Middle Pleniglacial to Holocene molluscan assemblages in the Marseille-Aubagne basin (Provence, France)

Des assemblages malacologiques du pléniglaciaire moyen à l’holocène dans le bassin de Marseille-Aubagne (Provence, France)

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ABSTRACT

A radiocarbon-dated sequence at Gémenos, near Marseille, has provided Pleniglacial and Holocene molluscan assemblages. The Pleniglacial succession shows only small specific changes within a malacofauna, in the main, common in periglacial deposits of south-eastern France. In the Middle Pleniglacial part of the sequence, a colluvial level dated to 38,690 ± 790 BP probably corresponds to a minor climate improvement during the marine isotopic stage (MIS) 3, potentially one of the oscillations of the Moershoofd-Pile interstadial complex. A deterioration then leads to loess accumulation with assemblages typical of cold open environments. A layer dated to 32,230 ± 490 BP appears to be only marked by an increase of humidity. It could be related to the Hengelo-Charbon interstadial. This is followed by a non-dated arid and cold phase characterized by aeolian sands that contain a very poor fauna. It may represent an undefined event in MIS 2. The subsequent warming phase is not dated, but its assemblages, in which both cold tolerant and thermophilous species can be found, are representative of the Early Holocene between 10,000 and 9,000 BP. Finally, the last levels of the sequence contain Late Holocene assemblages (ca. 4,000 BP) including several synanthropic Mediterranean snails. The present findings contradict the assumptions that the open-country snail *Pupilla muscorum* (which today is rather hygrophilous in the Mediterranean area) is not to be found in the loess of Provence, and that there is a climate-related biogeographic gradient within the malacofauna of the “Würmian” loess in south-eastern France with more xerophilic and Mediterranean assemblages near the littoral. A comparison with other MIS 3 land snail assemblages in Provence suggests a more complex regional pattern which remains difficult to comprehend owing to the lack of dated and well developed sequences in the different sub-regions of south-eastern France.

Keywords: Mediterranean France, land snails, aeolian deposits, loess, palaeoclimatic, marine isotopic stage 3, interstadials

1 - INTRODUCTION

Some fifty years ago, Bonifay (1965) published in this journal a synthesis on loess stratigraphy in south-eastern France. He noted that, before 1950, only limited loess sites were known in the Rhône and Durance valleys, providing little information on the age and stratigraphy of the deposits. From 1950, several major infrastructure works allowed the observation of more comprehensive sections in Provence (Tricart, 1952; Bourdier, 1961-1962; Bonifay, 1968).
Mazenot authored several publications on the land-snail fauna he found, mainly in the loess deposits studied by Bonifay, and revealed a progressive transition from typical northern malacofauna, near Lyon, to a southern one, with a threshold situated at the approximate 44°N latitude (Mazenot, 1956, 1965; Magnin, 1991). Unfortunately most of the molluscan assemblages were not dated as often elsewhere in the Mediterranean area (Brunnacker & Lozek, 1969; Morel, 1975; Paul, 1982). The first radiocarbon dates obtained from charcoals found in paleosoils interbedded with aeolian deposits (Ambert et al., 1974; Dubar, 1979) began to cause the relative chronology to be revised. But the fact remains that Pleistocene deposits in the Rhône valley and south-eastern France – and particularly loess and loess-like sequences – are in general lacunar, often without dating evidence, frequently with strong carbonate remobilization-accumulation, and regularly rich in coarse inclusions stressing the role of discrete sedimentary events.

Loess-like deposits near Aubagne and Gémenos were investigated as soon as 1953 by Bonifay who later distinguished, as in the Durance valley, old (Rissian) and recent (Würmian) sandy-silts separated by a red interglacial soil (Bonifay, 1962). This chronology was based upon the relations of these sediments with the Huveaune terraces (middle “Rissian” terrace at 35 m, low “Würmian” terrace at 12-15 m). Molluscan assemblages collected by Bonifay and Mazenot between 1957 and 1962 (Bonifay, 1962) do not seem to have been published. Mazenot (1956) only described, in one site (Aubagne, Les Paluns), a very poor assemblage whose the Mediterranean and xero-thermophilous nature seemed to him in accordance with a Würmian age. He thought that the typical Mediterranean assemblages found in loess-like deposits near the coast were the ending point of a north-south gradient in which the part of xero-thermophilous snails was increasing and reflected a milder climate near the Mediterranean Sea during the last cold Würmian stage (Mazenot, 1956, 1965).

That a part of the Mediterranean region experienced milder climates than north-western Europe during the cold stages, and thus harboured temperate species in refuge areas, is still a valuable paradigm (Preece, 1991; Hausdorf & Hennig, 2003; Médail & Diadema, 2009; Tzedakis et al., 2013). For this reason it was particularly important to study land snail assemblages from radiocarbon-dated cold and transition stages near the present day Mediterranean coastline.

