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Incidence and persistence of reversed-coiling in Quaternary land snails

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This paper reviews evidence for the incidence and persistence of reversed-coiling in different species of land snail based on studies of Quaternary sequences in Britain, Ireland and Siberia. Most sequences lack evidence for reversed-coiling but the relative proportions of dextral and sinistral specimens are presented for a few that do. Such data are reported for thirteen specimens belonging to seven species from seven sites in Britain and Ireland, mostly calcareous tufas of Holocene age. Sinistral specimens of *Acicula fusca* were recovered from three different sites but reversed-coiled specimens of other species were confined to single localities. The frequencies of reversed-coiling in most European samples are generally extremely low (zero to <1%) and relatively short-lived, although reversed-coiled specimens were recovered from adjacent stratigraphical horizons at three of the sites reported here. This situation contrasts with a Holocene floodplain sequence in Siberia, where sinistral specimens of *Cochlicopa* occurred in 12/18 samples, with a mean frequency of 9.8% (38/385) for the whole profile. Not only are the frequencies of reversed-coiling much higher than in most European sites but it appears to have persisted for much longer, indeed for much of the last 6000 ^{14}C yr BP. Reasons for this unusual situation are discussed. A plea is made for more assiduous recording of reversed-coiled specimens from Quaternary sequences.

Key words: Sinistrality, reversed-coiling, Holocene, tufa, *Acicula fusca*, *Cochlicopa*, Siberia.

INTRODUCTION

In the shells of most species of land snail the direction of coiling is clearly either dextral (right-handed) or sinistral (left-handed). Over 90% are dextral, a clear minority are sinistral (e.g. the Clausiliidae), whereas a few species are polymorphic for the direction of coiling. Many in the last category live in South-East Asia (e.g. *Amphidromus*) or on Pacific Islands (e.g. *Partula*). In general both the bilateral asymmetry of the internal anatomy, as well as coiling direction, is reversed between sinistral and dextral snails (Sutcharit et al., 2007). In the few species that have been characterized, the genetic control of both anatomical and coiling chirality is determined by the maternal genotype at a single locus, with either dextral or sinistral alleles being dominant (Asami et al., 1998; Schilthuizen & Davison, 2005). Bantock et al. (1973), however, concluded from breeding experiments that sinistrality in the helicid *Cepaea hortensis* (Müller, 1774) was probably not heritable, a conclusion also reached by Pelseneer (1920) for *Helix pomatia* L.,1758. In these species, as in many others, sinistrals are almost always found as single individuals in otherwise dextral populations.

Reversed-coiling can lead to reproductive isolation because it is associated with a shift in the position of the genital apparatus, which may inhibit successful interchiral mating. This can act as a barrier against hybridization between sympatric species (Gittenberger, 1988; Uit de Weerd et al., 2006) and has even been claimed to lead to "single gene" speciation (Ueshima & Asami, 2003), although the situation may be rather more complicated (Davison et al., 2005). Reversed-coiled individuals are extremely rare in most populations because it is assumed that strong frequency-dependent selection would act against the establishment of new chiral types since the chiral minority would have difficulty finding a compatible mating partner. Mixed populations should therefore not persist since any population with both forms should become two species if successful interchiral mating does not occur (but see Davison et al., 2005) or revert to one or other chiral type if it does (Van Batenburg & Gittenberger, 1996).

Pulmonate land snails have shells that are essentially either high-spired (tall and slender) or low-spired (globular to flat), with few intermediates (e.g. Cain, 1977). Flat-shelled species mate reciprocally, face-to-face, whereas tall-shelled species mate non-reciprocally, where the 'male' copulates by mounting the shell of the 'female', mutually aligned in the same direction. The sexual asymmetry in the latter situation permits interchiral copulation with small behavioural adjustments, relaxing the intensity of frequency-dependent selection, and so potentially explaining the observation that reversed-coiling is more prevalent in slender shells than in flat ones (Asami et al., 1998).

Much of the work on reversed-coiling has been undertaken on tree snails in Asia and on Pacific Islands, where the phenomenon is far more common and where populations of some species (e.g. almost all 35 *Amphidromus s. str.* species) can be made up of equal numbers of each chiral type. This coexistence appears to be true at all spatial scales, even down to populations on individual trees (Craze et al., 2006; Sutcharit et al., 2007). In some populations of molluscs, rare sinistral specimens are selectively favoured because predators exhibiting 'handedness' in their method of attack, such as crabs (Dietl & Hendricks, 2006) or snakes (Hoso et al., 2007), are less successful in dealing with this 'unusual' prey. In the case of *Amphidromus* it has been shown that sympatric populations occurring in roughly equal proportions of sinistrals and dextrals might be maintained not by predator-mediated selection but by sexual selection favouring chiral dimorphism. In other words, mating is non-random and favours the pairing of shells of opposite coil. Anatomical investigations have shown that the chirality of the spermatophore and female reproductive tract probably allow a greater fecundity in such interchiral matings (Schilthuizen et al., 2007). Incorporating these new findings into computer models showed that chiral dimorphism is relatively easy to achieve and is stable in the long term.

