide figures for this feature nor does Ellis (1969) for what would definitely be British material. Neither of these sources comment on the occasional attachment of the shell lip to the adjacent whorl but some older texts state that it is free (Gray 1857, Tate 1866, Rimmer 1880). The contribution of increased pitch to greater shell height in *C. bidentata* (Table 6) is of interest because, in contrast, Baur (1988) found that for *Chondrina clienta* on the island of Öland, Sweden, snails of a given size had the same whorl number.

Boycott (1919) studied populations of *C. bidentata* occurring on stone walls composed of slate at Portmadoc, north Wales and subsequently (Boycott 1920) at Tower Hill Plantation, a beech wood near Boscombe, Wiltshire, England. Some of the results are compared with those of the present study in Table 10. The most notable points of interest are the differences in the ranges of mean heights of the populations studied in each of the three regions and, in contrast, the similarity of the ranges of mean breadths. There is no overlap in the ranges of mean heights for Boycott's two studies, a point that the author did not comment upon at the time. Comparable figures for the present study are more varied and somewhat intermediate. Population samples from the walls of north Wales were, in general, the tallest and because apparently not greater in mean breadth, one would expect them to have possessed more whorls and/or whorls of greater pitch (Boycott did not provide data on whorl number).

Apart from the differences in shell height between these three regions, it should be emphasized that there were often statistically significant differences between pairs of population samples within each region (Tables 2 & 10). This raises the obvious question of the relative contributions of genes and environment to the observed differences. The investigation at Tower Hill Plantation (Boycott 1920) indicated an environmental influence. Here, Boycott also measured heights of the snail *Merdigera obscura*, a species with similar habits to *C. bidentata* in that it is often present on the trunks of deciduous trees, either at rest or actively crawling. It was found that size variation in the two species ran parallel i.e. the rank order of the five populations investigated within the wood was the same with respect to mean shell height for both species. It is hard to imagine how this correspondence could be due to other than an environmental cause. In the present study the preservation of an almost perfect correspondence in rank order of sites for mean shell height over the three year period could conceivably be due to either genetic or environmental differences but the synchronous rise and fall (Fig. 2) must have

Table 10 *Clausilia bidentata*: comparison of results with those of Boycott (1919 & 1920).

	Present study	Boycott (1919)	Boycott (1920)
Location	North-east Yorkshire	North Wales	Wiltshire
Years	2012–2014	1913–1914	1918
Habitat	Four woodland, one coastal dunes	Stone walls (slate)	Beech wood
No. of populations studied	5 (x 3 years) 15 data sets	10	5
Total sample size(all populations)	502	2,198	2,955
Height: overall range (mm)	8.6–12.8	8.3–13.7	8.0–12.5
Height: range of means for all populations (mm)	9.70–11.22	11.02–11.47	9.66–10.13
Breadth: overall range (mm)	2.3–2.8	2.2–3.1	2.2–2.9
Breadth: range of means for all populations (mm)	2.48–2.62	2.46–2.62	2.55–2.60

an underlying environmental cause operating at a regional level (see below).

At Tower Hill Plantation (Boycott 1920), population samples of greatest mean shell height came from the two areas that the author considered to be the most sheltered whilst the site deemed the most exposed yielded the second shortest population sample. With respect to the Portmadoc populations, Boycott (1919) commented "exposed, windy places *and densely shaded places* produce shorter shells, whilst moderately shaded loci [= habitats] are most favourable for largest growth" (my italics). It was suggested that this difference might be due to close shelter on the Wiltshire chalk of Tower Hill providing 'agreeably damp conditions' but the wetter climate of Portmadoc, where the strata are less porous, resulting in excessive moisture which could be detrimental. The study at Portmadoc was repeated by Boycott (1927) after an interval of ten years and the characteristic shell height at each site was found to be unchanged although breadths were somewhat less than in the earlier survey.

Shelter and exposure are complex phenomena and with respect to *C. bidentata* the relevant factor may be the duration of suitably moist conditions during which the animals have the opportunity to be active and to feed, an environmental feature in turn influenced by local ventilation conditions. With respect to the present study, the two localities yielding samples of least mean height give the subjective impression of being the most exposed: Cattersty dunes facing north-east on the North Sea coast and Rievaulx Terrace, a linear plantation which occupies an area at the top of a west facing scarp slope and thus exposed to the prevailing wind. The tallest shell samples were from the interior of two old woodlands, Oakrigg Wood occupying a steep sided valley and Airy Holme Wood in an area of complex but sheltered terrain. Yearby Wood yielded shell samples of intermediate mean height; these were collected from a narrow arm of the wood projecting from its north-east corner and possibly more exposed, in the sense described above, when compared with Oakrigg and Airy Home Woods. Determining exactly which component (or components) of 'exposure' has a direct (or indirect) effect on shell growth would be very difficult and of course the contribution of genetic differences between populations to shell size remains a possibility.

