MALACOLOGIA, 1982, 22(1–2): 727–730

PROC. SEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS

NON-MARINE MOLLUSCA OF THE LAST GLACIAL PERIOD (DEVENSIAN) IN BRITAIN

D. T. Holyoak

Department of Geography, University of Reading,
2 Earley Gate, Whiteknights, Reading RG6 2AU, England

The rôle of historical factors in explaining the geographical distribution of European non-marine Mollusca is open to critical investigation through the fossil record. Consideration of the history of the fauna of the British Isles, as of northern Europe generally, involves study of fossils from the Last Glacial Period (Devensian, roughly corresponding to the Weichselian and Würm of continental Europe, and the Wisconsin of North America). Some authors have suggested that southern England might have provided a refuge for thermophilous Mollusca during the Devensian (*e.g.* Ant, 1969) while others have questioned whether any Mollusca survived throughout the Devensian in Britain (Kerney, 1977a). This paper reviews fossil records as a basis for comment on the origins of some modern distribution patterns. The evidence of Devensian climates provided by fossil Mollusca is also considered.

SUMMARY OF DEVENSIAN STRATIGRAPHY

The Devensian is conventionally taken as the period from 70,000 to 10,000 radiocarbon years Before Present (a.B.P.). However, there is some uncertainty about the age of the lower boundary because radiocarbon dating is useful mainly over the past 50,000 years (commencement of mid-Devensian) so there are few estimates of the absolute age of early-Devensian deposits.

Information on British Devensian fossil Mollusca is mainly from England, especially the south and east. Fossils have been studied mainly from silts interbedded in river gravels, muds of pools and slope-wash deposits on chalk downland. The nature of the deposits in which shells are preserved inevitably means that shells from calcareous habitats are better represented than those from acid sites, although fluvial deposits may contain inwashed material from a wide range of habitats. Unfortunately, fluvial deposits often contain shells reworked from older deposits, so that many published records are open to doubt when lists of Devensian Mollusca are being prepared. Here, records are regarded as reliable only when a species occurs in fair quantity and in appropriate associations with floral and other faunal remains.

The climate during much of the Devensian was much colder than now, with tundra or steppe-tundra vegetation predominating over long periods. The colder periods with open vegetation (*stadials*) were punctuated by *interstadials*, which mostly had boreal forest vegetation. The following sequence of stadials and interstadials is known in England:

	^{14}C age a. B.P.	Vegetation in S. England
Loch Lomond Stadial	10,300–11,000	Open
Windermere Interstadial	11,000–12,300	*Betula* woodland
(stadial)	12,300–38,000	Open
Upton Warren Interstadial	38,000–43,000	Open; thermophilous Coleoptera present
(stadial)	43,000–50,000	Open
Brimpton Interstadial	?	*Betula-Pinus* woodland
(stadial)	?	Open
Chelford Interstadial	c. 60,000 ?	*Pinus-Picea-Betula* woodland
(stadial)	?	Open
Wretton Interstadial	?	*Betula-Pinus-Alnus* woodland
(stadial)	?	Open
(Ipswichian Interglacial)	(to c. 125,000)	(temperate forests)

Assemblages of fossil Mollusca are known from most of these periods, although information from the early-Devensian is fragmentary.

FAUNAS OF THE DEVENSIAN STADIALS

Molluscan faunas from the different stadials (excepting the Loch Lomond Stadial, which is discussed separately below) are generally similar, consisting of few species that mostly have modern ranges extending into the Arctic. However, much more is known of faunas from the long stadial extending from c. 38,000–14,000 a. B.P. than of earlier stadials, so the following discussion and lists refer to this period. Terrestrial species for which there are numerous records are:

Catinella arenaria
Oxyloma pfeifferi
Columella columella
Vertigo genesii
Pupilla muscorum
Arion sp.
Deroceras sp.
Limax sp.

Other species for which the few records might be due to reworking or occurrence only during warmer periods are:

Cochlicopa lubrica
Vallonia pulchella
Punctum pygmaeum
Trichia hispida

Succinea oblonga has frequently been reported. Many Devensian shells resemble this species rather than *Catinella arenaria* but it may not be possible to separate them reliably.

