Quaternary non-marine Mollusca and palaeoclimates in Mediterranean France.

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Research in southeastern France, on both Recent and Pleistocene land gastropods, enables us to interpret compositional changes in Pleistocene communities in terms of altitudinal shift of bioclimatic zones. This permits reliable quantitative estimates of palaeotemperatures.

Contents

Introduction

For a long time research on the Quaternary land snails from the Mediterranean region of France by Mazenot (1956, 1957) and Dubar (1980, 1984) remained obscure.

This area is still thought to have been a refugium for temperate woodland snails during the cold stages when the ice and the periglacial environment pushed these species out of Northern and Central Europe (Ložek, 1969; Holyoak, 1989; Rousseau, 1989).

From the beginning of our study, however, we made three basic observations:

1) In Provence, at the end of the Rhône corridor, we did not find any woodland snail communities in the Pleistocene cold stages, but only assemblages from dry open environments (Mazenot, 1956, 1957; Dubar, 1980, 1984; Magnin, 1991).

2) During these periods, southwards from the middle Rhône Valley, we found neither the cold arctic-alpine nor the asiatic species which characterise glacial stages in northern Europe, for example *Columella columella* (Mazenot, 1956, 1957; Magnin, 1989, 1991).

3) Two species, *Trochoidea geyeri* and *Phenacolimax annularis*, which are frequently

found in periglacial sediments at low elevation in the Provence and as far as the present day coast line, still live in this region, but only in upland refugia from c. 900-1000 m above sea level (Magnin, 1989, 1991).

Taking all this into account, we have tried to answer the following question: Is it possible to interpret compositional changes in Pleistocene snail communities in terms of altitudinal shifts of climatic zones ?

Pleistocene land snail assemblages

The loess sequence of Pont-de-Mirabeau

The loess sequence of Pont-de-Mirabeau (Jouques, Bouches-du-Rhône) (Magnin, 1991, 1992) is located at 260 m above sea-level, on the left bank of the Durance River (Fig. 1). Two loess units are separated by a red colluvial soil (Fig. 2). Two dates were

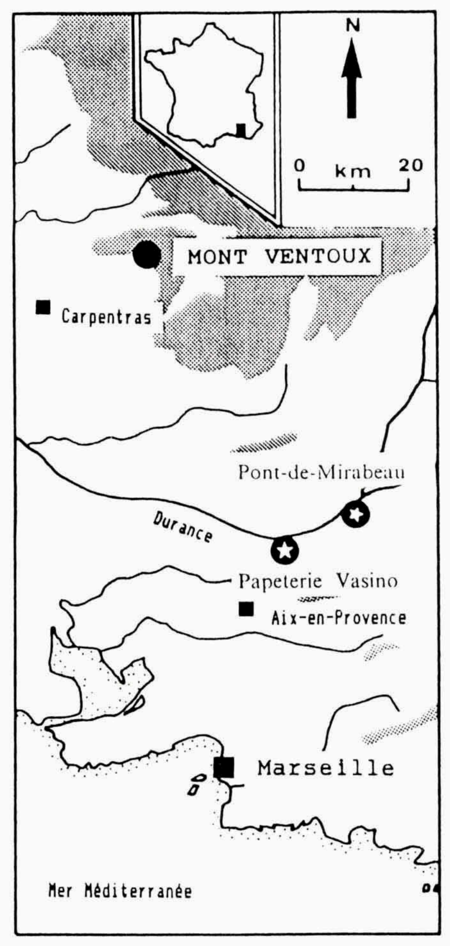

Fig. 1. Location of the Pleistocene sequences (Pont-de-Mirabeau and Papeterie Vasino) and of the modern reference area (Mont Ventoux).

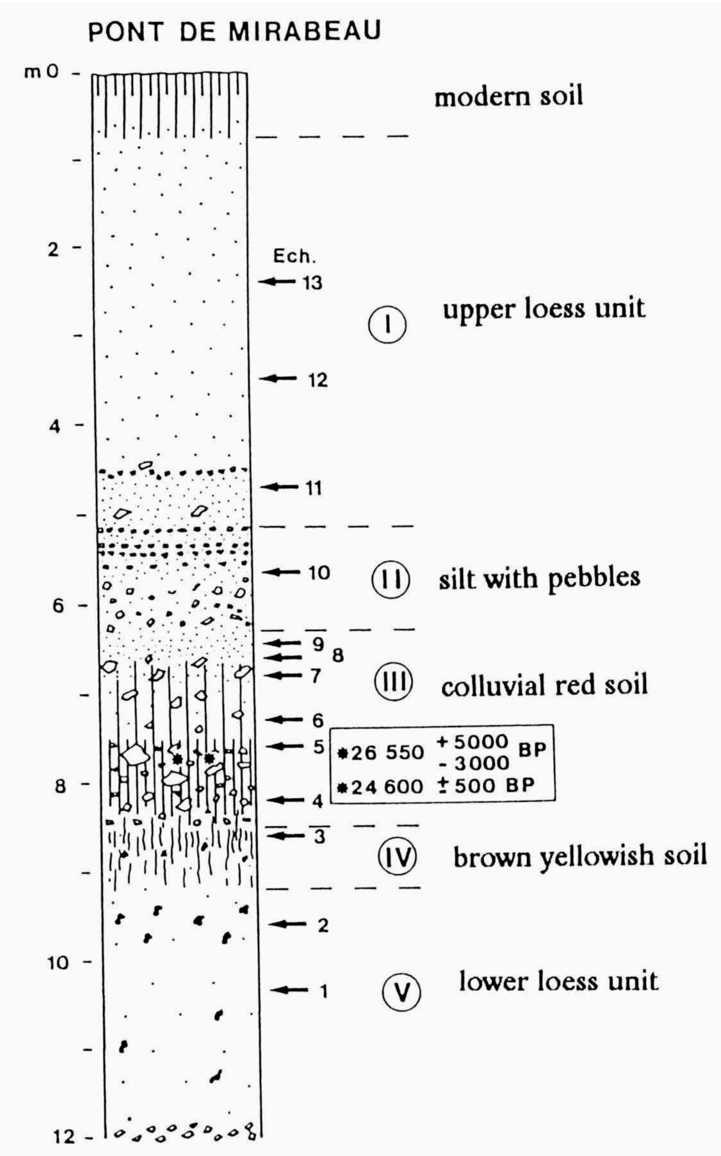

Fig. 2. Section of Pont-de-Mirabeau (Jouques, Bouches-du-Rhône). Lithostratigraphy and ^{14}C datings.