This situation appears to be exceptional and populations of the same species composed of equal numbers of sinistrals and dextrals are virtually unknown elsewhere. Indeed, apart from reports of the occasional reversed-coiled specimen, virtually no information exists on the frequency of reversed-coiling amongst smaller species of European land snail. Indeed, since reversed-coiling is so rare in most natural populations it is extremely difficult to obtain data on its incidence and frequency amongst different species. A detailed search through the literature (e.g. Pelseneer, 1920) may provide a list of species that have exhibited reversed-coiling but there will inevitably be a bias towards larger and more conspicuous species and it would be hazardous to draw any general conclusions from such data.

Quaternary malacologists routinely count large numbers of snails from successive stratigraphical levels through sedimentary sequences that may cover several millennia. It is not uncommon for them to analyse tens of thousands of specimens from a single profile and inevitably the occasional reversed-coiled specimen will be encountered. Such records have two advantages. First, the data are quantitative and not biased by size, since all specimens above 0.5 mm are usually counted. Second, the sampling covers timescales beyond the scope of ecologists and geneticists, who usually work only on modern populations. Using such datasets it is therefore possible to provide information, lacking in existing literature, to estimate both the incidence of reversed-coiling in each sample and its persistence throughout the entire profile.

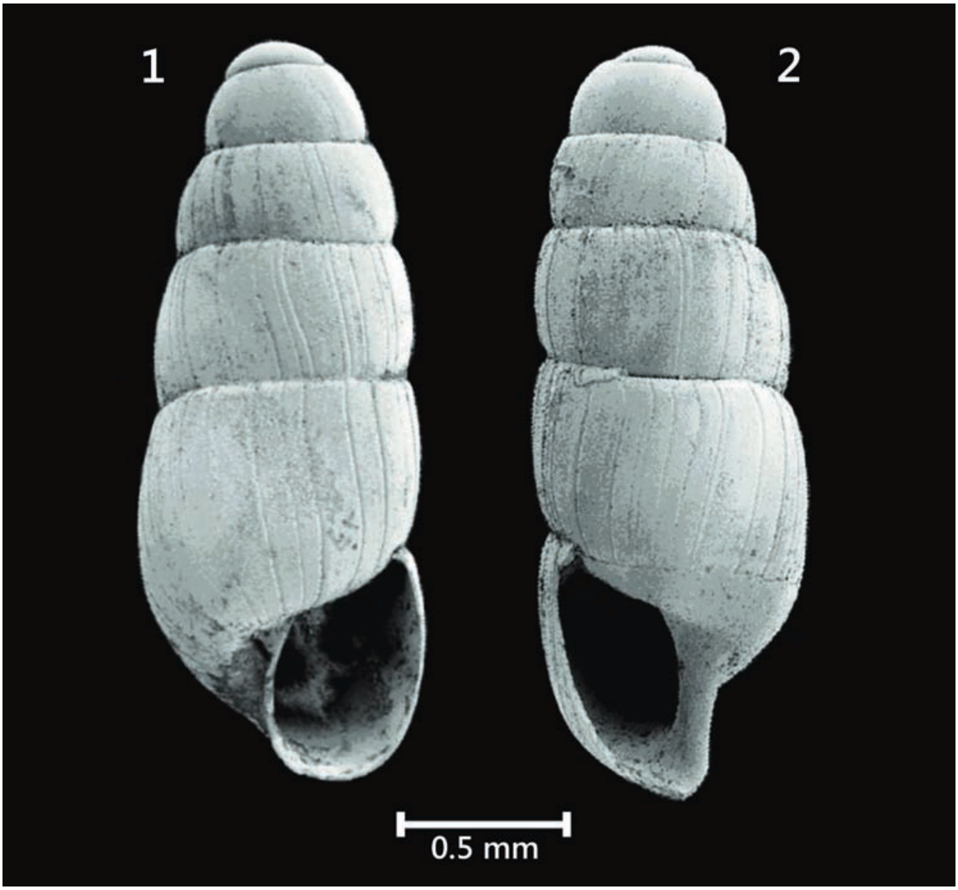
THE EUROPEAN SITUATION

In Europe, students of snail chirality have focused their attention on larger helicid taxa especially *Helix pomatia*, *Cornu aspersum* (Müller, 1774), *Arianta arbustorum* (L., 1758) or *Cepaea* spp. Mating difficulties have been observed in reversed-coiled specimens that attempt to mate with individuals of the opposite coil. There are many records of isolated specimens of reversed-coiling in the literature but few give any estimates of their relative frequency (cf. Gould et al., 1986). Rarer still are the instances of populations of sinistral shells of normally dextral species. Morrell (1979) reported a colony of sinistral *Cepaea nemoralis* (L., 1758) from waste ground in Nottingham in the English Midlands, where on one sampling occasion in September 1976, 13/20 living *Cepaea* were found to be sinistral. Taylor (1911: 322) also mentioned “a local race of reversed shells” of this species from sand dunes at Bundoran in Donegal, Ireland, which yielded “nearly 2,000 specimens, mostly Holocene fossils”. Examples of sinistral *C. nemoralis* from this locality are well represented in museum collections. No estimates are given of the proportion of sinistral specimens in this population but dextral shells were obviously far more common and were even used by the locals to make necklaces sold to tourists and visitors (Taylor, 1910: fig. 338). Moreover, although Kennard & Woodward (1917: 127) record *C. nemoralis* as “common” in the dune deposits at Bundoran, they do not mention the occurrence of sinistral specimens, suggesting that they were not as frequent as Taylor implies (see also Boycott & Diver, 1925; Clarke et al., 1968).

