A RELICT POPULATION OF *RETINELLA OLIVETORUM* IN SOUTHERN FRANCE. BIOGEOGRAPHICAL AND HISTORICAL IMPLICATIONS

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Abstract *We consider* Zonites herculeus *Rambur, a Pleistocene fossil land snail of the French Riviera described at the end of the 19th century, a synonym of* Retinella olivetorum *(Gmelin), a shade loving species until now considered endemic to Italy. We report the recent discovery of both living and Holocene* R. olivetorum *near Aix-en-Provence (France), about 250 km from the western boundary of its main range. The origin of this disjunct range is discussed. The most consistent hypothesis is the fragmentation of a large Eemian range during the succeeding glacial stage. The persistence of the species through scattered refugia is considered. The resilience of the only French* R. olivetorum *population to wildfires is also examined.*

Key words Retinella, olivetorum, *Eemian, Neolithic, refugia, disjunct range, wildfire*

INTRODUCTION

Retinella olivetorum (Gmelin 1791) is a large member of the Oxychilidae (8–15×17–33 mm) considered to be endemic to Italy. Its distribution is centred on the Ligurian and Tuscan Apennines but reaches southern Italy and Sicily. Alzona (1971) listed subspecies *R. olivetorum olivetorum* (Gmelin 1791) from north-western and central Italy (Fig. 1) and subspecies *R. olivetorum icterica* (Tiberi 1872) from Campania, Lucania and Calabria.

Zonites herculeus, a subfossil species described from Monaco, is said by Rambur (1868, 1869) to be larger than typical *H. olivetorum*. Collecting in Quaternary land-snail deposits in the neighbourhood of Menton, Nevill (1880) found a single specimen of *Hyalina* (*Retinella*) *herculea* (*Zonites herculea*) together with *Hyalina* (*Retinella*) *olivetorum* "by thousands", in coastal deposits. He observed that *R. olivetorum* evidently abounded during some stages of the Quaternary although it no longer survives on the French Riviera. He outlined a zonation of the deposits based on molluscan assemblages and believed that the assemblage with *R. olivetorum* and *R. herculea* "have immediately preceded the present fauna, without any very marked break, either of change in the climate or otherwise", for it contained a profusion of "present-existing species". Dubar (1984, 1986) has shown that a zone characterised by *R. olivetorum* actually exists but must be attributed to a climatic optimum of the Eemian interglacial. This interpretation has recently been

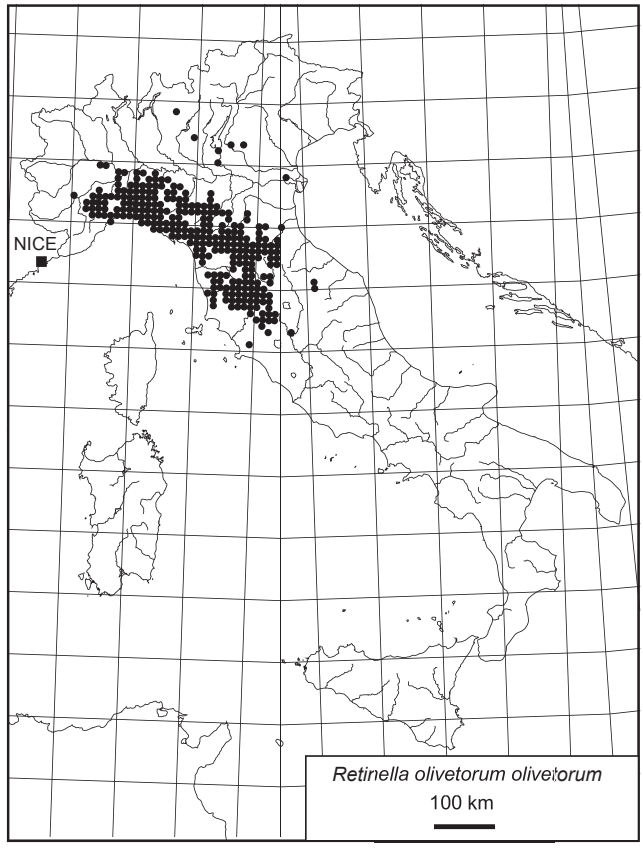

Figure 1 Distribution map of *Retinella olivetorum* (Gmelin) in Italy (unpublished data courtesy of Marco Bodon, Simone Cianfanelli, Folco Giusti and Ettore Bo).