obtained from this soil at the level of mollusc sample 5 (Ly 1587: 26 550 +5000, -3000 BP (Ambert, 1980) and MC 2390: 24 600 ± 500 BP (Bazile-Robert, 1981), enabling us to place it at the boundary between oxygen isotope stages 2 and 3 of the oceanic chronology.

The data obtained (13 samples) were studied using a correspondence analysis (Benzecri & Benzecri, 1984; Rousseau, 1987). A data matrix comprising of 32 species and 13 assemblages was taken into account.

Axis 1 (Fig. 3) is the most important factor (32.1% of the total variance). It opposes temperate forest species on its positive side, to cold open ground species on its negative side.

The most typical snails of the first group are *Cochlostoma septemspirale, Pagodulina pagodula, Discus rotundatus,* and *Pomatias elegans,* a thermophilous species (Kerney, 1968). This indicates a rather damp forest environment, comparable to that of the present day supra-mediterranean bioclimatic level.

In the second group we find *Phenacolimax annularis* (a high alpine species), *Abida secale, Pupilla triplicata, Vallonia costata, Clausilia parvula,* and *Perforatella ventouxiana.* Such an assemblage today characterises open altimediterranean (= sub-alpine) environments.

The meaning of axis 2 is not clear. It opposes *Helicodonta obvoluta, Vallonia costata, Abida secale,* and *Granaria variabilis* on its negative side, to *Truncatellina claustralis, Clausilia parvula, Trochoidea geyeri,* and *Perforatella ventouxiana* on its positive side.

A plot of the 13 samples on the first factor plane (Fig. 3) enables us to follow the molluscan succession from the bottom of the sequence (sample 1), which corresponds to a moderately cold climate and open vegetation, to the top of the sequence (sample 13) which corresponds to a very cold climate, via the soil which is an interstadial stage at c. 25 ka BP.

Notice, we do not have a real Mediterranean fauna during this temperate stage, but a community which we find in woodlands at c. 1000 m above sea-level.

On Fig. 4, the 13 malacological samples are placed in their stratigraphic position and with regard to their coordinates on the first axis of the previous analysis. This gives us a semi-quantitative view of climatic changes in the Provence at the end of isotopic stage 3.

At the bottom of the sequence (samples 1 and 2), the lower loess unit corresponds with an open environment and a dry and moderately cold climate, but sufficiently warm to support *Pomatias elegans.* The snail community is dominated by *Granaria variabilis* and *Trochoidea geyeri,* indicating grassland environments. At the level of samples 3, 4 and 5 we observe the establishment of a damp woodland environment with a cool temperate climate of supra-mediterranean type (note the occurrence of *Pomatias elegans,* today rare above 1000 m, and of *Trochoidea geyeri,* rare below 1000 m). *Cochlostoma septemspirale, Pagodulina pagodula, Pomatias elegans,* and *Discus rotundatus* are the most numerous taxa at this time. Above the level of sample 5, however, we find that the tree cover begins again to diminish and the climate cools. The most typical woodland species: *Pagodulina pagodula, Sphyradium doliolum* and *Acicula lineata* are the first to disappear, while the open ground species *Granaria variabilis* and *Abida secale,* begin to develop. Finally, unit I corresponds with the coldest climate of the sequence (assemblage with *Phenocolimax annularis*).

The travertine section of the Papeterie Vasino

This section (Meyrargues, Bouches-du-Rhône) (Figs. 1 and 5), situated 15 km downstream of the Pont-de-Mirabeau section, presents a complex lithostratigraphic sequence comprising two travertine units dated at 170 ka BP and 145 ka BP, respectively, alternating with detrital sediments (Magnin, 1990, 1991). Eight samples were col-