The sequence of Plaine de Jouques at Gémenos, composed mainly of aeolian sand and loess-like sediments, provided such an opportunity to take a new step towards knowing more about Upper Pleistocene and Early Holocene land snail communities in southern Provence.

2 - STUDY SITE AND STRATIGRAPHY

The site of Plaine de Jouques at Gémenos (Bouches-du-Rhône, France) is located 15 km eastward from Marseille, and at the same distance from the coastline (fig. 1). The

sections studied in this paper are at an elevation of 110 m, on the bottom of the northern slope of the Douard (496 m) – a karstified Urgonian limestone mountain –, between the Cuges-les-Pins polje and the Huveaune valley. They were sampled during the construction of the “Plaine de Jouques” industrial park. At this place, Quaternary deposits – mainly aeolian sand and silt veneers – form a short talus slope between the Douard and Les Paluds depression which is an ancient marsh reclaimed during the xvth century (Masson & Estrangin, 1928). The particular geomorphological setting may have favoured deflation in the depression, by the dominant wind that comes from the NW sector (present-day Mistral wind), and aeolian deposits in the form of sand and silt ramps on the north-facing slope of the Douard mountain. Such a disposition can be observed elsewhere in Provence and Langedoc (Ambert, 1973, 1974, 1988, 2013).

Two sections were studied less than 100 m away from each other (fig. 2). Section I, against the mountain slope, allowed the observation of the lower part of the deposit,
down to the substratum, the upper part of the deposit being visible downstream, in section II.

The stratigraphy of section I (fig. 3) was as follows, from bottom to top:

- 6.40 m: karstified limestone filled with red clay;
- 6.40 to 6.06 m: angular limestone clasts with a red sandy silt matrix (sample 1);
- 6.06 to 5.95 m: greyish sandy silt (sample 2);
- 5.95 to 3.00 m: sandy silt (samples 3-8). In the mid-part (3.70 m to 5.00 m), three more coloured layers (brown, whitish and orange), containing some charcoals, fill a small rill;
- 3.00 to 0.75 m: aeolian cross-bedded sand (sample 9). Several lenses of limestone clasts, mostly in the lower part. This layer rests with a disconformity on the former;
- 0.75 to 0 m: unsorted clasts deposit with a sandy matrix; variable thickness; rests with a strong disconformity on the underlying aeolian unit (solifluction deposit?).

Section II showed the following stratigraphy, from bottom to top (fig. 3):

- 5.00 at least to 4.20 m: aeolian cross-bedded sand (dunes), interlayered with a bed of clasts and a bed of settled silt (sample 10). This layer would be the same as that in section I between 3.00 and 0.75 m and can be used to correlate the two sections;
- 4.20 to 3.60 m: unsorted clasts with a sandy matrix, and lenses of sand; wind-polished clasts. This layer rests with a disconformity on the former;
- 3.60 to 3.50 m: aeolian cross-bedded sand (dunes), interlayered with a bed of clasts and a bed of settled silt (sample 10). This layer would be the same as that in section I between 3.00 and 0.75 m and can be used to correlate the two sections;
- 3.50 to 2.10 m: bedded silty sand with layers of irregular calcareous concretions (samples 11-13);
- 2.10 to 1.45 m: sandy silt with scattered small irregular concretions (sample 14);
- 1.45 to 1.00 m: whitish bioturbed and calcareous unit, with rare concretions (sample 15);
- 1.00 to 0.70 m: bioturbed transition unit, with red soil aggregates (sample 16);
- 0.70 to 0.30 m: brown-red soil, well structured (sample 17);
- 0.30 to 0 m: stony horizon, disturbed by ploughing.

Fig. 3: Stratigraphy of sections I and II (Plaine de Jouques, Gémenos).

Fig. 3 : Stratigraphie des coupes I et II (Plaine de Jouques, Gémenos).
3 - RADIOCARBON DATES

Small charcoal fragments were extracted from three layers and submitted to the NSF-Arizona AMS Facility laboratory at the University of Tucson. The AMS dates obtained (tab. 1) concern sample 1 (section I, 6.30 m depth), sample 5 (section I, 4.50 m depth) and sample 16 (section II, 0.85 m depth).

4 - MOLLUSCA

4.1 - SAMPLING METHOD

A series of 17 samples was taken from the two sections for molluscan analysis (fig. 3). Very coarse-grained deposits were not sampled. Samples of about 10 litres of sediment (10-cm-thick samples) were dried out and then washed and sieved at the laboratory through a 0.5 mm mesh to extract the shells. A small quantity of 35% hydrogen peroxide was used in some cases to segregate the sediment. Molluscs were picked out under a low-power binocular microscope, and counted taking into account only whole shells, apical or apertures fragments. The method follows broadly that of Evans (1972). The systematic nomenclature used in this paper is based on Welter-Schultes (2012).

