CHAPTER 20

Land and Freshwater Molluscs

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Introduction

Any study of past extinctions and introductions is based upon a sound knowledge of the current distribution of species. From its inception in 1876, The Conchological Society of Great Britain and Ireland had a strong interest in species' geographical distribution and was able to build upon earlier work at a county level (e.g. Lowe 1853, and others quoted in Kerney 1999). In 1961 the Society formally launched its latest major national mapping initiative based upon 10 km national grid squares, with the preliminary results published in Kerney (1976) and a more detailed update published in Kerney (1999). As pointed out in the 1999 update, the level of detail which we know about molluscan distributions in the British Isles and Ireland is probably unparalleled with comparison to any other invertebrate group.

The national mapping scheme has given us a superb database of what species presently live where within Britain and Ireland. Above and beyond that, the scheme has also incorporated fossil occurrences from molluscan studies concerned with late-Quaternary landscape change (e.g. Kerney *et al.* 1980; Preece 1980) and with the setting of prehistoric archaeological sites (e.g. Evans 1999; Evans *et al.* 1988). The combination of modern and past occurrences within the scheme has allowed us to determine whether species are likely to be native (that is, arrived in the British Isles under their own powers of dispersal), probably native (likely to have arrived under their own accord but not definitively proven to have done so by the fossil record), or are introductions (brought here by accident or deliberate introduction, Tables 12 and 13). It also clearly highlights some species that the fossil record shows were here in the past but for which there are no modern records (i.e. they are now extinct in Britain and Ireland, Table 14). However, it is necessary to point out that this has only been possible for those molluscan species with a recognisable shell, since it is the shell that is preserved in ancient deposits. While the present distribution of non-shelled Mollusca (i.e. slugs) is therefore known, the fossil record is unable to shed light on their native or non-native status.

Period in which introduced	Species	Notes
Prehistory	*Cochlicella acuta*	Most probably a late prehistoric introduction. Present in a pre-later Iron Age soil at Stackpole Warren, Dyfed (Benson *et al.* 1990).
	Monacha cartusiana	A 'weed' species present from the Neolithic period onward.
Roman/Romano-British	*Oxychilus draparnaudi*	A Mediterranean species.
	Balea biplicata	Known from a few Roman sites only and presently restricted to the Thames area near London.
	Candidula gigaxii	A 'weed' species.
	Cernuella virgata	A 'weed' species.
	Monacha cantiana	A 'weed' species probably introduced in the late Roman period.
	Helix aspersa	A mainly Mediterranean species probably introduced accidentally via trade routes.
	Helix pomatia	Probably introduced during the Roman period for food.
Medieval	*Oxychilus helveticus*	Known only from Post-Roman sites.
	Cecilioides acicula	A Mediterranean species. Although found in prehistoric deposits the species can burrow to about 2m and it is therefore probably intrusive in pre-Medieval deposits.
	Candidula intersecta	No pre-Medieval records in the UK.
Recent	*Paralaoma caputspinulae*	First recorded in 1985. Originally Australasian.
	Helicodiscus singleyanus	First recorded in 1975. Origin in North America.
	Semilimax pyrenaicus	Found in Ireland only. Probably an 18th or 19th Century introduction.
	Bradybaena fruticum	A 20th Century introduction with a few occurrences recorded in south east England. Now probably extinct.
	Trochoidea elegans	Recorded in 1890 from Kent.
	Cochlicella barbara	Probably introduced in the 1970s. Restricted to a few south-western coastal parts of the UK
	Hygromia cinctella	First recorded at Paignton, Devon in 1950. The species is now expanding northwards.
	Hygromia limbata	First recorded in 1917 in Devon. Now spreading northwards.
	Theba pisana	A Mediterranean 'weed' species probably introduced in the 19th Century.

TABLE 12. Introduced terrestrial species. Data from Kerney (1999).

Late-Glacial and Postglacial faunal changes

Studies of well-dated fossil sequences have allowed a very detailed picture of molluscan colonisation of the British Isles and Ireland since the last glacial period. Kerney (1977) first proposed molluscan biozones (in effect the molluscan equivalent of the well established Late-glacial and postglacial pollen zones) for south-eastern England, and these have since been amended in the light of further intensive study and dating at Holywell Coombe near Folkestone (Preece and Bridgland 1998; 1999). The molluscan biozones are set out in Table 15.