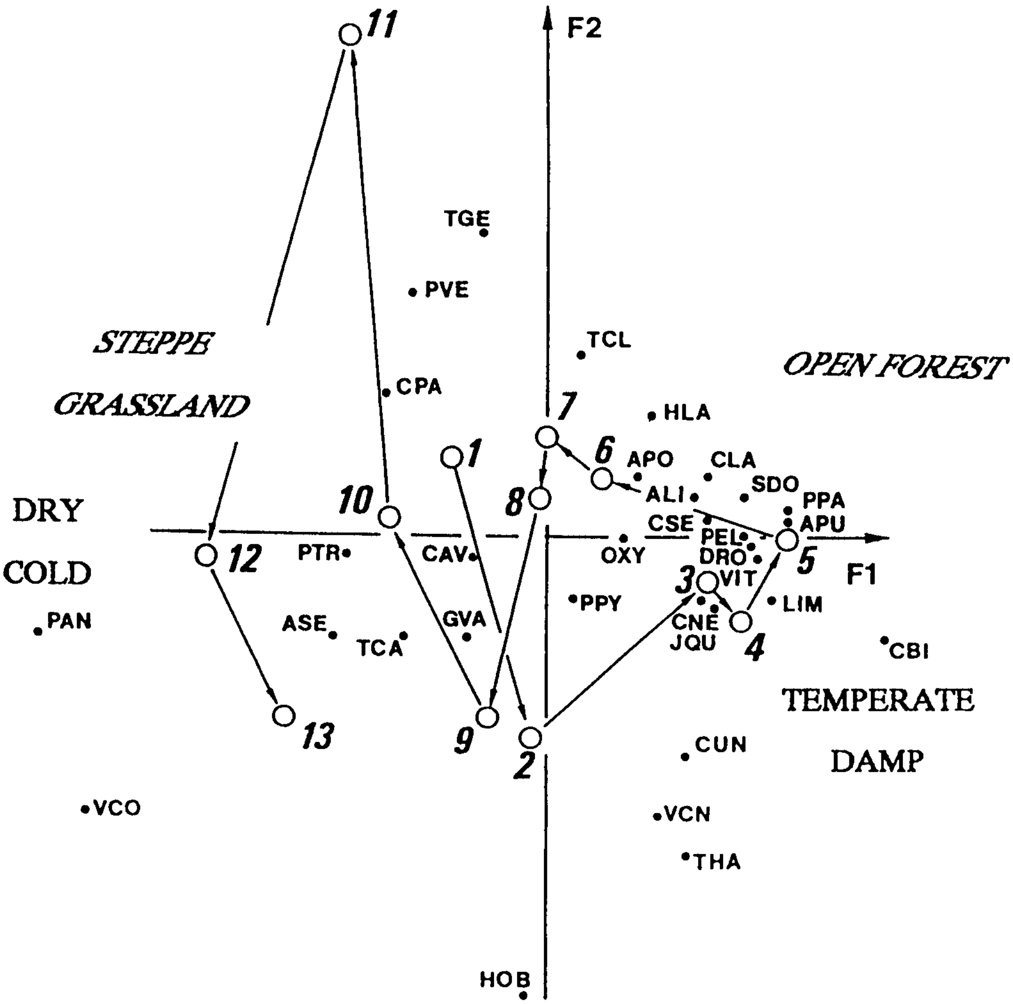

Fig. 3. Correspondence analysis of the malacofauna from the section of Pont-de-Mirabeau. Plot of the species (variables) and of the samples (individuals) on the first factor plane.

PAN: *Phenacolimax annularis*; VCO: *Vallonia costata*; ASE: *Abida secale*; PTR: *Pupilla triplicata*; TCA: *Truncatellina callicratis*; CAV: *Chondrina avenacea*; HOB: *Helicodonta obvoluta*; CPA: *Clausilia parvula*; PVE: *Perforatella ventouxiana*; TGE: *Trochoidea geyeri*; TCL: *Truncatellina claustralis*; APO: *Abida polyodon*; HLA: *Helicigona lapicida*; CLA: *Cochlodina laminata*; ALI: *Acicula lineata*; SDO: *Sphyradium doliolum*; CSE: *Cochlostoma septemspirale*; PEL: *Pomatias elegans*; PPA: *Pagodulina pagodula*; APU: *Aegopinella pura*; OXY: *Oxychilus* sp.; DRO: *Discus rotundatus*; VIT: Vitrinidae; PPY: *Punctum pygmaeum*; LIM: Limacidae; CNE: *Cepaea nemoralis*; JQU: *Jaminia quadridens*; CBI: *Clausilia bidentata*; CUN: *Candidula unifasciata*; VCN: *Vitrea contracta*; THA: *Testacella haliotidea*.

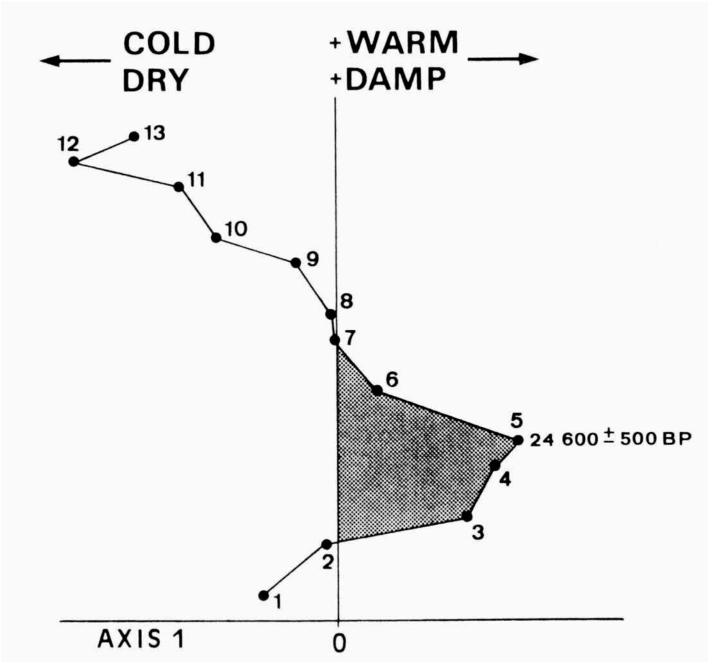

Fig. 4. Reconstruction of environmental and climatic changes from the section of Pont-de-Mirabeau: plot of the samples on the first factor axis.

lected from the soft levels of the travertine.

Figure 6 shows the factor planes 1-2 and 1-3 of a correspondence analysis applied to a data matrix composed of 8 assemblages and 44 land snail species.

The first axis (31.1% of the variance) opposes Mediterranean snail communities from open woodland or scrubland environments, to cold upland communities from grassland or steppe vegetation.

Thus, on the right hand-side (F1 > 0), there are *Candidula unifasciata, Pomatias elegans, Monacha cantiana, Cernuella cespitum, Vitrea contracta,* and *Rumina decollata.* In this group, *R. decollata* is a typical interglacial indicator species. Its strictly Mediterranean range implies, at least, a mean temperature of Tm > 4°C for the coldest month, and an annual mean temperature of T > 12°C (present day values at Meyrargues: Tm=4.7°C; T=12.5°C).