Kemp & Bertness (1984) investigated the role of the environment in shell growth in the marine gastropod *Littorina littorea.* Two groups of snails drawn from the same population in New England, USA were maintained in laboratory conditions. One had a plentiful food supply, the other did not. The former grew faster and, interestingly, developed low spired shells with a larger body whorl and larger aperture. Variation in shell height of *C. bidentata* could be due to variation in food availability or feeding opportunity as a result of exposure effects. In contrast, Baur (1988) studying the pulmonate land snail *Chondrina clienta* at 30 different sites on the island of Öland, Sweden found that shell height was not influenced by habitat type (exposed rock surface, stone pile or stone wall) or by the proportion of calcareous stones in the habitat. It was however correlated with local population density (which did vary greatly, from 5 to 794 individuals per m^2) suggesting intraspecific competition, and with extent of plant cover. Also there was a population density effect exerted by the snail *Balea perversa* on shell size of *C. clienta* presumably as a result of interspecific competition. Breeding experiments using *C. clienta* from different sites and carried out under uniform conditions caused most of the phenotypic variation to disappear, demonstrating the high phenotypic plasticity of this species. However, underlying genetic links to variation in shell morphology should not be discounted. In *Cochlicopa lubrica* two groups of homozygous genotypes are known. One group is more common in exposed habitats and has, on average, slightly smaller shells. The other, larger shelled form occurs more frequently in moist, shady habitats (Armbruster 2001). Possible factors influencing shell height in molluscs thus appear to be many.

Returning to the synchronous variation between years in mean shell height noted in the five populations of the present study (Fig. 2), this was greater in extent than anticipated at the start of the investigation. Some association between this pattern and year to year variation in climatic conditions of the region as a whole might be expected, providing life cycle and reproduction in *C. bidentata* follow a seasonal pattern. One early text states that *C. bidentata* takes 22 to 24 months to reach its adult age (Gray 1857, page 73). Here it is worth stressing that the salient feature is time to achieve full shell growth, which is not necessarily the same as reproductive maturity. Shells in the study area often show an interruption to growth at about the start of the last whorl, suggesting a pause in development during the previous winter and therefore growth over two seasons. However, frequency of partially grown snails in warmer months seems less than expected if they do take two years to become fully grown. Thus perhaps variation in some aspect of either temperature, rainfall or both at some time during the two years prior to sampling could be the underlying factor influencing shell growth. However, in the absence of detailed information on the life cycle of *C. bidentata* in the region where this study was carried out, any suspected correlation with weather patterns would at present be highly speculative. Nonetheless, Meteorological Office data for the study area was inspected and no obvious correlation with weather patterns was evident.

Acknowledgements

Fig. 1 was produced by MapMate using Digital Map Data © Bartholomew 2002. I would like to thank two anonymous referees for their helpful comments on a draft of this article. I am grateful to my wife Moira Wardhaugh for her unfailing support in the work described above, for her help with the field work and for commenting on a draft of this article.

References

Armbruster GFJ 2001 Selection and habitat-specific allozyme variation in the self-fertilizing land snail *Cochlicopa lubrica* (O.F. Muller). *Journal of Natural History* **35**: 185–199.

Baur B 1988 Microgeographical variation in shell size of the land snail *Chondrina clienta*. *Biological Journal of the Linnean Society* **35**: 247–259.

Boycott AE 1919 Observations on the local variation of *Clausilia bidentata*. *Journal of Conchology* **16**: 10–23.

Boycott AE 1920 On the size variation of *Clausilia bidentata* and *Ena obscura* within a "locality". *Journal of Molluscan Studies* **14**: 34–42.

Boycott AE 1927 Further observations on the local variation of *Clausilia bidentata. Journal of Conchology* **18**: 131–135.

Ellis AE 1969 *British Snails.* Clarendon Press, Oxford.

Gray JE 1857 *Manual of the Land and Fresh-water Shells of the British Islands.* Longman, London.

Kemp P & Bertness MD 1984 Shell shape and growth rates: Evidence for plastic shell allometry in *Littorina littorea. Proceedings of the National Academy of Sciences USA* **81**: 811–813.

Kerney MP & Cameron RAD 1979 *A Field Guide to the Land Snails of Britain and North-west Europe.* Collins, London.

Rimmer R 1880 *The Land and Freshwater Shells of the British Isles.* John Grant, Edinburgh.

Tate R 1866 *The Land and Fresh-water Molluscs of Great Britain.* Robert Hardwicke, London.

Vermeij GJ 1993 *A Natural History of Shells.* Princeton University Press, Princeton, New Jersey.