Remains of voles (Microtus sp.) from Fox holes cave, High Wheeldon, Derbyshire, UK
Resten van woelmuizen (Microtus sp.) uit Fox holes grot, High Wheeldon, Derbyshire, UK

SMALL IS BEAUTIFUL: FOSSIL ARVICOLIDS (VOLES) AS STRATIGRAPHIC AIDS

When you walk through the countryside you will not very often come across a vole. However, they are present in most temperate habitats and indeed they are the most successful and abundant of small mammals, widely distributed in Eurasia and North America. Many vole species are specialised for burrowing. They are adapted to eat hard vegetation such as grasses which are very abrasive due to the presence of silica spicules. So, many vole species have evolved continuously growing molar teeth (three upper and three lower), as well as having the continuously growing incisors typical of rodents. This evolution took place largely in the last five million years. For this reason, fossil remains of voles are very useful for helping us to unravel the stratigraphy of deposits from the Pliocene and Pleistocene periods. This article emphasises the Early Pleistocene, but voles are of course found in deposits right up to the present time.

We are talking here of quite small fossils, for example the molar teeth are between 1 and 4 mm in size, so where and how are they found?

In cave and fissure deposits, such as the Holocene locality Foxholes at High Wheeldon, Derbyshire, UK, many thousands of specimens can be found. Often such localities have no stratigraphic context other than the contained fauna. However, the material, coming from e.g. owl pellets, may be very complete (skulls and lower jaws, limb bones).

Teeth can also be recovered from open continental sediments of various types. Most promising are poorly sorted freshwater sediments (such as the base of channel fillings) of a grey colour containing mollusc shells, since these are not oxidised or decalcified. The Upper Freshwater Bed at West Runton has long been well known for the relatively abundant remains of small mammals.

It is extraordinary and of great scientific value that fossil vole remains can even be found in marine sediments, for example in the crags of East Anglia (Weybourne Crag, Norwich crag).

In the Netherlands, fossil vole remains of arvicolids are known from the Maassluis Formation inshore marine deposits of the Early Pleistocene. These can be reached by boreholes extending down to more than 40m in the Zeeland area, and deeper further North. In 2008 we made a borehole at Moriaanshoofd,

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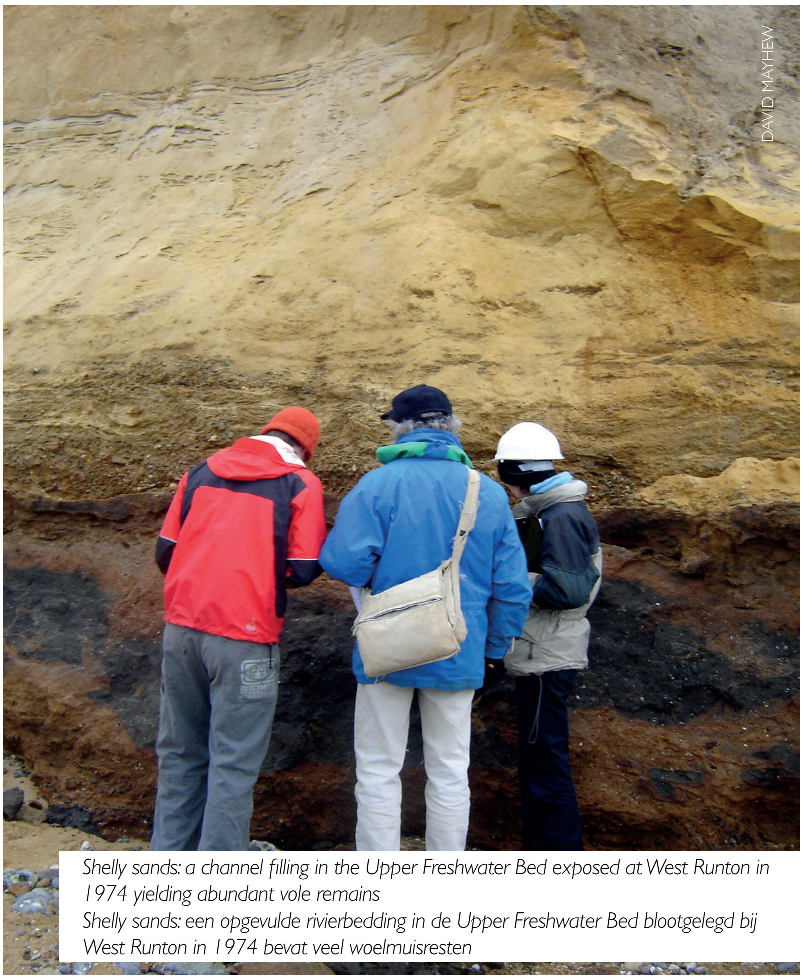
Schouwen-Duiveland and extracted some small mammal remains suitable for stratigraphy. Much more impressive are the results of the Zuurland boreholes near Brielle, where thousands of teeth have been recovered.