On the left-hand side (F1 < 0) we have *Vallonia costata, Pupilla triplicata, Perforatella ventouxiana, Granaria variabilis,* and *Trochoidea geyeri.* Today *T. geyeri* no longer lives on the site and is very rare in the whole Mediterranean bioclimatic zone. This species is generally limited to upland refugia and can tolerate harsh climates (minima values at Mont Ventoux, Vaucluse: Tm = -7.6°C; T = 2.1°C).

Axis 2 opposes hygrophilous and paludal species (*Carychium minimum, Zonitoides nitidus, Oxyloma elegans, Vertigo moulinsiana*) on its negative side, to some more xerophilous species (*Pupilla triplicata, Vallonia costata, Granaria variabilis, Perforatella ventouxiana, Acanthinula aculeata, Pomatias elegans, Aegopinella nitidula, Candidula unifasciata*) on its positive side.

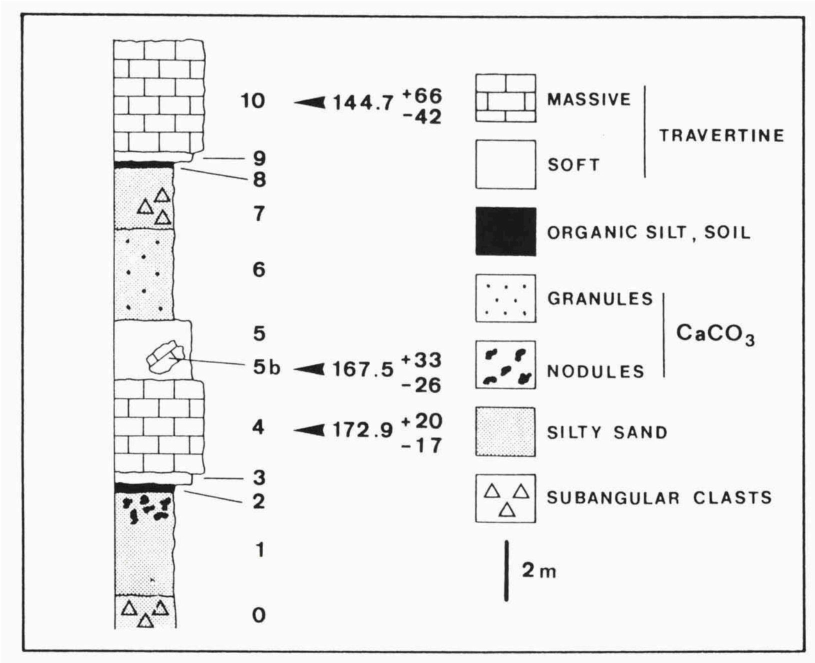

Fig. 5. Section of the Papeterie Vasino (Meyrargues, Bouches-du-Rhône). Lithostratigraphy and U/Th datings.

Finally, within the group representative of Mediterranean bioclimates, axis 3 highlights the differences between sample 2, corresponding to forest vegetation, and sample 5, characteristic of a more open vegetation of scrubland type.

From this analysis it is possible to draw two climatic curves using the coordinates of each sample on the factor axes 1 and 2 (Fig. 7). Thus, axis 1 clearly expresses a thermal gradient signifying changes in regional climate; whereas axis 2 indicates variations in local dampness which is only partly related to changes of rainfall (we have also to take into account the proper functioning of the travertine system).

The assimilation of all the data (molluscs, leaf impressions, charcoal) allows us to reconstruct the climatic history of the site.

The first climatic stage, corresponding with the lower detrital accumulation (level 0 and 1), is moderately cold and rather damp. The following interglacial stage (levels 2, 3, 4, and 5), with an annual mean temperature of 11.8°C, enables the growth of a Mediterranean deciduous oak forest. After this optimum, a second climatic deterioration is characterised by a dry and fairly cold context with a pine steppe vegetation (levels 6 and 7), becoming damper and slightly more temperate at levels 8 and 9. Level 5 marks the transition between the first temperate stage and the second climatic cooling. This provides evidence of a forest recession (*Candidula unifasciata* becoming abundant) without any climatic cooling (presence of *Rumina decollata*). Moreover, aridity seems to play an important part in the progress of steppe vegetation, as is shown by the constant presence of molluscs with relatively high thermal requirement (*Pomatias elegans*). At the top of the sequence, leaf impressions of the second