4.2 - MOLLUSCAN ASSEMBLAGES AND SUCCESION

4.2.1 - Phase A (section I)

The malacoфаuna is well preserved. The small subterraneean land snail Cecilioides acicula is possibly intrusive in samples 1 and 7. The assemblages (tab. 2, fig. 4) are poorly diversified with 15 terrestrial and 5 freshwater taxa. The average number of species per sample is 8.5. Only 7 terrestrial species are well represented by numerous shells in several samples: Vallonia costata, Abida secale, Granaria variabilis, Clausilia rugosa parvula, Xerocrassa geyeri, Pupilla triplicata and Pupilla muscorum. Apart from P. muscorum, they constitute the basis of the classical loess malacoфаuna in south-eastern France (Mazenot, 1956, 1957; Granier, 1976; Magnin, 1989, 1991, 1993a), and are the major components of most open ground communities on the mountain tops of the region (Magnin, 1991; Labaune & Magnin, 2002; Aubry et al., 2005). Indeed, the most frequent species in grazed dry grasslands between 1,450 m and 1,909 m on the Mont Ventoux are X. geyeri, P. triplicata, V. costata, A. secale and/or G. variabilis, i.e. a poor species assemblage very similar to the set of basic species found in the loess deposits in Provence. In addition, Jaminia quadridens, Oligolimax annularis and Urticicola glabellus are frequently associated with the former species, both in loess and in modern mountain assemblages. Punctum pygmaeum, and Truncatellina callicratis are however rarer in these contexts.

Along this phase, only slight changes in the malacoфаuna are noticeable, indicating modest environmental variations. Nevertheless, some original features are evidenced.

4.2.2 - Phase A1

Granaria variabilis belongs to the molluscan fauna of Mediterranean France and may have evolved during the Pleistocene in the Alpine borderland (Gittenberger, 1984). It is an open ground species, generally abundant in loess deposits in Provence (Mazenot, 1956, 1957; Magnin, 1989, 1991), and commonly found up to 1,600 m or 1,800 m in the Alps (Kerney et al., 1983; Boschi, 2011) and even 2,375 m in Queyras (Aubry, 2003). In section I, this species, as well as Jaminia quadridens and Truncatellina callicratis, occur only in the bottom samples 1 and 2. Today J. quadridens is rare above 1,300-1,400 m in the Alps (Germain, 1930-1931) although it can reach 2,000 m (Kerney et al., 1983), 2,100 m in Switzerland (Boschi, 2011) and 2,400 m in the Queyras (Aubry, 2003). Truncatellina callicratis does not jut out above 750 m near Geneva but 2,450 m in the Vaïas (Mermod, 1930). It reaches at least 1,400 m on Mont Ventoux (Magnin, 1991; Aubry, 2003) and 2,440 m in the Queyras (Aubry, 2003).

4.2.3 - Phase A2

Sample 3 displays a poor malacoфаuna, typical of loess deposits in Mediterranean France, with only four species: Abida secale, Clausilia rugosa parvula, Xerocrassa geyeri, Pupilla triplicata. In the present day, similar communities live mainly above 1,700 m in grazed, dry grasslands (Magnin, 1991; Labaune & Magnin, 2002; Aubry, 2003). Sample 4 shows the same assemblage with some Pupilla muscorum.

<table>
<thead>
<tr>
<th>Laboratory ref.</th>
<th>Sample</th>
<th>Depth (m)</th>
<th>Fraction of modern 14C</th>
<th>14C age (BP)</th>
<th>Calibrated age</th>
</tr>
</thead>
<tbody>
<tr>
<td>16473</td>
<td>Co1</td>
<td>6.3</td>
<td>0.0081 ± 0.0008</td>
<td>38,690 ± 790</td>
<td>44,263 – 41,932</td>
</tr>
<tr>
<td>16474</td>
<td>Co5</td>
<td>4.5</td>
<td>0.0181 ± 0.0011</td>
<td>32,230 ± 490</td>
<td>38,434 – 35,406</td>
</tr>
<tr>
<td>16475</td>
<td>Co16</td>
<td>0.7 to 1</td>
<td>0.5968 ± 0.0041</td>
<td>4,145 ± 55</td>
<td>4,830 – 4,528</td>
</tr>
</tbody>
</table>

*Calibrations are by Calib 6.1 software using INTCAL09 (Reimer et al., 2009).*
4.2.4 - Phase A3
The presence of *Pupilla muscorum* from sample 4 to sample 8 may be due to the development of damper habitats. The occurrence of *Vallonia costata* during the same period may confirm this hypothesis or, alternatively, that of an increasing shrub or tree cover. *P. muscorum*, however, rarely enters open woodlands or other shaded places (Evans, 1972).