Quantitative data regarding reversed-coiling in smaller species of land snail are extremely sparse and most Quaternary sequences do not yield any examples. Table 1 lists every reversed-coiled specimen encountered by the first author in his analyses of Quaternary sediments over the last 35 years, together with other examples from the literature. It only includes examples where the relative proportions of reversed-coiled specimens can be given. Most of the samples are Holocene in age, although one Late-glacial site (Dover Hill, Folkestone) is also included. Doubtless many other examples have been overlooked but because these records are often mentioned only incidentally, listed as footnotes or included in appendixes to archaeological reports, this is not surprising. Many examples may not even have been recorded at all, since the primary focus of much of this work is palaeoenvironmental analysis. Indeed, several colleagues have also encountered reversed-coiled specimens in their analyses but frustratingly have failed to record the details.

The provenance of 13 reversed-coiled specimens from seven species is listed in table 1. Of these, three species possess slender shells and four have flat ones, although there are five independent instances of reversed-coiling in slender shells compared with four amongst the flat-shelled taxa. It is noteworthy that six of the 13 records relate to *Acicula fusca* (Montagu, 1803), the only prosobranch represented, found as sinistral shells at three different sites; figs 1-2 illustrate specimens from Graffy, County Mayo. Kennard &

Species	Shell shape	Site (Grid reference)	Sample, Depth (cm)	Number of reversed-coiled specimens in the sample/total for that species	Number of reversed-coiled specimens in the profile/total for that species (%)	Approximate age (^{14}C years BP)	Reference
Acicula fusca (Montagu, 1803)	Slender	Holywell Coombe, Folkestone, Kent (TR220379)	Trench 3, 175-184	1/15	1/37 (2.7)	7650 ± 80	Preece, 1998
Acicula fusca (Montagu, 1803)	Slender	Graffy, Co Mayo, Ireland (G343046)	A2, 200-210 A2, 240-250	1/20 1/9	2/270 (0.74)	3500-3000	Speller, 2006
Acicula fusca (Montagu, 1803)	Slender	Crabble Mill, Dover, Kent. (TR29954311)	65-70 90-95	1/28 2/276	3/597 (0.5)	7100-4000	Bates et al. 2008
Lauria cylindracea (da Costa, 1778)	Slender	Totland Bay, Isle of Wight (SZ32128671)	90-95	1/10	1/76 (1.3)	7000	Preece, 1979
Discus rotundatus (O.F. Müller, 1774)	Flat	Crabble Mill, Dover, Kent (TR29954311)	70-75	1/188	1/849 (0.1)	7100-4000	Bates et al. 2008
Nesovitrea hammonis (Ström, 1765)	Flat	Broughton-Brigg, Lincolnshire (SE977086)	Bulk sample	1/1127	1/1127 (0.08)	9000-6000	Kennard & Musham, 1937
Aegopinella nitidula (Draparnaud, 1805)	Flat	Holywell Coombe, Folkestone, Kent (TR220379)	Trench HV, 120-125	1/49	1/819 (0.12)	7000	Preece, 1998
Clausilia bidentata (Ström, 1765)	Slender	Waddingham, Lincolnshire (SK963951)	40-45	1/4	1/24 (4.1)	8500	Preece & Robinson, 1984
Trochulus hispida (Linnaeus, 1758)	Flat	Dover Hill, Folkestone, Kent (TR235376)	105-115 120-130	1/113 1/63	2/1694 (0.1)	11,000-10,000	Kerney, 1963



Figs **1-2**. SEM photographs of *Acicula fusca* from a Holocene tufa (Profile A2, 200-210 cm) at Graffy, County Mayo, Ireland. **1**, dextral specimen; **2**, sinistral specimen.