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confirmed with an absolute age of circa 130 ky (Dubar, Innocent & Sivan, 2008).

Fagot (1880), Germain (1930–1931), and all authors succeeding them agreed that *R. olivetorum* is no longer extant in France. Recently we have found both a living population of *R. olivetorum* and numerous Holocene shells in an area near Aix-en-Provence (Bouches-du-Rhône, France).

In this paper we intend to: (1) review the status of *Retinella olivetorum*, *Retinella herculea* and related taxa; (2) summarize the available data regarding *R. olivetorum* in the last interglacial deposits in Provence and the French Riviera; (3) describe the postglacial assemblages with *R. olivetorum* recently discovered near Aix-en-Provence; (4) report the first living population in France, found in the same area. Subsequently we shall examine the main question raised by these new observations, i.e. the origin of the present day disjunct range of *R. olivetorum* and its consequences both to Pleistocene biostratigraphy and to species conservation.

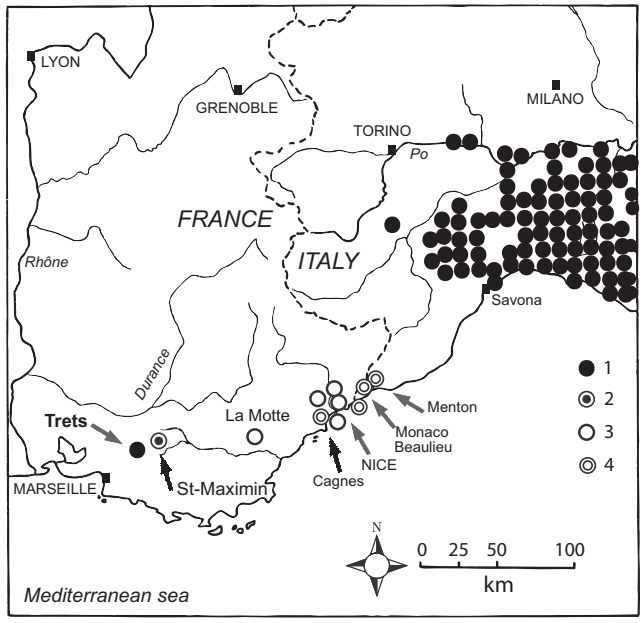

Figure 2 Distribution map of *Retinella olivetorum* (Gmelin) from Provence (France) to Ligurian Apennines (Italy), Pleistocene to Recent. 1 Recent disjunct range, 2 Neolithic and Bronze Age locality, 3 Eemian locality, 4 Pleistocene localities according to 19th century authors.

Material and methods

Holocene sediment samples from Saint-Maximin (Var) were extracted according to the classical methods of Evans (1972) and Puisségur (1976). A recent leaf litter sample (Trets, Bouches-du-Rhône) was dried in a drying oven, and then immersed in water. Floating particles were collected in a 0.5 mm mesh sieve and shells were separated under magnification from plant material.

Results

Review of Retinella olivetorum, Retinella herculea *and related taxa* Rambur (1868) gave a short Latin diagnosis of "*Zonites herculeus*", a subfossil species from Monaco (Fig. 2). Soon after (Rambur, 1869) he added a full French description of the shell and of the geological context. According to Rambur the shell of "*Z. herculeus*" has a diameter larger than typical for *R. olivetorum*. However, in his Latin diagnosis a size ("Diam. Maj. 19½, min. 16, alt. 10 mill.") smaller than that of typical *R. olivetorum* is quoted. In the same diagnosis, although none of the three specimens he collected had a complete aperture, he compares the aperture with that of "*Helix nitida*" (= *Zonitoides nitidus* (Müller 1774)). These deficiencies underline the weakness of the original diagnosis of *R. herculea*. Maury & Caziot (1906) include a brief description of the species and note the incompleteness of the shells.