Finally the aspect of reworking must be considered. When the fossil material is found in extensively reworked sediments such as pumped sand used for reinforcing beaches or making new ground (e.g. Maasvlakte) less can be said about age. Nevertheless, such specimens are valuable in documenting previous geographical distribution.

Small mammal material collected over the course of many years in the UK and the Netherlands has proved very valuable, even though consisting largely of isolated teeth. Many scientifically significant specimens including new species have been found by collectors, who generally have better local knowledge than research workers located at a distance.



Shelly sands: a channel filling in the Upper Freshwater Bed exposed at West Runton in 1974 yielding abundant vole remains
Shelly sands: een opgevulde rivierbedding in de Upper Freshwater Bed blootgelegd bij West Runton in 1974 bevat veel woelmuisresten

Norwich Crag Shell Beds at Easton Bavents
Norwich Crag Shell Beds bij Easton Bavents

STRATIGRAPHIC VALUE

Teeth from many open sites have a stratigraphic context, consisting of the lithostratigraphy, the other contained animal and plant remains (e.g. pollen, foraminifera and dinoflagellates in marine sediments) and perhaps also palaeomagnetic information. This means that they are generally more useful for regional and international correlation of deposits than teeth from caves and fissures.

The remains of voles from the Early Pleistocene UK Crags include the ubiquitous *Mimomys pliocaenicus* (Weybourne Crags) and its precursor *Mimomys praepliocaenicus* (found in the Norwich Crags).

They can be seen as early versions of the present water vole *Arvicola terrestris*, although the precise evolutionary connections of these forms is not as clear-cut as was previously thought. At West Runton (Middle Pleistocene), the species *Mimomys savini*, very probably ancestral to *Arvicola*, is present. Several other extinct species used for stratigraphy are known from the UK and the Netherlands. Using voles, we can easily distinguish in the UK between the Norwich Crag deposits at Bramerton and Bulcamp, and those of later age such as the Weybourne Crag sediments at Weybourne, Sidestrand, and East Runton.

In the Netherlands, the small mammal fauna of Tegelen (channel filling, TC5 stage) contains several vole species including *Mimomys pliocaenicus*. Using these, it is possible to determine the age of the Tegelen assemblage relative to UK material. In this way a joint regional stratigraphic sequence of localities can be built up.

RECOVERING FOSSIL VOLES FROM OPEN SITES

Exceptionally, whole jaws may be found on the weathered surface of outcrops of sands muds and clays.

More generally, the teeth are isolated and not visible, and can be only recovered by wet sieving of sediments through various mesh sizes down to 1 or even 0.5 mm., followed by drying, and picking out the teeth using a low powered binocular microscope. A trial sample of a bucket of sediment may be sufficient to indicate the presence of bone, and often fish remains are relatively abundant. Finding fragments of vole incisors or molars is a certain clue that further sampling is worthwhile. The amount of sediment to be sieved depends on locality, but it should be ex-

Mimomys pliocaenicus m1, Weybourne Crag, West Runton

Lower first molar of Mimomys savini: eroded by digestion by predator
Eerste onderkaaksmolaar van Mimomys savini: geërodeerd door vertering door roofdier

Lower jaw of Mimomys praepliocaenicus from Norwich Crag of Bramerton
Onderkaak van Mimomys praepliocaenicus uit de Norwich Crag bij Bramerton

Lower jaw of Mimomys savini from Cromerian deposits at West Runton
Onderkaak van Mimomys savini uit de Cromerian afzettingen bij West Runton

pected that several hundred kilograms yields a few identifiable teeth plus many fragments. When the Tegelen locality was sampled in the 1970s, many tons of sediment were processed.