Musham (1937: 376) mention another sinistral example of this species (as *Acme lineata*) from a Holocene tufa at Broughton-Brigg in Lincolnshire, near the site that yielded the sinistral *Nesovitrea hammonis* (Ström, 1765), but no quantitative information is given. There are other instances of sinistral *Acicula fusca* in the literature. Jeffreys (1862: 308) described an immature specimen from flood debris of the River Avon near Bristol as *Acme lineata* var. *sinistrorsa*, which was subsequently illustrated by Boeters et al. (1989: fig. 45). Brown (1852) also listed sinistral '*Acme fusca*' from "upper Tertiary beds" (now known to be a Holocene tufa- see Kerney et al., 1980: 35-36) at Copford, Essex, a record also mentioned by Jeffreys (1862: 309). Reversed-coiled specimens of other species listed in table 1 were confined to single localities.

The incidence of reversed-coiling in these populations is generally extremely low, at least when the percentages are calculated for the whole profile. Most populations of

◀ Table **1**. Incidence of reversed-coiled specimens of land snails from Late-glacial and Holocene deposits in Britain and Ireland. With the exception of Dover Hill, Folkestone, the sediment at all the sites was calcareous tufa.

reversed-coiled shells listed in table 1 seldom reach frequencies higher than about 1%; the exceptions are all samples with less than 80 shells. The calculated percentages of reversed-coiled specimens will also be governed, to some extent, by the number of samples analysed, which is usually determined by the thickness or complexity of the sedimentary sequence. Looking at the three samples in table 1 giving anomalously high percentages: the sinistral *Lauria cylindracea* (da Costa, 1778) came from one of 12 samples taken through a 65 cm thick tufa; the dextral *Clausilia bidentata* (Ström, 1765) came from one of 15 bore-hole samples (sample weights only 50-150 g) through a 75 cm thick tufa; and the sinistral *Acicula fusca* from Holywell Coombe came from one of only eight samples in this profile that could potentially have yielded this species. It is important to stress that these particular values should not be taken as typical. More realistic values can be provided for the frequency of sinistrality in both *A. fusca* and *Aegopinella nitidula* (Draparnaud, 1805) at Holywell Coombe because several different profiles have been analysed through the Holocene tufa deposits within this dry valley (Kerney et al., 1980; Preece, 1998). *Acicula fusca* occurred in four profiles analysed by Preece (1998), as well as in the original sequence (Pit 1) analysed by Kerney et al. (1980). Only one sinistral *Acicula* was detected amongst 227 specimens of this species, a frequency of 0.4%. *Aegopinella nitidula,* which in Britain has a much longer history than *Acicula* during the Holocene, occurred in seven different profiles (Kerney et al., 1980; Preece, 1998). Of the 6814 specimens of this species analysed from these profiles, again only a single sinistral specimen was recorded, this time representing a frequency of 0.01%.

Two of the sites listed on table 1 have reversed-coiled populations of more than one species, although the sinistral *Acicula fusca* and *Aegopinella nitidula* from Holywell Coombe came from different profiles less than 200 m apart (Preece, 1998). These were the only two examples of reversed-coiling amongst the ~94,500 shells analysed from 10 profiles from this site. It should be noted that the numbers given in table 1 relate to totals for that species in that profile and not to a composite total amalgamating the data from neighbouring profiles (see above).

At three of the sites listed in table 1, sinistral specimens of the same species were recovered from more than one stratigraphical horizon. The horizons yielding the sinistral specimens have not been individually dated so it is not possible to be precise about the exact duration of the episode of reversed-coiling. However, radiocarbon dates are available from each of these three sequences that together with other information, allow the construction of general age models. The sediments at Graffy and Crabble Mill, Dover, were both calcareous tufa, deposited in the vicinity of springs. In the case of Crabble Mill, the sinistral *Acicula* probably occurred a few centuries after 7000 ^{14}C yr BP (Bates et al., 2008), whereas those at Graffy were younger, occurring between 3500 and 3000 ^{14}C yr BP (Speller, 2006). The sediments at Dover Hill, Folkestone, containing the sinistral *Trochulus hispida* (L., 1758) were colluvial slopewash, which accumulated during the Younger Dryas between 11,000 and 10,000 ^{14}C yr BP (Kerney, 1963; Preece, 1994). At all of these sites the sinistral shells occurred in adjacent (sometimes successive) samples, so the episode of reversed-coiling can probably be constrained to a relatively narrow time interval, perhaps a few decades or centuries, between the dates given.