Nevill (1880) found a single specimen of *R. herculea* described as a "rare, well-marked, and very distinct species" in deposits at Cap Mortola. At the same time he collected numerous *R. olivetorum* between Monaco and Cap Mortola. He noted that the largest form of this polymorphic species closely resemble specimens he possessed from Lucca (Italy) although "the spire in the Menton specimens is more depressed, slightly less convex, and markedly more central". Nevill also described two new varieties of *R. olivetorum* (var. *macrobiotus* and subvar. *subincerta*) and a new species (*R. likes*) "easily distinguished from all varieties of *R. olivetorum*".

In their synthesis of the Pleistocene land-snails of the French Liguria and Alpes-Maritimes, Caziot & Maury (1909) considered the following species related to *R. olivetorum*: *R. herculea* (Rambur), the most frequent form according to the authors

who found it at several sites near Menton, Nice and Beaulieu, in deposits older than the most recent part of the Upper Pleistocene; *R. olivetorum* (Gmelin) and its forms *macrobiotus* Nevill and *subincerta* Nevill, a species with the same stratigraphical distribution as *R. herculea* and found at Menton; *R. subolivetorum* (Maury & Caziot 1905), described from the Middle Pleistocene and the lower part of the Upper Pleistocene at Cap Martin, a species closer to *R. olivetorum* than *R. herculea; R. likes* (Nevill 1880), a slightly different species that Germain (1930–1931) includes in the *R. olivetorum* complex.

In a later paper (Caziot & Maury, 1912), mention of *R. herculea* is omitted, and instead *R. olivetorum* is listed from Quaternary deposits between Cros de Cagnes and Cagnes, and at Beaulieu-sur-mer. Germain confirmed most of the shells collected.

In fact Germain (1930–1931) considered *R. herculea* and *R. olivetorum* to be synonyms. *R. olivetorum* is mentioned as a species endemic to Italy that lived on the French Riviera during the Quaternary, together with the forms *macrobiotus* and *subincerta*, and with the closely related *R. likes*. In contrast, Granier (1976) mentioned *R. herculea* as an extinct species from the lower and middle Pleistocene of the Côte d'Azur (Menton, Monaco, Nice, Beaulieu etc.) implicitly suggesting that *R. olivetorum* never lived in the area where it had been replaced by the closely related *R. herculea*. Granier had no direct experience of these two species and gave a superficial and curtailed account of the literature on the subject, overlooking the changes of opinion that had taken place. Unfortunately the opinion of Granier influenced subsequent authors (Dubar, 1984).

The profuse material collected by Dubar since 1980 enables a clarification of both the status of the fossil *Retinella* on the French Riviera and the age of the corresponding sediments.

Retinella olivetorum *in the last interglacial deposits of South-eastern France* During his field researches on the Quaternary deposits of the Nice area, Dubar (1984) found four of the reputed extinct species described at the end of the 19th century, i.e. *Glandina antiqua* Issel 1867, *Cepaea paretiana* (Issel 1867), *Daudebardia isseliana* Nevill 1880 and *Retinella herculea* (Rambur 1868), the latter species considered by him to be a large form of *R. olivetorum* since large forms of modern species such as *Cepaea nemoralis* (Linnaeus 1758) and *Pomatias elegans* (Müller 1774) are found in these deposits. All the specimens collected by Dubar from different sites belong to one species and are very similar in shell shape to *Retinella olivetorum*. Maximum major diameter of well-preserved specimens is 30.0 mm (Fig. 3) and compatible with the maximum shell size recorded for living *R. olivetorum* in Italy of 33.0 mm (Cianfanelli, 2009; Cianfanelli & Lori, 2007).

The age of the deposits studied above is uncertain. Dubar (1984) showed that the "extinct species" and *R. olivetorum* were index fossils of the last interglacial (Eemian) in the Nice area. Further researches on newly discovered sites enabled Dubar (1986; 1995; Dubar *et al.*, 2008) to confirm this chronological attribution (Fig. 2, Fig. 3, Table 1). Most of these species do not exist in Quaternary deposits of this area either older or younger than the Eemian. They are thought to have extended their range westward under the favourable bioclimatic conditions of this interglacial (Dubar, 1984). A zonation has been proposed for the order of appearance of these species in the region using heavy isotope ratios (Dubar, 1986): first appearance of the "extinct species" with *Glandina isseli* during OIS 6 lateglacial; optimum occurrence with *Retinella olivetorum* during OIS 5e; regression phase with *Cepaea paretiana* during OIS 5d and 5C; the "extinct species" and *R. olivetorum* no longer in OIS 5b.