4.2.5 - Phase B (sections I and II)
The assemblages are very poor with few whole shells, and fragments most often worn or corroded. This is due to the harsh depositional environment. Therefore, aeolian fluxes would have been more or less continuous during sediment accumulation. Thus, aeolian fluxes would have been more or less continuous during sediment accumulation.

4.2.6 - Phase C (section II)
Rather scarce, the malaco fauna may have suffered a redistribution of carbonate in the sediment.

4.2.7 - Phase C1
An important change can be observed in sample 13 where *Candidula rugosioscula* and *Candidula gigaxii* are associated for the first time with *Xerocrassa geyeri*. While *X. geyeri* is tolerant of harsh climate, *C. unifasciata* is an endemic species of Provence, typical of Mediterranean scarcely vegetated and dry environments, and *C. gigaxii* a land snail non-tolerant of harsh conditions, living in Mediterranean and west-European open habitats. Usually, the modern distributions of *X. geyeri* and of the two *Candidula* do not overlap. In some cases, however, the three species can be found in true Mediterranean open wood habitats, at about 400 m above sea level in Provence and Languedoc (Magnin, 1991). Here, the assemblage evidences a clear climate improvement.

4.2.8 - Phase C2
From sample 14 to sample 16, the two *Candidula* species constitute a major part of the assemblages which become more diversified. This diversification is due to the arrival (or return) of more or less open ground Mediterranean species: *Monacha cartusiana*, *Granopupa granum*, *Jaminia quadridens*, *Testacella haliotidea*. Such an assemblage of snails is typical of Mediterranean dry grasslands or open shrublands with a well developed herbaceous layer. Cold tolerant species are no longer present.

4.2.9 - Phase D (section II)
The malaco fauna of the most recent assemblage (sample 17) collected in the upper brown red soil is strongly altered. It contains several strictly Mediterranean xerophilous and thermophilous species, some of which seem to have been introduced in this area during the Neolithic period (*Oxychilus hydatinus*, *Cernuella virgata*) or even latter (*Microxeromagna lowei* / *Xerocrassa geyeri*, *P. muscorum*, *Radix putris*, *Oxyloma elegans* / *Succinea planorbidis*, *Planorbus planorbis*, *Gyraulus crista*, *Pisidium* sp. or, at least, marsh species living on the edge of water bodies (*Oxytoma elegans* / *Succinea putris*). It is likely that these marsh, xerophilous and freshwater molluscs have been transported with aeolian sand blown from temporary marsh deposits in the depression of Les Paluds, deflated by a strong NW sector wind. Therefore, aeolian fluxes would have been more or less continuous during sediment accumulation.

4.3 - COMMENTS ON SELECTED TAXA

4.3.1 - Freshwater and marsh species
Unexpectedly, fragmented shells of freshwater and marsh taxa are present in almost each sample, and even in aeolian sands. This is not in accordance with:
- the dominant snails which characterises dry habitats;
- the steepness of the deposit, about 55°;
- the silty or sandy texture of the sediment which do not show any hydromorphic traits;
- the configuration of the site, on the piedmont of the mountain, but far from the possible location of temporary marshes.

There is no evidence for the presence of a marsh environment at the place of the section. Such evidence would have been found with the occurrence of marsh species but, apart from one shell of *Vallonia pulchella* – a hygrophilous snail – in sample 9, these species are lacking. All the taxa from damp habitats found in this section are true freshwater species: *Radix bathica*, *Stagnicola fuscus* / *Stagnicola palustris*, *Planorbus planorbidis*, *Gyraulus crista*, *Pisidium* sp. or, at least, marsh species living on the edge of water bodies (*Oxytoma elegans* / *Succinea putris*). It is likely that these marsh, hygrophilous and freshwater molluscs have been transported with aeolian sand blown from temporary marsh deposits in the depression of Les Paluds, deflated by a strong NW sector wind. Thus, aeolian fluxes would have been more or less continuous during sediment accumulation.

4.3.2 - *Urticicola glabellus* (Draparnaud)
Kerney et al. (1983) made *U. glabellus* a synonym of *U. ventouxiannus* and, in my opinion, they are right. Falkner et al. (2002) provide a very complex scheme for *Urticicola* in France, with 5 species and 3 subspecies, but I believe that this interpretation needs to be tested using unified criteria. Welter-Schultes (2012) is of the same view. Today *U. glabellus* lives in rather dry, very open or light wooded habitats, from 200 m to more than 2,000 m in the Alps (Maguin, 1991; Aubry, 2003). It seems to be more frequent today in upland grasslands (Mont Ventoux, Lure mountain) than in periglacial Pleistocene deposits. Only two shells were collected here in sample 7.