As one would expect, these biozones clearly mirror the climatically-driven vegetation changes in the Late-glacial to mid-postglacial periods, with open-country, cold-climate faunas (Zones *y* and *z*) giving way to shade-tolerant or shade-demanding faunas indicative of mid-postglacial temperate woodland (Zones *a–d*). The most recent zones (*e–f*) show the re-emergence and expansion

Species	Notes
Potamopyrgus antipodarium	Introduced sometime prior to 1852. Probable New Zealand origin.
Physa spp.	One species (*Physa fontinalis*) is native, but other poorly-defined species are probably 19th Century introductions from North America.
Menetus dilatatus	First recorded in 1869, origin probably eastern USA.
Ferrissia wautieri	A very recent (1976) introduction from North Africa.
Musculium transversum	First recorded in 1856, of North American origin
Dreissena polymorpha	An introduction from the Caspian/Black Sea around 1820, probably via timber imported from the Baltic.

TABLE 13. Introduced freshwater species. Data from Kerney (1999).

of open-country faunas, though now temperate rather than cold-climate ones, as prehistoric and historic farming activity transformed the British Isles into a mosaic of grassland, arable and woodland.

Several points are worthy of note. First, some species that colonised the British Isles as the last glacial maximum came to an end, and (relatively) warmer Late-glacial and early postglacial conditions persisted, themselves subsequently became extinct as conditions became warmer still and temperate woodland developed. *Columella columella*, for example, is an arctic-alpine species which was a characteristic element of the Late-glacial and early postglacial periods (Table 15), but which became extinct from the British Isles as conditions warmed further (Table 14). Second, it is also evident that it is not just species that can become extinct: communities or species-associations can too. Notwithstanding the actual geographical extinction of *Columella columella* it is evident that the association of the other species in Zone *z* has no modern parallel within the British Isles, having only existed for the limited period of periglacial conditions in the Late-glacial and very early postglacial. Third, as vegetation changes followed temperature changes and the landscape became one of temperate mixed-woodland, thermophilous (i.e. warmth-loving) shade-requiring species such as *Spermodea lamellata* were able to move into the British Isles for the first time. The first few thousand years of the postglacial period was therefore a time in which the molluscan fauna of these islands was altering as a result of temperature, and later vegetation, changes. Some of our native species did not finally reach Britain until well into the postglacial period, just before the land bridge attaching the British Isles to the European mainland was cut off by rising sea level. This severing of the land bridge fixed our 'native' molluscan fauna and hindered the migration of other species from the European mainland which otherwise may also have become established here. Finally, it can be said that as a result of later human impacts these islands have a richer molluscan fauna than they would have had had woodland clearance not occurred (Kerney 1968). Without such clearance some of the open-country species which are now widespread and characteristic of grazed or otherwise managed land might well have been marginalised to the point of extinction. In addition, some of the more recent 'accidental' introductions (see Table 12) would not have become so readily established within wooded conditions.

Introductions and extinctions

The species considered as introduced are given as Tables 12 and 13. It is noticeable that 21 terrestrial species are considered as introductions (Table 12), some 20 per cent of the entire current terrestrial molluscan fauna. Only two species seem to have been prehistoric introductions, the other 19 being Roman/Romano-British, medieval or more recent introductions. Only one (*Helix pomatia* – Figure 42) is considered a deliberate introduction, as a food source; the rest appear to have been 'accidental'.

The status of many of the freshwater and brackish species is less certain. Kerney (1999) only lists five species and elements of one taxon (*Physa* spp.) as definite introductions. They are all recent and the dates of first occurrences well documented (Table 13). However, a further 14 freshwater or brackish gastropods and seven freshwater bivalves are only listed as probably native or query (?) native. This uncertainty reflects the relative paucity of well-dated fossil occurrences as compared to terrestrial Mollusca.

Table 14 lists the terrestrial and freshwater species currently considered as once native but now extinct. As mentioned earlier, the majority of these are species that were able to colonise the British Isles during the Late-glacial or early postglacial period but were disadvantaged as temperate woodland conditions became fully established. Although these extinctions seem to be securely recorded, a word of caution is necessary. As the mapping scheme data accumulated, at least one species (*Vertigo genesii* an arctic-alpine species thought to have only inhabited the British Isles during the Late-glacial and early postglacial) was 're-discovered' as an extant species, albeit in a single locality in Teesdale (Coles and Colville 1980). It remains possible that some of

Species	Notes
Cochlicopa nitens	A central and eastern European species which is known only from UK Late-Glacial and early postglacial deposits (see Preece 1992 and Davies 2006).
Columella columella	An arctic alpine species found only in Late-glacial and early postglacial deposits in the UK.
Discus ruderatus	A Holarctic species found in early postglacial deposits but replaced by *Discus rotundatus* between 8630 ±120 and 7650 ±80 BP (Preece and Bridgland 1998; 1999).
Trochoidea geyeri	Seemingly extinct from much of the UK by the early-mid postglacial as open country was replaced by closed woodland. However, it was present at Gwithian, Cornwall, in the Bronze Age but seems to have become extinct shortly after, possibly as a result of competition from other helicellines.
Helicopsis striata	Extinction in early-mid postglacial due to loss of open habitat as woodland cover increased.
Nesovitrea petronella	Presently a boreal-alpine species. Extinction from UK due to postglacial warming.
Margaritifera auricularia	Climatic change (postglacial warming) probably responsible for extinction.
Pisidium vincentianum	A cold water bivalve now found in western Siberia and The Himalayas. Only found in early postglacial lake deposits in the UK.