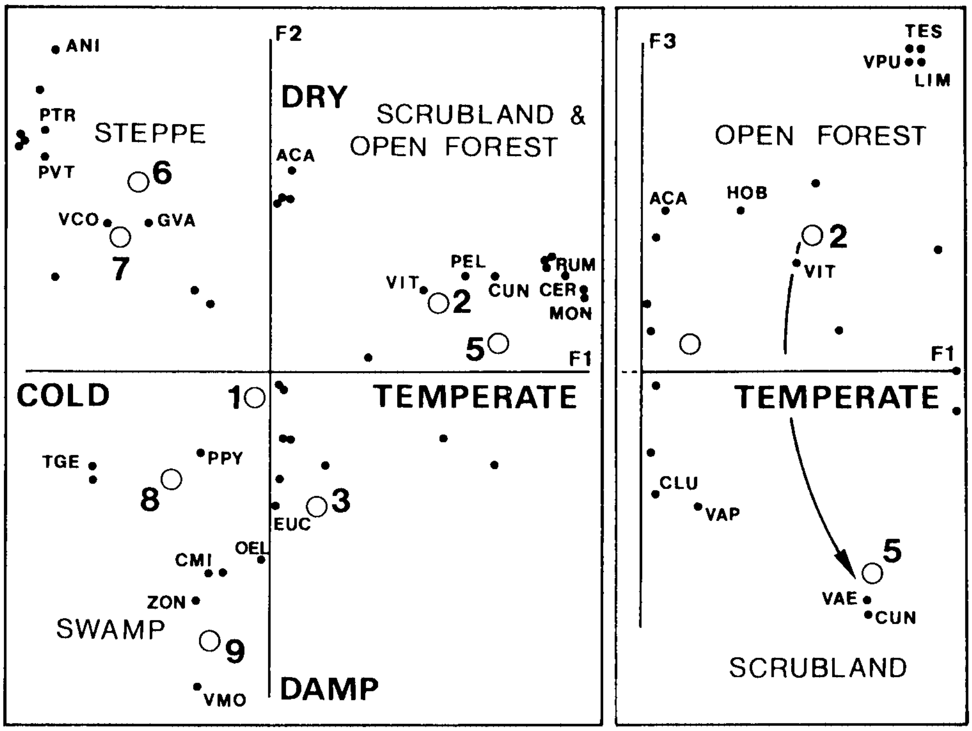

Fig. 6. Correspondence analysis of the malacofauna from the section of the Papeterie Vasino. Plot of the species (variables) and of the samples (individuals) on the factor planes 1-2 and 1-3.
Species with high contributions: CUN: *Candidula unifasciata*; PEL: *Pomatias elegans*; MON: *Monacha cantiana*; CER: *Cernuella cespitum*; VIT: *Vitrea contracta*; RUM: *Rumina decollata*; VCO: *Vallonia costata*; PTR: *Pupilla triplicata*; PVT: *Perforatella ventouxiana*; GVA: *Granaria variabilis*; TGE: *Trochoidea geyeri*; CMI: *Carychium minimum*; ZON: *Zonitoides nitidus*; OEL: *Oxyloma elegans*; VMO: *Vertigo moulinsiana*; PPY: *Punctum pygmaeum*; EUC: *Euconulus fulvus*; ACA: *Acanthinula aculeata*; ANI: *Aegopinella nitidula*; HOB: *Helicodonta obvoluta*; VPU: *Vertigo pusilla*; TES: *Testacella haliotidea*; LIM: *Limax* sp.; CLU: *Cochlicopa lubrica*; VAP: *Vallonia pulchella*; VAE: *Vallonia enniensis*.

travertine (level 10) provide evidence of a mixed forest with a supra-mediterranean climate, cooler than that of today (warmth of interglacial rank).

Comparison of the Pleistocene assemblages with modern analogues

Choice of the modern analogues

Recent snail assemblages were taken from Mont Ventoux (1909 m) which offers a whole range of bioclimatic variation, from the Mediterranean zone to the altimediterranean zone (= sub-alpine zone). Mont Ventoux is situated only 60 km to the north of the Pleistocene sequences described above (Fig. 1). Most species from these sections are found on Mont Ventoux (Magnin, 1991). Thus it is possible to compare fossil assemblages with their modern analogues that live in various bioclimatic zones.

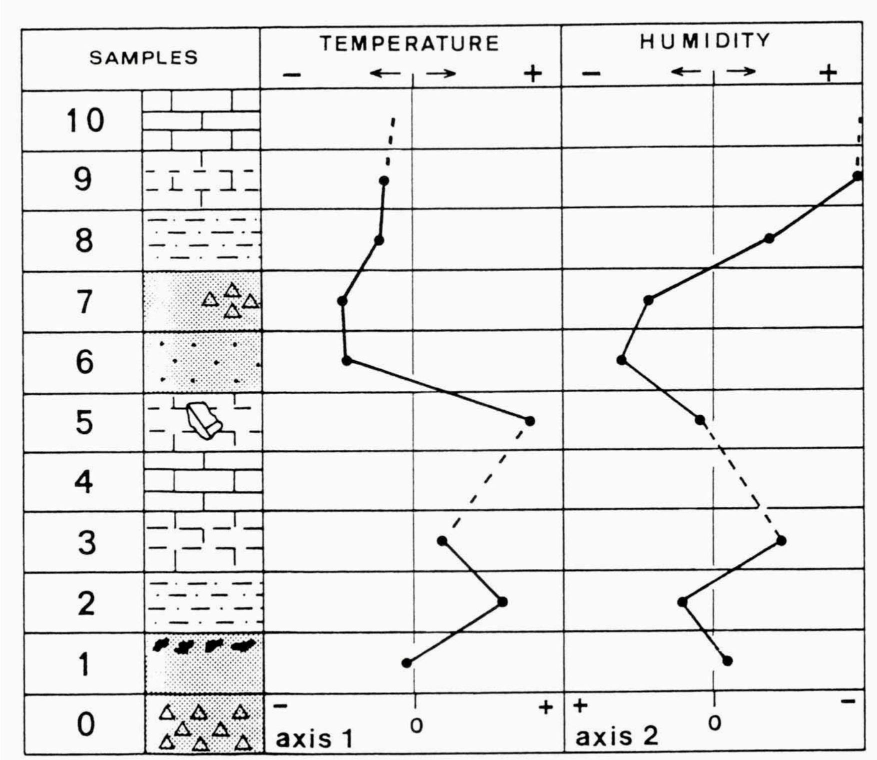

Fig. 7. Reconstruction of climatic changes from the section of the Papeterie Vasino: plot of the samples on the factor axes 1 (temperature) and 2 (humidity).

Fifty-seven Recent assemblages were sampled from different climatic and vegetational zones.

Bioclimatic significance of the Pleistocene assemblages

A data matrix comprising the 57 Recent assemblages and 42 species was constituted and studied using a correspondence analysis. Figure 8 represents the factor plane 1-2 of this analysis on which the 57 mollusc assemblages have been plotted.

Axis 1 (14.1% of the variance) clearly expresses the altitudinal gradient as is shown by the increasing size of the points from the negative to the positive side.