4.3.3 - *Vallonia costata* (Müller)
Climatically very tolerant, abundant in loess deposits throughout Europe – except during extreme climatic conditions in north-west Europe –, this species is generally known to characterise open habitats (Evans, 1972; Puisségur, 1976). Nevertheless it has been shown that...
Triplicata can live in several kinds of habitats, although it is more prevalent in grasslands than in open woodlands (Evans, 1972). In Provence, V. costata is an open-ground species at high elevation (e.g., above 1,650 m on Mont Ventoux) and a woodland species living in leaf litter in the Mediterranean and supra-Mediterranean zones (Magnin, 1991; Martin & Magnin, 2002). It is also found occasionally in marshes (Evans, 1972 and pers. obs.). We are in the case of a compensation of ecological factors (Rübel, 1935), i.e. the condition when one or a group of limiting factors for an organism is counteracted by an excess or difference of other factors. For instance, on the Ventoux mountain top grasslands, dew – or maybe snow cover –, could replace the humidity that occurs in the litter of shaded woodlands at lower altitude. Within Plaine de Jouques section I, V. costata characterizes molluscan phase A3 but it is very difficult to determine the meaning of this occurrence. An increase of relative humidity during selected seasons would be a plausible assumption.

4.3.4 - Papilla muscorum (Linnaeus) and Papilla triplicata (Studer)

Papilla muscorum is a Holarctic open-ground species, characteristic of grassland habitats, but rarely entering woods and other shaded places (Evans, 1972). It attains 2,500 m in Switzerland (Boschi, 2011). P. muscorum is one of the commonest land snails of the cold periods during the Pleistocene in Britain and north-west Europe (Rousseau, 1985; Limondin-Lozouet & Gauthier, 2003). It is frequent and abundant in loess deposits in the middle Rhône valley (between Vienne and Orange), rarer southward, and totally lacking in Provence (Mazenot, 1956; Granier, 1976) apart from the suspicious site of “Clos Marie-Louise” near Aix-en-Provence (Mazenot, 1956; Granier, 1976). It is frequent and abundant in loess deposits of northern Europe and the Quaternary deposits of Provence and Durance valley. This observation is confirmed by more recent studies such as those of Dubar and Magnin (Dubar, 1979; Aubry, 2003).

Papilla triplicata is a mountain alpine and East European species, generally more xerophilous than P. muscorum (although it can occasionally live, as P. muscorum, in wetter places). It exhibits a large altitudinal range extending to 2,800 m in the French Alps (Aubry, 2003). P. triplicata exhibits the same kind of pattern as V. costata: frequently living in Mediterranean woods, it is also found in subalpine and alpine grasslands (Magnin, 1991; Aubry, 2003).

Mazenot (1956, 1965) has shown that P. muscorum, frequent in loess deposits of northern Europe and the middle Rhône valley, is replaced by P. triplicata in the Quaternary deposits of Provence and Durance valley. This observation is confirmed by more recent studies such as those of Dubar and Magnin (Dubar, 1979;
Fig. 4: Malacological diagram for Plaine de Jouques. All values are expressed as percentages of total shells. Grey bars indicate very poor assemblages.

**Fig. 4 :** Diagramme malacologique de Plaine de Jouques. Toutes les valeurs sont exprimées en pourcentages du total de coquilles. Les assemblages très pauvres sont en grisé.
Magnin, 1991, 1992). The presence of *P. muscorum* in the Gémenos deposits shows, however, that this species was not completely absent in the Mediterranean region during certain Upper Pleistocene cold stages.

The frequencies of *P. muscorum* and *P. triplicata* in this sequence present a pattern which is difficult to interpret. *P. muscorum* appears in sample 4 and increases up to sample 7 where *P. triplicata* disappears. In sample 8, *P. triplicata* becomes more abundant whilst the *P. muscorum* population collapses. One hypothesis is that *P. muscorum* benefited from more humid conditions during the deposit of the mid-part of section I (mainly phase A3).

### 4.3.5 - *Candidula rugosiuscula* (Michaud)

*Candidula rugosiuscula* is an endemic snail in Provence. It has long been considered as synonym of *C. unifasciata* (Kerney et al., 1983) but it has been shown that *C. unifasciata* and *C. rugosiuscula* are sister species, the speciation of the latter being probably a result of climatic events around 3.2 Myr (Pfenninger & Magnin, 2001; Pfenninger & Posada, 2002). Morphometric shell analysis reveals that the divergence between the sister species is a result of desiccation-resistant shell characters (Pfenninger et al., 2003a). Unfortunately shell characteristics are sometimes poor discriminating markers owing to a strong polymorphism of *C. unifasciata*, with a convergence of the two species toward coarse ribbed forms in arid habitats. The shells collected at Gémenos have very coarse ribs and most likely belong to *C. rugosiuscula*.