In the Nice area, *R. olivetorum* is actually characteristic of the Eemian interglacial (OIS 5e, between 130 and 125 ky). Uranium-Thorium dating of *R. olivetorum* shells gives ages of 131 and 132 ± 1 ky (Table 1) (Dubar *et al.*, 2008) in conformity with this interpretation. *R. olivetorum* was also recently collected in an Eemian tufa at La Motte (Var) (Fig. 2, Table 1). This is the most western known Eemian locality for the species.

The rich Eemian assemblages which contain *R. olivetorum* are typical of woodland habitats (Table 2). Charcoal analysis (unpublished data) indicates a deciduous oak forest in which hop hornbeam (*Ostrya carpinifolia* Scop.) and beech (*Fagus sylvatica* L.) are present. Thus, mesophilous woodlands may have spread out from western Liguria to the Nice area and even beyond during this period. The climatic optimum at this time is attested by the occurrence of *Strombus bubonius* (Lamarck 1822) in contemporary marine deposits along the coast. This thermophilous

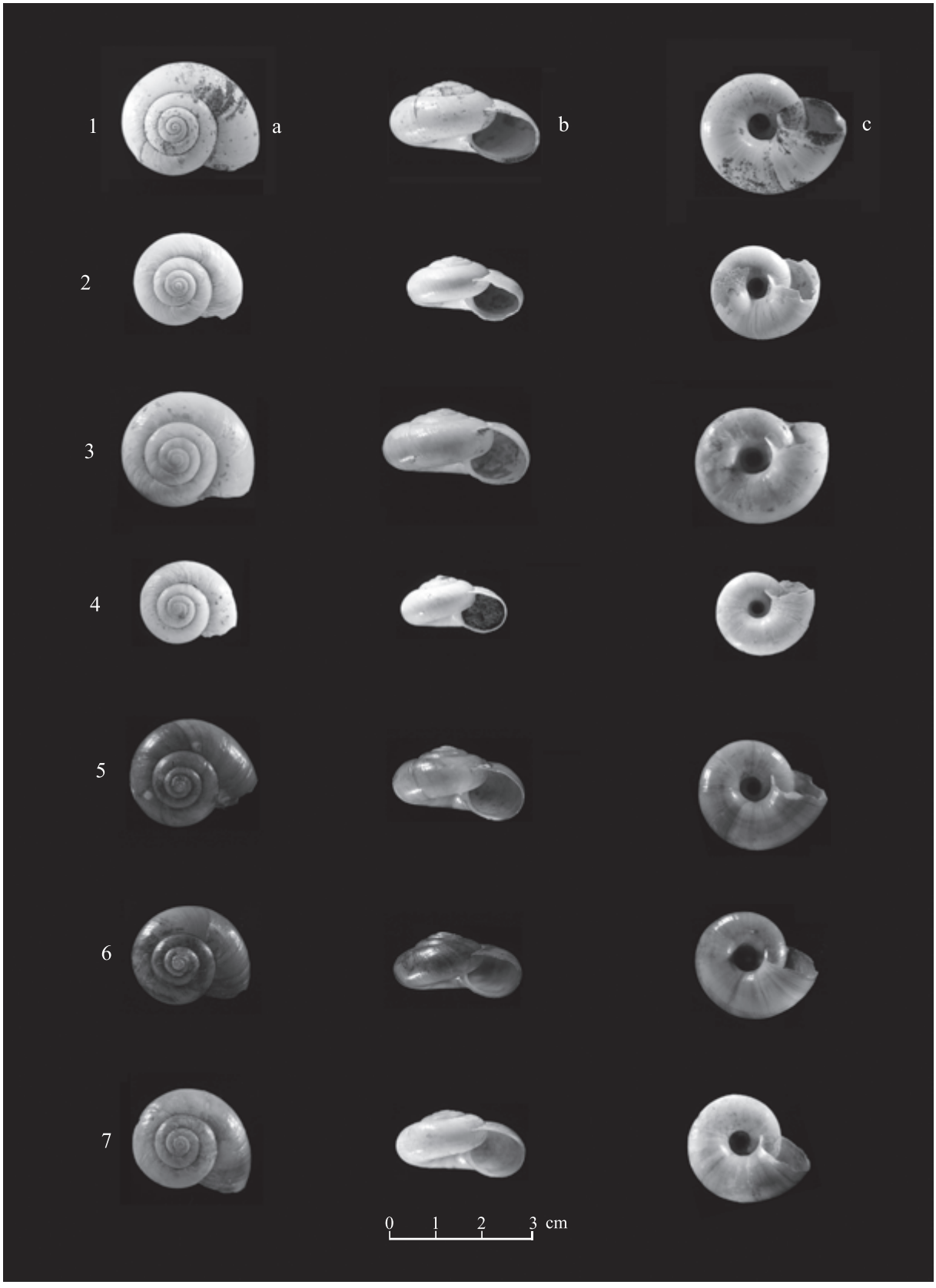

Figure 3 *Retinella olivetorum* (Gmelin) shells from Eemian to Recent localities in Provence. a apical view, b frontal view, c umbilical view. Eemian: 1 Les Amandiers (Cagnes-sur-Mer, Alpes-Maritimes); 2 La Motte (Var); 3 La Verdiane (Nice, Alpes-Maritimes). Neolithic: 4 Chemin de Barjols (Saint-Maximin, Bouches-du-Rhône). Recent: 5, 6 and 7 Vallat de Bourgaille (Trets, Bouches-du-Rhône).

Table 1 Eemian sites with *Retinella olivetorum* in Var and Alpes-Maritimes (France)

Site name	Type of deposits	Stratigraphy	Absolute age	Reference
Le Gattamua (Rue Gattamua, Nice)	Alluvial loam	Eemian coastal terrace	—	—
Le Matisse (Avenue Grinda, Nice)	Alluvial loam	Eemian coastal terrace	—	—
Clos de Fabron (Avenue de la Lanterne, Nice)	Calcareous brown paleosoil	Eemian colluvial deposits	—	Dubar, 1984
Chemin de la Ginestière (Saint-Isidore)	Calcareous brown paleosoil	Eemian slope complex	—	Dubar, 1984