Aquatic faunas of the different Devensian stadials are also rather monotonous and consist mainly of species that have modern ranges extending into the Arctic. The following have been reliably recorded from deposits of 38,000–14,000 a. B.P.:

Valvata piscinalis
Lymnaea truncatula
Lymnaea peregra
Anisus leucostomus
Gyraulus laevis
Sphaerium corneum
Pisidium amnicum
Pisidium casertanum
Pisidium obtusale
Pisidium subtruncatum
Pisidium henslowanum
Pisidium nitidum
Pisidium vincentianum

Less reliable records, possibly due to reworking or presence only in warmer periods (perhaps the Upton Warren Interstadial) are:

Bithynia tentaculata
Lymnaea stagnalis
Lymnaea palustris
Armiger crista
Hippeutis complanatus
Anodonta cf. *anatina*
Pisidium milium
Pisidium supinum

The foregoing rather short lists of hardy species suggest harsh climatic conditions during Devensian stadials. This evidence from Mollusca is in accordance with evidence of generally cold conditions from fossil Coleoptera (Coope, 1975, 1977), palaeobotany (Godwin, 1975) and geomorphological evidence for at least intermittent occurrence of permafrost well outside the glaciated regions (Worsley, 1977).

Ant (1969) postulated that refugia allowing survival through colder parts of the Last Glaciation existed in southern England for such apparently thermophilous species as *Acicula fusca* and *Ashfordia granulata*. Such refugia appear most unlikely to have existed in view of the evidence for periods during which harsh climatic conditions existed over at least most of southern England. Furthermore, the earliest of numerous records of fossils of *Acicula* and *Ashfordia* are from the Atlantic Period of the Post-Glacial.

Kerney (1977a) questioned whether any Mollusca survived in England through the period between 26,000–14,000 a. B.P., parts of which had glacial ice extending over northern England. However, deposits at Barnwell Station, Cambridge radiocarbon dated to 19,500 ± 650 a. B.P. (Coope, 1968, 1980) had previously yielded a molluscan fauna with seven aquatic and five terrestrial species (Kennard & Woodward, 1922). This and less securely dated deposits may suggest pre-glacial survival of a few species, but the interrupted nature of the fossil record may prevent this from being firmly established.

THE EARLY-DEVENSIAN INTERSTADIALS

The molluscan faunas of the interstadials of the early-Devensian are very poorly known. Nothing is known of the fauna during the Wretton Interstadial, and faunas securely attributed to the Chelford and

Brimpton Interstadials are known only from Brimpton, Berkshire (Holyoak, 1980). Besides many of the tolerant species that also occur in stadials, species recorded from the Chelford Interstadial include *Vertigo substriata, Discus ruderatus* and *Nesovitrea hammonis*. There are records from the Brimpton Interstadial of *Valvata cristata, Myxas glutinosa, Bathyomphalus contortus, Cochlicopa lubrica, Vertigo pygmaea, Vallonia pulchella, Punctum pygmaeum, Euconulus fulvus* agg. and *Trichia hispida*. Many of these species have modern ranges that extend into the Arctic. However, a fauna that may be of early-Devensian interstadial age at Pitstone, Buckinghamshire includes such apparent thermophiles as *Azeca goodalli* and small numbers of *Discus rotundatus* (Kerney, 1977a).

THE UPTON WARREN INTERSTADIAL

Evidence for one or more warm periods around 43,000–38,000 a. B.P. is derived mainly from studies of fossil Coleoptera. The vegetation over this period appears to have consisted of herbaceous and dwarf-shrub associations, with no trees.

Land snail faunas consist mainly of the species that occur during stadials, but also:

Succinea cf. *putris*	*Vallonia pulchella*	*Trichia hispida*
Vallonia costata	*Punctum pygmaeum*	

The occurrence of *T. hispida*, which now has a northern range limit that barely penetrates the Arctic in Scandinavia, may be associated with increased warmth during this interstadial. The aquatic faunas are notably richer than those of stadials, the additional records comprising:

Bithynia tentaculata	*Anisus vortex*	*Anodonta anatina*
Lymnaea stagnalis	*Ancylus fluviatilis*	*Pisidium milium*
Lymnaea palustris	*Acroloxus lacustris*	*Pisidium supinum*
Planorbis planorbis		

and perhaps also *Pisidium moitessierianum*.

THE WINDERMERE INTERSTADIAL AND LOCH LOMOND STADIAL

Faunas of the Windemere Interstadial (12,300–11,000 a. B.P.) are better known than those of earlier interstadials. About forty species are known. In addition to the tolerant species present during the stadials a number of apparently thermophilous land snails of open habitats occurred in at least south-eastern England, notably *Abida secale, Helicella itala* and *Trochoidea geyeri* (cf. Kerney, 1963).