### 4.3.6 - *Oligolimax annularis* (Studer)

This species has a wide modern range from the Cantabrian Mountains, the Pyrenees and central Spain, to the mountains of Iran (Gittenberger & Goodfriend, 1993). This is an almost exclusively high Alpine snail, reaching elevations of 2,800 m (Turner et al., 1998). On the Dolomites, it lives between 1,250 and 2,718 m with a peak frequency between 2,200 and 2,718 m (Forcart, 1956). It has been recorded in the Hautes-Pyrénées at only 600 m by Colas et al. (1983) who suggested that this is not strictly a mountain species. In Valais, Mermod (1930) has shown that *O. annularis* lives either in dry habitats of the bottom of the Rhône valley or in true high Alpine environments.

In Provence and Hautes-Alpes, it has been found up to 2,700 m on Queyras mountains and between 1,600 to 1,800 m on Mont Ventoux (Magnin, 1991). However, close to Gémenos, on the Sainte-Baume mountain, *O. annularis* lives at 900 m in elevation together with thermophilous and Mediterranean species (Magnin, 1991). Such populations, located in small temperate refuges, would indicate that the species is not strictly limited by climatic factors although the main populations have a high mountain distribution.

*O. annularis* can be found in several Pleistocene deposits in Provence, down to the present day sea level (Mazenot, 1956; Magnin, 1991, 1993a). The same altitudinal changes in distribution between Pleniglacial and recent populations of *O. annularis* has been observed in southern Greece by Gittenberger and Goodfriend (1993). This is an open ground species, frequent in rocky and karst habitats although it is tolerant of a tree cover not to exceed 40 %. A few shells were recovered from the two dated Pleistocene samples 1 and 5 and could indicate a light tree cover.

### 4.3.7 - *Xerocrassa geyeri* (Soós)

Quaternary dynamics of *X. geyeri* populations must be compared to that of *O. annularis* although the former species is more frequent than the latter, today as in the past. In south-east France, *X. geyeri* now presents a very discontinuous range, limited to mountain tops, dwelling in dry grasslands and open scrublands generally above 900-1,000 m (Magnin, 1989). It is rarely found in open woodlands, as it prefers a tree cover below 10 %. It is still found near Gémenos on the Sainte-Baume mountain top, together with *O. annularis* (Magnin, 1991). However, low-altitude populations can be found and there is some evidence that a temperate climate is not a prime limiting factor for this species, present day distribution being explained partly by competitive interaction with *C. unifasciata* (Magnin, 1993b).

*X. geyeri* is a common element of cold Pleistocene assemblages from the middle Rhône valley and western Languedoc, down to the present Mediterranean coastline (Magnin, 1989). This is undoubtedly a cold tolerant species since populations would have survived the Late Glacial Maximum in Germany (Pfenninger et al., 2003b). Nevertheless, in south-east England, Normandy, Charente and Burgundy, *X. geyeri* is found only in interstadial or transitional assemblages indicating a dry or very dry and moderately cold climate (Magnin, 1989). In addition *X. geyeri* occurs in particular interglacial deposits in England (Sparks, 1953; Preece, 1990, 2001).

*X. geyeri* is by far the commonest snail at Plaine de Jouques. It only makes room for more thermophilous Hygromiidae (*C. rugosiuscula* and *C. gigaxii*) in the younger assemblages, following a succession already described (Magnin, 1993b).

### 4.3.8 - *Candidula gigaxii* (Pfeiffer)

Provence is the area of origin of *C. gigaxii* (Pfenninger et al., 2007). The first fossil occurrence of the species is dated to 12,720 ± 170 BP in a site at Bouc-Bel-Air, between Aix-en-Provence and Marseille (Magnin, unpubl. data). Populations of this snail seems to increase dramatically at 8,905 ± 90 BP (Magnin, 1997) together with *Candidula unifasciata* (or *C. rugosiuscula*) whilst the occurrence of *X. geyeri* progressively decreases at low altitude (Magnin, 1993b). Today *C. gigaxii* has a Mediterranean and Atlantic range due to temperature requirements. In Provence it can be found in dry grassland, garrigues and open woodlands up to 950 m, and generally below 600 m (Magnin, 1991; Aubry, 2003).
At Plaine de Jouques, the progressive replacement, from sample 13, of *X. geyeri* by the two ecologically related species *C. gigaxii* and *C. rugosiussula*, most likely take place during the Early Holocene, between approximately 10,000 and 9,000 BP according to a similar succession observed at Laudun, Gard (Magnin, 1997).