A SIBERIAN EXCEPTION

A very different picture is emerging from a site that we are investigating in the Baikal region of south-central Siberia. The site is located near the cliff sections of Krasniy Yar (N 55^{o} 42′ 32″, E 107^{o} 48′ 26″) in the Kirenga Valley (Lena River tributary), about 100 km to

Depth (cm)	Number of dextral shells	Number of sinistral shells	% sinistral	^{14}C yr BP	Lab Ref. Number
0-5	33	0	0		
5-15	13	0	0	355 ± 30	Poz-25691
15-25	43	2	4.4		
25-40	17	3	15		
40-50	35	4	10.2		
50-60	35	5	12.5	1185 ± 30	Poz-25692
60-70	39	13	25		
70-80	5	1	16.7	1915 ± 30	Poz-25693
80-90	4	1	20		
90-100	8	0	0		
100-110	11	0	0	1720 ± 30	Poz-25694
110-120	0	0	0		
120-130	23	2	8		
130-135	11	2	15.4	4580 ± 35	Poz-25695
135-145	29	2	6.4		
145-155	25	1	3.8		
155-165	11	2	15.3	6100 ± 40	Poz-25696
165-175	5	0	0		
TOTAL	**347**	**38**	**9.8**		

Table **2**. Incidence of sinistrality in shells of *Cochlicopa* from Holocene floodplain sediments at Krasniy Yar in the Kirenga Valley, Siberia, together with details of the AMS radiocarbon dates obtained on charcoal. The dates were measured at the Poznañ Radiocarbon Laboratory, Poland.

the west of the northern tip of Lake Baikal. The floodplain sediments here are 175 cm thick and appear to span much of the middle and late Holocene (last ~6000 ^{14}C yr BP) (table 2). Several weakly developed buried soils occur within the sequence just below the ground surface and at 50-60 cm, 70-85 cm and 130-135 cm. Units of unfossiliferous gravel occur at 110-120 cm and below 175 cm (fig. 3). Apart from the lowermost samples, which yielded a predominantly aquatic fauna, land snail assemblages dominate this floodplain succession (fig. 3B). Eighteen 2 litre bulk sediment samples were taken through this sequence, 12 of which yielded sinistral specimens of *Cochlicopa* (table 2).

There is some uncertainty regarding the species involved but they appear to be a small form of *lubrica* (Müller, 1774) or *lubricella* (Rossmässler, 1834), which are both recorded from the Baikal region. Starobogatov (1996) listed a number of other species from Siberia but several of these are of dubious validity since shell characters are not always reliable in this genus (Armbruster, 1997). In his extensive review of *Cochlicopa* from Eurasia, Starobogatov (1996) does not describe any sinistral taxa as distinct and the dextral and sinistral shells from the Kirenga Valley superficially appear to be mirror images of one species (figs 4-7). However, in a detailed morphometric analysis of *Cerion*, Gould et al. (1986) showed that there were subtle interchiral differences in size and coiling late in growth, leading sinistrals to have relatively small apertures and a slight twist in the axis of coiling. It is not possible to provide detailed comparative measurements of the two chiral morphs of *Cochlicopa* at the Kirenga site because only two complete sinistral adults were recovered (figs 6-7); most of the other sinistral (and dextral) specimens were repre-