Axis 2 (14.0% of the variance) indicates a gradient within the structure of plant formations, from grassland on its positive side to forest on its negative side.

Now we have to answer the following question: At what height would the fossil assemblages be if they were collected today on the Mont Ventoux ? To this end we have introduced as passive individuals the 13 samples from the Pleistocene sequence of Pont-de-Mirabeau. We can thus determine the 'apparent altitude' of each fossil assemblage. For example, the samples from the top of the sequence are very similar to present day assemblages collected between 1600-1800 m in a tree-less environment, while the soil assemblages are similar to present day malacofaunas collected in

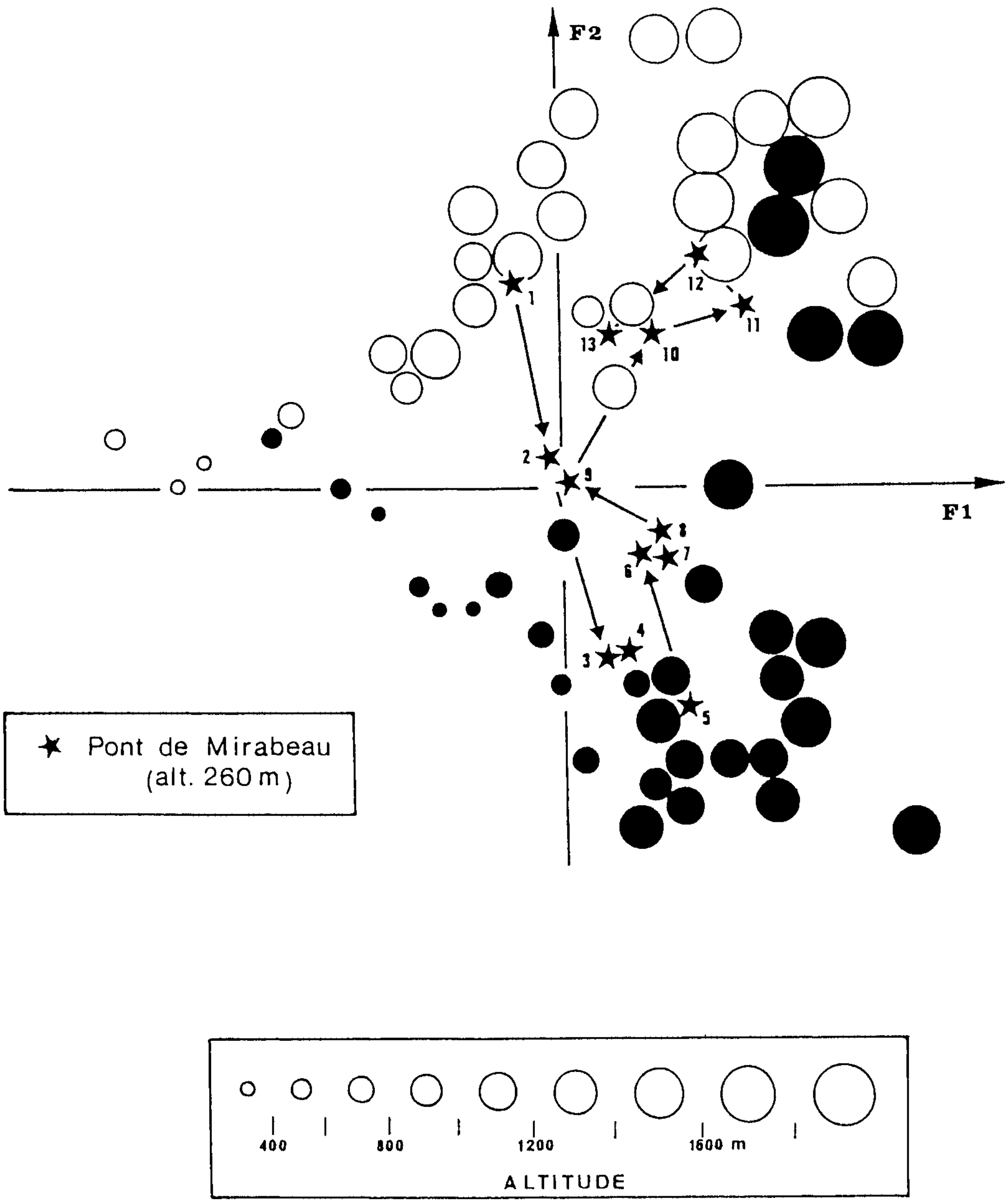

Fig. 8. Correspondence analysis of the present day Mont Ventoux malacofauna (dots), and plot of the Pleistocene assemblages from the section of Pont-de-Mirabeau, as supplementary or passive individuals, on the first factor plane of this analysis (stars).