5 - PALAEENVIRONMENTAL IMPLICATIONS OF THE MOLLUSCAN SUCCESSION

As stated above, the Pleistocene molluscan succession shows only small specific changes. All the assemblages characterize a very open vegetation with a cold and arid climate. However, several molluscan phases can be identified. Phase A1 corresponds to samples 1 and 2 and seems to indicate a climate dryer and less severe than that of the following phases, since one can find some xerophilic species (*J. quadridens*, *G. variabilis*, *T. callicratis*) which are lacking in the remainder of the Pleistocene sequence, and which now are not very frequent at high altitude in the Alps. Such species disappear in phase 2 in which we found assemblages maybe representative of a slightly more humid and cold climate. Phase A3 corresponds to samples 5 to 8 where *P. muscorum* – a species usually missing in Provence loess deposits – could indicate an increase of humidity supported by the fact that these layers fill a small rill. The presence of charcoals and of fragments – of the least wooded environment which, however, must have existed.

6 - CHRONOLOGICAL HYPOTHESES

One can summarise the paleoenvironments at Gémenos in the following manner. The red and grey layers at the bottom of the sequence (phase A1, samples 1 and 2), dated 38,690 ± 790 BP (in sample 1) probably corresponds to a minor climate improvement during the Middle Pleniglacial (MIS 3). However, this slight climatic amelioration does not lead to woodland but only to dry grasslands or scrublands, possibly with a very clear tree cover. The temperature was comparable to that of the present day supra-Mediterranean belt in Provence, between 1,000 and 1,500 m in elevation. An estimate using Mont Ventoux modern analogues (Magnin, 1991) gave a mean annual temperature of 6°C and a mean temperature for January above 0°C (the present day mean annual temperature at the site is 13°C). Such temperatures are not sufficient to account for the non-appearance of woodland, which must be explained either by an arid climate or by a time-lag due to the distance from tree (and/or snail) refugia and the short duration of the climate improvement. This slight climatic amelioration may correspond to a MIS 3 interstadial that could be contemporary with Hengelo-Charbon (MIS 3: 38-37 ka BP; Guiter et al., 2003) corresponding to Lazio III and Monticchio PAZ 9 (40-37.6 ka cal. BP; Allen & Huntley, 2000) or more likely with one of the oscillations of the Moershoofd-Pile interstadial complex (MIS 3: 50-43 ka BP) corresponding to Lazio II and Monticchio PAZ 11 (50-42.3 ka cal. BP).

A deterioration led to loess deposition with snail assemblages typical of cold open environments, impoverished and devoid of any thermophilous species (phase A2, samples 3 and 4). Estimate mentioned above provided a mean annual temperature between 6 and 4°C, the mean temperature for January being below 0°C.

The same estimate did not show any rise of temperature during the remainder of the loess deposit and the layer dated to 32,230 ± 490 BP (sample 5) which appears to be marked only by an increase of humidity, shown by the presence of species more tolerant of moisture (*V. costata, P. muscorum*) and perhaps of shade (*V. costata, O. annularis*). This is consistent with the rill erosion/sedimentation observed during phase A3 (samples 5 to 8). We can hypothesize from the 14C date in sample 5 that this phase could be related to the Hengelo-Charbon interstadial. Van Huissteden and Pollard (2003) reports, from Dutch fluvial sequences, increased atmospheric precipitation during the Hengelo interstadial. This does apply at Gémenos where an increase in precipitation is consistent with the assemblages of samples 5–8.

Non-dated phase B (samples 9-12) was roughly arid and probably cold. Powerful winds formed sand dunes.
which contain a very poor malacofauna owing to such depositional environment. A solifluxion or brief torrential event occurred. The whole phase B may represent an undefined part of the Upper Pleniglacial (MIS 2 pro parte: 29-15 ka).

The beginning of the following warming phase C (sample 13 at least) is not dated. However its malacofauna is typical of the Early Holocene between approximately 10,000 and 9,000 BP. This first warming step did not allow shade-loving species to immigrate from their refugia, but only led xero-thermophilous open-ground species (e.g. *C. gigaxii*) to expand in the area. The age of sample 16 (4,145 ± 55 BP) is in agreement with the malacofauna and the presence in the preceding sample of *Cernuella virgata*, a synanthropic snail that has undergone a wide range expansion during the Middle and Late Neolithic in Mediterranean France (Magnin & Martin, 2012).

The upper part of the sequence (phase D, sample 17) probably follows a long period of human impact on the landscape, accompanied by the introduction and/or range expansion of several Mediterranean species. Soil erosion seems to be responsible for the hiatus between Early Holocene deposits and this Late Holocene soil.

From these results it is clear that Mazenot was wrong when he generalized a biogeographical gradient within the malacofauna of the “Würmian” loess in south-east France, the assemblages of the Durance valley being more xerophilic than those of the Durance valley and Mediterranean than those of the Rhône valley. The malacofauna of Plaine de Jouques exhibits some affinities both with Rhône and Durance assemblages. *P. muscorum*, for instance, present in the Rhône valley, but replaced by *P. triplicata* in the Durance, is present in several samples in loess-like deposits at Plaine de Jouques.