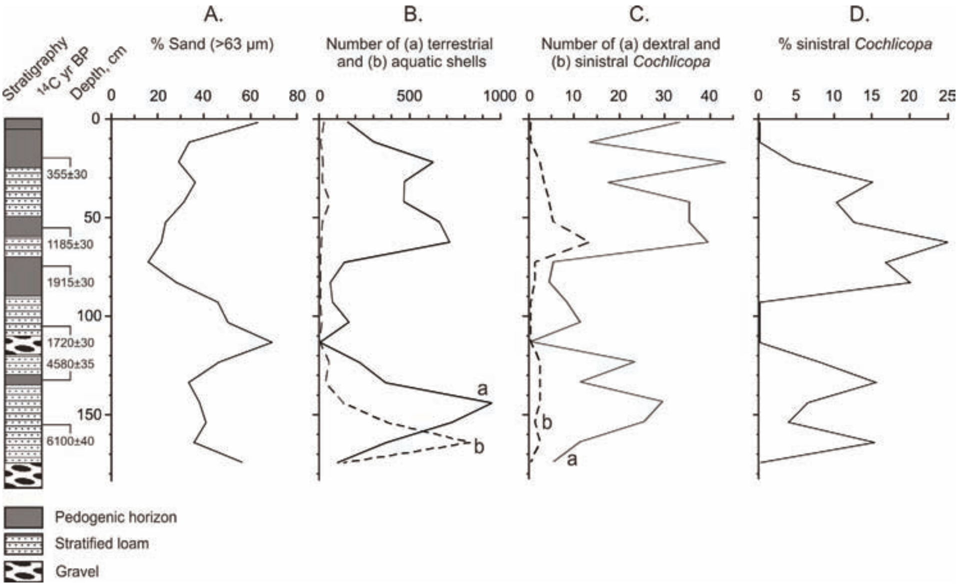


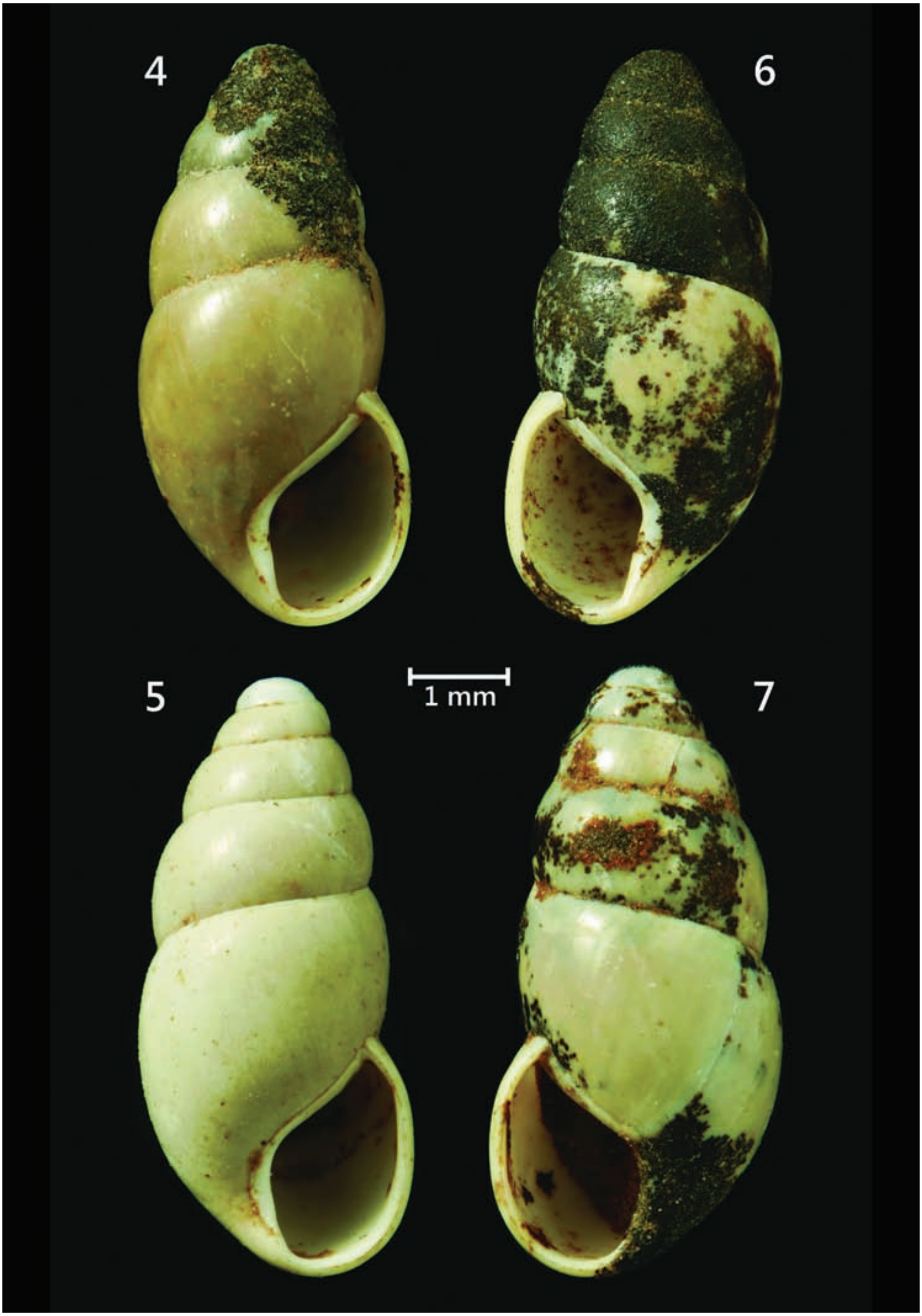
Fig. **3**. The stratigraphical sequence at Krasniy Yar, Kirenga Valley, Siberia, showing: **A**. % sand; **B**. number of (a) terrestrial and (b) aquatic molluscs; **C**. number of (a) dextral and (b) sinistral *Cochlicopa*; **D**. % of sinistral *Cochlicopa*/total *Cochlicopa.* The radiocarbon dates (^{14}C yr BP) suggest the existence of a hiatus coinciding with the emplacement of the gravel between 110-120 cm.

sented by juveniles or by broken fragments of adults.