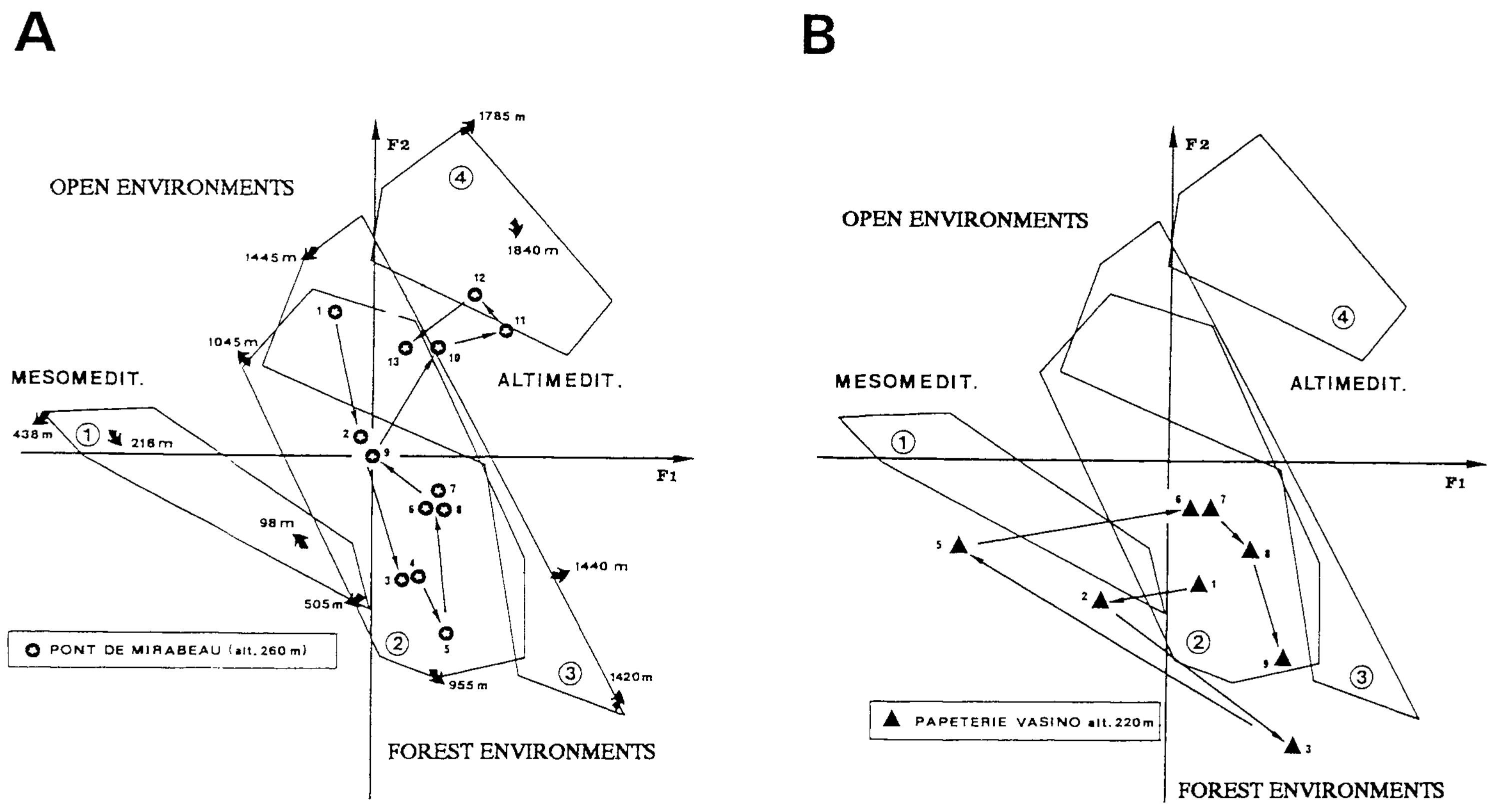

Fig. 9. Correspondence analysis of the present day Mont Ventoux malacofauna (samples regrouped according to their corresponding climatic zone), and plot of the Pleistocene assemblages (as supplementary individuals) from the sections of Pont-de-Mirabeau (Fig. 9a) and Papeterie Vasino (Fig. 9b) on the first factor plane of this analysis.
Climatic zones: 1 = meso-mediterranean; 2 = supra-mediterranean; 3 = oro-mediterranean; 4 = alti-mediterranean (or sub-alpine).