Corniche des Pugets (Saint-Laurent-du-Var)	Calcareous brown paleosoil	Eemian slope complex	—	Dubar, 1984
Les Amandiers (Cagnes-sur-Mer)	Lagunal marl and paleosoil	Eemian coastal terrace	131 ± 1 ky 132 ± 1 ky	Dubar *et al*., 2008
La Motte (Var)	Travertine	Eemian travertine	—	—

gastropod only penetrated in the Mediterranean Sea during OIS 5 (5e, 5d and 5c).

Recent discovery of late Holocene assemblages with R. olivetorum *near Aix-en-Provence* Post-glacial *R. olivetorum* shells were discovered during two archaeological excavations in 2008 at Saint-Maximin-la-Sainte-Baume (Var), situated between Nice (Alpes-Maritimes) and Aix-en-Provence (Bouches-du-Rhône), but only 35 km east of Aix, that is to say 70 km westward from the most western known Eemian locality for this species.

The first excavation was at Chemin de Barjols, north to Saint-Maximin (Fig. 2), near the A8 motorway (Cockin & Furestier, 2009). The archaeological context belonged to the late Neolithic and the early Bronze Age. The late Neolithic occupation was represented by more than 50 pits (silos, dishes…), a well and two dog burials. According to radiocarbon dating and artefact, the occupation may be placed within the interval 5300–5100 yr BP. Only three of the late Neolithic structures were sampled for molluscan analysis. Two furnished *R. olivetorum* shells.

In Structure 1189 in this study *R. olivetorum* shells were particularly abundant in the upper part of the fill and thus clearly visible in the section during excavation. Samples have been taken both in the upper (US 1190; samples 129 and 130) and the lower part of the fill (US 1200; samples 131 and 132).

The four assemblages obtained are quite similar (Table 3). That of sample 129 is more diversified and abundant but these characteristics are amplified by the volume of sediment examined (3 litres against 1 for the other samples in the structure).