The Kirenga Valley data therefore differ in two important respects from the NW European records just discussed. First, the incidence of reversed-coiling is far higher. In eight (of the 12) samples the frequency of sinistral *Cochlicopa* exceeded 10% of the population, whereas in one a maximum value of 25% (13/52 shells) was attained (table 2 and fig. 3D). Taking the *Cochlicopa* profile as a whole, sinistral individuals occurred with a mean frequency of 9.8% (38/385). Second, there is evidence here for long-term persistence of a reversed-coiled population, not merely on multi-decadal to centennial timescales but maintained over several millennia (table 2; fig. 3).

The record of sinistral *Cochlicopa* (fig. 3C and D) appears to be bimodal, suggesting that two distinct populations containing relatively high proportions of sinistrals became established, initially at the base of the sequence (>6100 ^{14}C yr BP) and again at 80-90 cm (~1900 ^{14}C yr BP). However, the bimodality might be an artefact, especially when taphonomic processes on the floodplain are taken into consideration. Note that the least fossiliferous part of the sequence (fig. 3B) coincides with the emplacement of gravel and other coarse sediments between 90 cm and 120 cm (fig. 3A). This coarse unit probably reflects a flooding event which resulted in the erosion of part of the sequence followed by rapid deposition, thus interrupting the succession of land snails and causing temporary declines in species records. Subsequent recolonization of the river banks from adjacent sites unaffected by this local flooding appears to have occurred relatively quickly. Such distal sites are therefore likely to show greater continuity in the record of sinistral *Cochlicopa* (and other taxa), which would confirm the spurious nature of the bimodality.

The numbers of shells were relatively low in the levels immediately above the gravel and it is noteworthy that among the *Cochlicopa* only dextrals were recovered (table 2).



Figs **4-7**. *Cochlicopa* from Holocene floodplain sediments at Krasniy Yar, Kirenga Valley, Siberia. **4-5**, dextral specimens; **6-7**, sinistral specimens. The dark encrustation is manganese dioxide.

Significantly, sinistral *Cochlicopa* reappear at 80-90 cm, which coincides with a pedogenic horizon. An interpretation could be that the assemblage from 90-110 cm, which includes only dextral *Cochlicopa*, represents allochthonous elements transported from neighbouring sites upstream, whereas the level where sinistrals reappear reflects a population living at the site. This would imply either that the sinistral population was spatially restricted or the absence of sinistrals in these coarse levels results from biases associated with small sample sizes.

A striking feature of the *Cochlicopa* data is the peak of sinistral specimens at 60-70 cm, immediately above a pedogenic horizon. The frequency of sinistral *Cochlicopa* falls sharply above this level and then progressively declines until 5-15 cm, where the sediments begin to coarsen and sinistrals disappear from the record (fig. 3C and D). The behaviour of the sinistrals is not matched by that of the dextrals, which maintain relatively high, but fluctuating, values throughout the upper levels (fig. 3C). Indeed, only dextrals were present in the two uppermost samples, indicating that the local environment remained suitable for *Cochlicopa*. This suggests either that selection may have been operating against the sinistrals or that they were lost from the population as the result of genetic drift. However, it must be remembered that the sample sizes are not large, so it is possible that a population containing relatively high proportions of sinistrals may still survive nearby. Unfortunately no litter samples were taken to test this possibility.

The spatial extent of this population of sinistral *Cochlicopa* is unclear, although it appears to be relatively localised. No sinistral *Cochlicopa* were encountered among 1923 shells of this genus analysed from Basovo, another Holocene floodplain sequence about 130 km to the west in the neighbouring upper Lena Valley (White et al., 2008), or among 2116 *Cochlicopa* shells from stratified floodplain sediments near Burdukovo, about 400 km to the southeast in the Selenga Valley (White, 2006). Moreover, we did not find any sinistral *Cochlicopa* in a survey of the modern molluscan fauna of the Baikal region undertaken in 2007. However, modern sinistral specimens of *Cochlicopa*, this time involving *C. nitens* (Gallenstein, 1848), have been reported from two localities near the village of Teguldet in the Tomsk region of Western Siberia (Udaloi & Novikov, 2005), about 1400 km west of Lake Baikal. The first site, 5 km south of Teguldet, yielded only one sinistral specimen but at the second site, on the floodplain of the Chet River 26 km south of Teguldet, six of the 10 *C. nitens* specimens recovered were sinistral (Udaloi & Novikov, 2005). Further afield, Starobogatov (1996) illustrated a sinistral specimen of '*Cochlicopa repentina* Hudec, 1960' from the Moscow Region ("railway station Turist"); the specimen is now in the Zoological Institute of the Russian Academy of Sciences.