HOW DO VOLES BECOME FOSSILISED?

To understand this we need to answer two questions: why are there so many vole teeth and how do they get into sediments?

There are so many teeth because voles are the most abundant of mammals and they reproduce extremely quickly. There can be hundreds of individuals in an acre of land, and they are mature at three months of age, being able to produce several generations per year. Therefore the absolute number of individuals is very high.

The study of the processes by which fossil remains accumulate in sediments is called taphonomy. Understanding of the taphonomy helps us to interpret the fossil remains correctly. Voles get into sediments and become fossilised largely because they are the prey of a wide range of predators including owls, hawks, herons, stoats, weasels and foxes. Several of these produce pellets or scats containing concentrated undigested (owls) or partly digested (hawks, foxes) bone material.

The fossil remains found in caves can often be seen to be derived from the pellets of roosting owls: the proportions of the skeletal element and their position to each other (lower jaws and skulls) may confirm this.

In open sites with disarticulated material it may be more difficult to say what the route of fossilisation was. However it is certain that predators were often involved, and the pellets or scats were transported into water, since this protects the bones (bones on the surface of the soil soon disintegrate or are eaten and destroyed by other animals). In some cases, characteristic erosion marks can be seen on fossil teeth and these indicate that the animals were eaten by predators.

Once in the water and sediments, there is the question of transport and

Breccia of fossil small mammal bones originating from owl pellets, Derbyshire
Breccie van fossiele kleine zoogdierbotten afkomstig uit uilenballen, Derbyshire

reworking of teeth. Some teeth in the marine crags appear rolled and mineralised (dark brown or black). Others are light, unrolled and very fragile. The question is, do we have teeth together which came from different times?

Perhaps remarkably, it can be said that up to now there is no clear evidence from the marine crag material that voles of different geological ages are mixed up together. In contrast, the fossil vole material found on the beach in the Netherlands seems to come from many different periods.

TAXONOMY

The taxonomy of arvicolids is exceedingly complicated. Some of the lineages have only been understood in the last twenty years, others still await clarification. For this reason no attempt has been made here to cover this point, or details of biozonation in what is intended as a general article. For those who wish to learn more, see further reading below.

CONCLUSIONS

Study of fossil voles has proved of great value in understanding the sequence of the Pleistocene Crag deposits of the UK and the Pleistocene deposits of the Netherlands. Further important discoveries including new species continue to be made. Detailed information is available from many continental European localities for comparison with the UK and the Netherlands. Further collecting can be expected to provide interesting and valuable information, as well as specimens which are, in their own small way, beautiful.

POSTSCRIPT

This article for general readership is adapted from a version first published in Deposits Magazine in 2006. I am grateful to many colleagues for collaboration during the course of my work and especially to the private collectors who continue to contribute so much to this field.

FURTHER READING

There are unfortunately no convenient review books in Dutch or English dealing with the latest situation of arvicolid taxonomy and stratigraphy.

For an up-to-date scientific description of Early Pleistocene arvicolids from the Netherlands:

Tesakov, A.S. (1998) Voles of the Tegelen fauna. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60,* 71-134.

This paper has good figures of the various species. This issue of the journal was a special volume for an INQUA meeting and contains other scientific papers dealing with arvicolids, including the description of *Mimomys hordijki* found for the first time in the Zuurland boreholes.

The UK Early Pleistocene material was reviewed by:

Mayhew, D.F., A.J. Stuart (1986) Stratigraphic and taxonomic revision of the fossil vole remains (Rodentia, Mammalia, Microtinae) from the Lower Pleistocene deposits of Eastern England. *Philosophical Transactions of the Royal Society of London B 312*, 431-485.

This article includes 15 pages of figures, but some of the taxonomy and ideas about dating have changed since.

The latest work on the Norwich Crags, with a description of a new species, is covered in:

Mayhew, D.F. (2011) West European arvicolid evidence of intercontinental connections during the Early Pleistocene. *Quaternary International doi:10.1016/j.quaint.2011.08.005.*, 1-12. (Corrected Proof, Available online August 2011).

The reference lists of these papers provide an entry into the literature.