TABLE 14. Terrestrial and freshwater species becoming extinct from the UK during the Holocene. Data from Kerney (1999) unless otherwise stated.

the other colder-climate species listed in Table 14 may survive as isolated extant populations in remoter areas of the British Isles.

Biozone	Characteristic species and dates
Zone *y*	*Pupilla muscorum, Vallonia* spp. and *Vitrina pellucida* dominated faunas. Dated from 13,160 ±400 yr BP to just before 11,530 ±160 yr BP and therefore covering the pre-interstadial phase of the Late-glacial.
Zone *z*	An open ground periglacial fauna with *Pupilla muscorum, Trichia hispida, Abida secale, Vallonia* spp., *Columella columella* and *Neosovitrea hammonis*. Dated from just before 11,530 ±160 yr BP until 9820 ±90 yr BP. Covering the Late-glacial (Windemere or Allerød) Interstadial and (Loch Lomond or Younger Dryas) Stadial phases of the Late-glacial period, as well as the very early postglacial period.
Zone *a*	As *z* but with *Pupilla* and other bare ground species declining and with ecologically catholic species increasing. Appearance of *Carychium tridentatum, Vitrea* spp. and *Aegopinella* spp.. Dated from 9760 ±100 yr BP until before 9530 ±75 yr BP and reflecting increasingly wooded conditions.
Zone *b*	Expansion of *Carychium* and *Aegopinella* and otherwise generally a woodland assemblage. First appearance and expansion of *Discus ruderatus*. Dated from just before 9460 ±140 yr BP until 8630 ±120 yr BP.
Zone *c*	*D. ruderatus* replaced by *D. rotundatus* Otherwise a closed woodland assemblage. Dated from 8630 ±120 yr BP until just before 7650 ±80 yr BP.
Zone *d*	A woodland fauna with the notable expansion of *Oxychilus cellarius, Spermodea lamellata, Leiostyla anglica* and *Acicula fusca*. Dated from 7650 ±80 yr BP until sometime before 5620 ±90 yr BP.
Zone *e*	Shade species decline. Re-emergence and expansion of open-ground species, particularly *Vallonia costata*. Lower boundary dating to between 5620 ±90 to 3980 ±70 yrs BP, reflecting the diachronous nature of substantial prehistoric woodland clearance.
Zone *f*	As Zone *e* but with *H. aspersa*. From sometime before 2850 ±70 yr BP.

TABLE 15. Molluscan biozones from south-east England as detailed by Preece and Bridgland 1999.

FIGURE 42. *Helix pomatia.*

Relict, declining and 'migrating' species

Another feature of the national mapping scheme is that it is possible to consider which extant species are relict and which are declining. Relict species are those which were once more widespread under different climatic conditions (e.g. the cooler, drier conditions of the early postglacial) and are now generally disadvantaged but just about maintaining viable populations in a few localities where conditions allow. *Vertigo genesii*, mentioned above, comes into this group. Other examples include *Vertigo modesta*, *Vitrea subrimata*, *Sphaerium solidum*, *Catinella arenaria*, *Pisidium conventus*, and *Pisidium lilljeborgi*. Declining species are those which were once far more widespread but are threatened by human-induced habitat loss (e.g. *Aplexa hypnorum* and *Lymnaea glabra* suffering from loss of ditches and ponds), the effects of pollution (e.g. *Myxas glutinosa* and *Segmentina nitida*) or climatic cooling since the mid-postglacial climatic optimum (e.g. *Pomatias elegans, Ena montana*).

Some species show very strong evidence of northward migration due to longer-term climate change. Both *Vertigo genesii* and *Vertigo geyeri* are boreal-alpine species intolerant of warmth and have migrated northwards since the earlier postglacial period. Unlike *Columella columella* they have not yet become extinct, but future warming could severely threaten their existence in the British Isles. Conversely, some of the more recent introductions, particularly the 'Mediterranean' species (e.g. *Theba pisana* and *Hygromia cinctella*) which currently have a limited distribution due to frost intolerance may well expand their distributions in the same way that *Monacha cantiana* seems to have done over the last century (Kerney 1999).