DISCUSSION AND CONCLUSIONS

The purpose of this paper is to highlight the potential value of Quaternary sequences in furnishing data on the incidence and persistence of reversed-coiling in land snails. We hope that it will stimulate others to provide comparable data from different regions and encourage everyone to keep more assiduous records when reversed-coiled shells are encountered. Despite the relatively limited scope of the present paper, several interesting points emerge. First, although reversal of the direction of coiling can potentially occur in all spiral shells, it appears to be much rarer in some species than in others. Previous studies have suggested that reversed-coiling is likely to be more frequent in slender shells than in flat ones but this is not really supported by our data (table 1). Moreover, we have never encountered sinistral specimens of either *Carychium* (slender-shelled) or *Vallonia* (flat-shelled), perhaps the most abundant genera found as fossils in the two regions discussed.

On the other hand, sinistral specimens of *Acicula fusca* were recovered from Holocene tufas at three different sites and two further records have been traced in the literature, again from Holocene tufas. *Acicula* is a prosobranch with separate sexes, so it has to mate with an individual of the opposite sex. From its incidence and the fact that sinistral shells occurred in more than one stratigraphical horizon at two of the sites, it appears that its reproductive strategy has not led to an immediate elimination of the mutation. Perhaps its slender shell allows relatively successful interchiral mating, as reported for other slender-shelled taxa.

The second point to emerge is the extreme rarity of reversed-coiling in most populations, where the frequency is usually between zero and <1%. Values higher than ~1% in table 1 are essentially statistical artefacts resulting from small sample sizes. We assume that mutations resulting in reversed-coiling are exceedingly rare for most European taxa and that in general they do not persist for more than a few centuries (cf. Bantock et al., 1973).

This is not the situation that we discovered with *Cochlicopa* in a Holocene floodplain sequence in the Kirenga Valley in Siberia. Here sinistral specimens occurred at much higher frequencies, up to 25% (13/52) in one sample, with an overall mean frequency of 9.8% (38/385) for the 18 samples taken through the entire profile. These values are therefore intermediate between the 'normal' situation in European land snails where the frequency of reversed-coiling is usually zero to <1% and the populations of some Asian tree snails, where the ratio of sinistral/dextral shells is roughly 50:50 (but see Sutcharit et al., 2007). The second unusual feature of the Kirenga site is that the reversed-coiling appears to have been maintained for much longer periods, indeed for >6000 ^{14}C yr BP.

Unlike *Acicula*, *Cochlicopa* is a hermaphroditic pulmonate that can potentially reproduce by either outbreeding or self-fertilization but it appears that self-fertilization is the more usual reproductive strategy adopted by this genus (Armbruster & Schlegel, 1994). However, a mutation resulting in sinistrality is likely to have produced a clutch of sinistral individuals, rather than just one, because of the maternal effect. Self-fertilization is therefore not necessary for successful reproduction because sibling mating could also occur. It would seem that in the Kirenga Valley, a sinistral clutch of *Cochlicopa* arose as the result of mutation and since these sinistral specimens were not at a selective disadvantage, they were able to persist in the population alongside dextral conspecifics for several millennia. They were not present in the uppermost samples, hinting that the sinistral population may have recently died out, although whether its disappearance resulted from selection, genetic drift or sampling bias remains unclear.

These simple explanations raise several questions. Since *Cochlicopa* is a widespread Palaearctic genus, why are there not more reports of sinistral populations across this enormous range? Apart from the single sinistral specimen of '*C. repentina*' from the Moscow region (Starobogatov, 1996), we have only been able to trace one other paper reporting sinistral populations of *Cochlicopa*, interestingly again from Siberia (Udaloi & Novikov, 2005). Indeed, why should other self-fertilizing snails not all produce occasional sinistral populations where the frequency of reversed-coiling reaches or exceeds values of 10%? Moreover, are we right to assume that sinistrality in this genus is selectively neutral or are other processes operating to maintain these relatively high frequencies over such long periods of time? The data presented in this paper pose interesting questions; perhaps some clearer answers will be forthcoming in future research.

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