All of the 'thermophiles' of the Windermere Interstadial appear to have survived through the ensuing Loch Lomond Stadial (11,000–10,300 a. B.P.), implying that climatic conditions in southern England were not too severe for them. This appears to conflict with evidence of widespread cryoturbation of soils in the lowlands of southern England and of glaciation in mountain areas at that time, but marked seasonality of climate may offer an explanation.

It is noteworthy that the fauna of the Windermere Interstadial (and apparently also faunas of the earlier Devensian interstadials) are poorer in 'thermophilous' woodland Mollusca than the better known Preboreal Period of the Post-Glacial. This difference might be explained by short duration of warm conditions during the interstadials, although the extent of forest development during some interstadials suggests this is unlikely to be sufficient explanation. The appearance of such species as *Carychium* spp., *Aegopinella* spp., *Vertigo pusilla, Ena montana* and *Clausilia bidentata* early in the Post-Glacial shows that the full development of temperate forest was not necessary for them to become established. Hence the poorer faunas of the Devensian interstadials than of the Preboreal Period may be most simply attributed to harsher climates during the interstadials.

BIOGEOGRAPHICAL COMMENTS

There can be little doubt that a majority of the species of Mollusca comprising the modern fauna of Britain would have been unable to survive there during long periods of the Devensian. The apparently

orderly sequence of colonisation and establishment of species through the Late-Devensian and Post-Glacial has received detailed study (Kerney, 1977b; Kerney, Preece & Turner, 1980).

The few land-snail species that were present in Britain during colder periods of the Devensian mostly became rarer early in the Post-Glacial. Some such as *Pupilla muscorum* have since become widespread again in Britain, but others have decreased greatly (*Catinella arenaria, Vertigo genesii*) or apparently become extinct in Britain (*Columella columella*). Reduction of the extent of open habitats as forests expanded seems more likely to account for the decrease of some of these species than any direct èffect of the warmer climate of the Post-Glacial. Thus, *Catinella arenaria* and *Vertigo geyeri* both survive in the British Isles only in relict areas of open habitat, but these areas are in warm lowland regions as well as in the colder uplands.

REFERENCES CITED

ANT, H., 1969, Zur Würm-Glazialen Überdauerung Europaischer Landgastropoden in Eisrandnahe. *Malacologia* 9: 249–250.

COOPE, G. R., 1968, Coleoptera from the 'Arctic Bed' at Barnwell Station, Cambridge. *Geological Magazine,* 105: 482–486.

COOPE, G. R., 1975, Climatic fluctuations in north-west Europe since the last Interglacial, indicated by fossil assemblages of Coleoptera. *In*, WRIGHT, A. E. & MOSELEY, F. Ice Ages Ancient and Modern, *Geological Journal Special Issue,* 6: 153–168.

COOPE, G. R., 1977, Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philosophical Transactions of the Royal Society of London,* B280: 313–340.

COOPE, G. R., 1980, The climate of England during the Devensian Glacial Maximum: evidence from fossil Coleoptera. *Quarternary Newsletter, London,* No. 30: 11–13.

GODWIN, H., 1975, *History of the British Flora.* Cambridge: C.U.P., 2nd ed.

HOLYOAK, D. T., 1980, Late Pleistocene sediments and biostratigraphy of the Kennet Valley, England. Unpublished Ph.D. thesis, University of Reading.

KENNARD, A. S. & WOODWARD, B. B., 1922, The Post-Pliocene non-marine Mollusca of the east of England. *Proceedings of the Geologists' Association, London,* 33: 104–142.

KERNEY, M. P., 1963, Late-glacial deposits on the chalk of south-east England. *Philosophical Transactions of the Royal Sociey of London,* B246: 203–254.

KERNEY, M. P., 1977a, British Quaternary non-marine Mollusca: a brief review, in, SHOTTON, F. W. (ed.) *British Quaternary Studies: Recent Advances.* Oxford: Clarendon Press, pp. 31–42.

KERNEY, M. P., 1977b, A proposed zonation scheme for Late-Glacial and Postglacial deposits using land Mollusca. *Journal of Archaeological Science,* 4: 387–390.

KERNEY, M. P., PREECE, R. C. & TURNER, C., 1980, Molluscan and plant biostratigraphy of some Late Devensian and Flandrian deposits in Kent. *Philosophical Transactions of the Royal Society of London,* B291: 1–43.

WORSLEY, P., 1977, Periglaciation, *in,* SHOTTON, F. W. (ed.) *British Quaternary Studies: Recent Advances.* Oxford: Clarendon Press, pp. 205–219.