Other molluscan assemblages were recently studied at Aix-en-Provence [Collège Mignet (Magnin & Bonnet, this issue)] and in the Grand Luberon mountain (Magnin in Ollivier, 2006, and Ollivier et al., 2014).

At Collège Mignet (Aix-en-Provence), several assemblages (one dated 38,273 ± 400 BP) could be contemporary to phase I (samples 1-2) at Plaine de Jouques. However they were found in alluvial and marsh deposits and have a higher species richness for they contain a mix of freshwater, marsh, woodland and open-ground molluscs. Furthermore, these assemblages include some typical Mediterranean thermophilous species that are lacking – as well as shade-loving species – at Plaine de Jouques, even if in both sites cold-tolerant species and more tolerant ones could coexist.

In the Grand Luberon, also shows a molluscan succession in which two dates (37,000 ± 700 BP and 38,900 ± 600 BP) could allow to relate it to both Collège Mignet and the oldest assemblages of Plaine de Jouques. Rich assemblages were collected in alluvial silts showing loess-like traits and in an upper-lying brown soil. They indicate a light woodland or pre-forest environment and a Mediterranean climate at least as warm as today, with thermophilous snails like *Pomatias elegans* and *Rumina decollata*. The latter species is known as characteristic of interglacials. Therefore, the MIR 11 succession has some common ground with that of Collège Mignet, despite variations mainly due to dissimilar geomorphological settings. The two ^14C dates would allow to ascribe MIR 11 assemblages to the Moershoofd-Pile interstadial (Ollivier, 2006). Such a correlation may be consistent with evidences from other proxies in northern Europe (Coope & Angus, 1975; Coope et al., 1997; Vandenbergh et al., 1998).

To recapitulate, the oldest assemblage of Plaine de Jouques, the whole succession of MIR 11 (Luberon) and a large part of that of Collège Mignet (Aix-en-Provence) could be placed within the Moershoofd-Pile interstadial which seems to be composed of a succession of short-term warm and cold phases (Guiter et al., 2003). Yet it would be difficult to classify these assemblages in what is called a biozone, and it is not possible to correlate the different sequences on the basis of their molluscan specific composition. There are at least two reasons for that. First, the Moershoofd-Pile interstadial is a complex of different short warm and cold periods whose ages are sometimes near the limit of the radiocarbon method (Guiter et al., 2003). It is therefore possible that the assemblages described do not correspond to the same temperate phase, even more because the sequences are usually short, discontinuous, and have little potential for high-resolution analyses. Second, Dubar (1983) noted that the loess malaco-fauna in the Durance valley varies according to the local geomorphology and topography, which can affect local climate and environment (slope proximity, shady or sunny side of a mountain, main stream or tributaries...). The physiographic diversity of the region, thus,
preclude the possibility of a biozonation, inter-site variability being possibly greater than potential intra-site variability between warm peaks.

Again in Provence, Dubar (1979) and Magnin (d’Anna et al., 1988; Magnin, 1991, 1992, 1993a) described Middle Pleniglacial assemblages largely dominated by shade-loving species. At La Tuilière de Saint-Saturnin (Villeuneuve, Alpes-de-Haute-Provence) an assemblage, radiocarbon-dated between 37,000 and 30,000 BP and attributed to the Hengelo interstadial, showed 81.15 % of woodland snails including a large number of Cochlostoma septemspirale and the rather thermophilous Pomatias elegans (Dubar, 1979). This assemblage was quite similar to that found by the same author (Dubar, 1979) 25 km southward at Saint-Paul-Lez-Durance (Bouches-du-Rhône) in a paleosol radiocarbon-dated to 26,550 + 5,000 - 3,000 BP. However, a new 14C dating for this latter soil gave a far older age at about 52,000 yr cal. BP (Diaz del Olmo, pers. com. in Ollivier, 2006). Further south, d’Anna et al. (1988) described at Roquevaire, near Gémenos, another Middle Pleniglacial woodland assemblage, with numerous Pomatias elegans, in a soil interlayered with a travertine and dated (14C and U/Th) between 30,000 and 50,000 BP.

These latter typical woodland assemblages, in which shade-loving snails are clearly more abundant than in MIR 11 (Luberon) and Collège Mignet (Aix) assemblages, may be connected to an indeterminate warm peak of the Moershoofd-Pile complex, but the dates currently available appear so questionable that they could be correlated as well with one of the interstadials at the beginning of the last glacial (MIS 5d-a).

New analyses should be conducted to clarify the chronology of these sites that have been studied long ago. There is certainly a complex pattern combining biogeographical, ecological and stratigraphical meanings which is difficult to comprehend owing to the lack of dated and well developed sequences in the different sub-regions of south-east France.

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