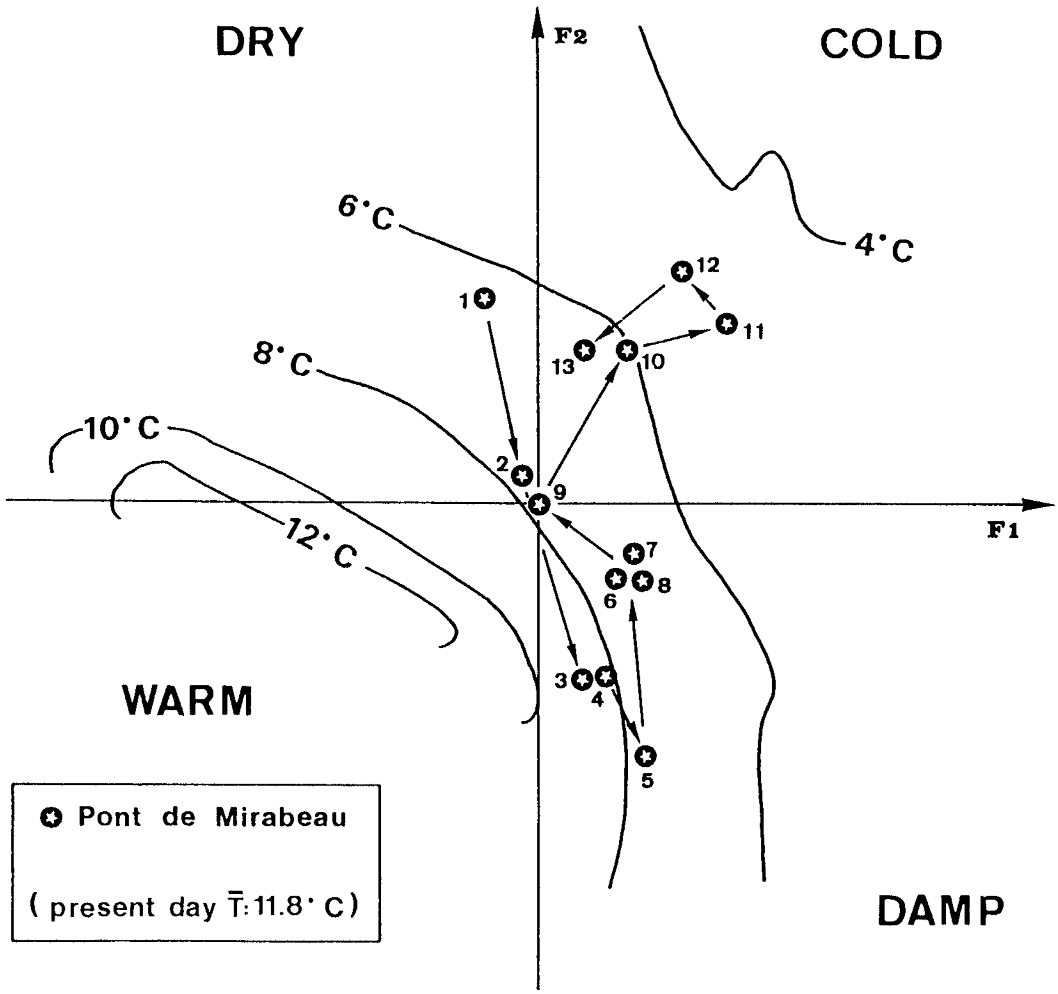

Fig. 10. Correspondence analysis of the present day Mont Ventoux malacofauna (samples regrouped according to the mean annual temperature of the sampling sites), and plot of the Pleistocene assemblages from the section of Pont-de-Mirabeau (as supplementary individuals) on the first factor plane of this analysis.

woodlands between 1000 and 1200 m (the section of Pont-de-Mirabeau is only at 260 m above sea level).

We can describe the following evolution:

- From sample 1 to sample 9 we can see the growth of a forest and then its recession; however, changes in apparent altitude are weak. From this we can hypothethise that the climatic changes were primarily concerned with rainfall rather than temperature.

- Concerning samples 11 and 12, it seems that the increasing aridity was coupled with a heavy cooling.

Cochlostoma (Cochlostoma) septemspirale (Razoumowsky, 1789)
Pomatias elegans (Müller, 1774)
Acicula (Acicula) lineata (Draparnaud, 1801)
Carychium minimum Müller, 1774
Oxyloma elegans (Risso, 1826)
Cochlicopa lubrica (Müller, 1774)
Columella columella (G. von Martens, 1830)
Truncatellina callicratis (Scacchi, 1833)
Truncatellina claustralis (Gredler, 1856)
Vertigo (Vertigo) pusilla Müller, 1774
Vertigo (Vertigo) moulinsiana (Dupuy, 1849)
Sphyradium doliolum (Bruguière, 1792)
Pagodulina pagodula (des Moulins, 1830)
Granaria variabilis (Draparnaud, 1801)
Abida secale (Draparnaud, 1801)
Abida polyodon (Draparnaud, 1801)
Chondrina avenacea (Bruguière, 1792)
Pupilla (Pupilla) triplicata (Studer, 1820)
Vallonia costata (Müller, 1774)
Vallonia pulchella (Müller, 1774)
Vallonia enniensis (Gredler, 1856)
Acanthinula aculeata (Müller, 1774)
Jaminia (Jaminia) quadridens (Müller, 1774)
Punctum (Punctum) pygmaeum (Draparnaud, 1801)
Discus (Discus) rotundatus (Müller, 1774)
Vitrinidae
Phenacolimax (Gallandia) annularis (Studer, 1820)
Vitrea (Crystallus) contracta (Westerlund, 1871)
Aegopinella pura (Alder, 1830)
Aegopinella nitidula (Draparnaud, 1805)
Oxychilus sp.
Zonitoides (Zonitoides) nitidus (Müller, 1774)
Limacidae
Limax sp.
Euconulus (Euconulus) fulvus (Müller, 1774)
Rumina decollata (Linnaeus, 1758)
Cochlodina (Cochlodina) laminata (Montagu, 1803)
Clausilia (Clausilia) parvula de Férussac, 1807
Clausilia (Clausilia) bidentata (Ström, 1765)
Testacella (Testacella) haliotidea Draparnaud, 1801
Candidula unifasciata (Poiret, 1801)
Cernuella (Xeromagna) cespitum (Draparnaud, 1801)
Trochoidea (Xeroclausa) geyeri (Soós, 1926)
Monacha (Monacha) cantiana (Montagu, 1803)
Perforatella (Monachoides) ventouxiana (Forcart, 1946)

Table 1. List of molluscan species mentioned in this paper (nomenclature after Kerney et al., 1983).

We can also express such a history in terms of altitudinal climatic zones. In the section of Pont-de-Mirabeau (pleniglacial and interstadial stages) the coldest assemblages correspond to the present day sub-alpine zone (= alti-mediterranean zone), while the warmest correspond with the supra-mediterranean zone (Fig. 9a).

The same method can be used for the section of the Papeterie Vasino (interglacial and interstadial stages). Here, the coldest assemblages correspond only with the supra-mediterranean zone, and the warmest with the meso-mediterranean zone (Fig. 9b).

Still using the same factor plane it is possible to express temperature changes. Thus, at Pont-de-Mirabeau (Fig. 10), we have an annual mean temperature of c. 8°C for the interstadial stage dated 25 ka BP (against 11.8°C today), and an annual mean temperature between 6°C and 4°C for the coldest pleniglacial stage, i.e. 6°C to 8°C below present temperatures.

Conclusions

We can interpret compositional changes in Pleistocene communities in terms of altitudinal shift of bioclimatic zones. Thus, in the Provence, pleniglacial assemblages are similar to Recent communities from sub-alpine grasslands and scrublands; interstadial assemblages correspond to communities from supra-mediterranean forests and interglacial assemblages with communities from meso-mediterranean woodlands.

This permits reliable quantitative estimates of palaeotemperatures.

However, some problems remain when attempting to estimate changes in rainfall, largely due to the difficulty in finding analogue ecosystems which are not modified by man.

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