Two ecological groups may be distinguished. The first one includes species which live preferentially in wooded habitats and in leaf litter. *Retinella olivetorum* is the most abundant species. This is not an exclusive woodland species although it needs fresh habitats and a loose substrate into witch it can burrow. *Vallonia costata* may belong to this group for, in Provence, it is frequent in leaf litter under deciduous oak woodland (Magnin, 1991; Martin, 1999). Other species found are less abundant – *Pomatias elegans*, *Acanthinula aculeata*, *Merdigera obscura*, *Punctum pygmaeum*, unidentified Vitrinidae, *Oxychilus* sp. and *Monacha cantiana*. All often live in leaf litter. One must underline the absence of woodland species characteristic of "old woodland" and, paradoxically, the feeble abundance of *P. elegans* and *M. cantiana*, two species frequently associated with open woodland. The second ecological group includes some open ground species which live in Mediterranean garrigue and dry grassland: *Granopupa granum*, *Truncatellina callicratis*, *Jaminia quadridens* and *Candidula rugosiuscula*. Only *C. rugosiuscula* is well represented. *Cecilioides acicula* and *Mediterranea hydatina* are two burrowing species frequent in open habitats. They may be recent for several shells were in a very fresh state.

It seems the environment in which *R. olivetorum* lived at Chemin de Barjols was moderately

Table 2 Land snail species associated with *Retinella olivetorum* in the Eemian sites of Var and Alpes-Maritimes (France)

Land Mollusca
Pomatias elegans (Müller 1774)
Pomatias elegans (Müller 1774) var. *major*
Carychium minimum Müller 1774
Carychium tridentatum (Risso 1826)
Cochlicopa lubrica agg.
Sphyradium doliolum (Bruguière 1792)
Argna ferrari blanci (Bourguignat 1874)
Vallonia enniensis (Gredler 1856)
Vallonia pulchella (Müller 1774)
Pupilla triplicata (Studer 1820)
Granaria variabilis (Draparnaud 1801)
Truncatellina callicratis (Scacchi 1833)
Vertigo angustior Jeffreys 1830
Vertigo antivertigo (Draparnaud 1801)
Vertigo pygmaea (Draparnaud 1801)
Jaminia quadridens (Müller 1774)
Merdigera obscura (Müller 1774)
Cochlodina laminata (Montagu 1803)
Clausilia rugosa (Draparnaud 1801)
Clausiliidae sp. indet.
Cecilioides acicula (Müller 1774)
Rumina decollata (Linnaeus 1758)
Punctum pygmaeum (Draparnaud 1801)
Discus rotundatus (Müller 1774)
Vitrea contracta (Westerlund 1871)
Vitrea crystallina (Müller 1774)
Vitrea diaphana (Studer 1820)
Euconulus cf. *Euconulus fulvus* (Müller 1774)
Daudebardia isseliana Nevill 1880
Aegopinella pura (Alder 1830)
Nesovitrea hammonis (Ström 1765)
Eucobresia diaphana (Draparnaud 1805)
Helicodonta obvoluta (Müller 1774)
Monacha cantiana (Montagu 1803)
Candidula unifasciata (Poiret 1801)
Hygromia cinctella (Draparnaud 1801)
Xerosecta cespitum (Draparnaud 1801)
Cepaea nemoralis (Linnaeus 1758)
Cepaea nemoralis var. *major*
Cepaea? paretiana (Issel 1867)

man-modified, but retained important woodland patches. An interpretation would be a mosaic of woodland and open habitat (garrigue), open enough to enable populations of *C. rugosiuscula* to develop. Anyway the true xerophilous Mediterranean species were lacking, especially *Cernuella* spp. which indicates in this area, at least from the middle Neolithic, the most man modified open landscapes.

In Structure 1193 the molluscan assemblages are similar to those of the previous structure, with a slight difference. One can observe the scarcity or disappearance of species like *V. costata* or *P. pygmaeum* which are now abundant in leaf litter. Some other woodland species are lacking: *E. obscura*, *A. aculeata*, undetermined Vitrinidae. *R. olivetorum* is still there but with lesser densities. On the other hand, open ground species seem to be more abundant. This is the case for *T. callicratis*, *J. quadridens* and *C. unifasciata*. Two relatively xerophilous species are present in this assemblage – *Monacha cartusiana* and *Candidula gigaxii*.

So, the assemblage of Structure 1193 indicates an environment comparable to that of Structure 1189, but slightly more open, with more expanded dry grassland. In the present case as in the preceding, there were no Mediterranean xerophilous species typical of a deeply man-modified landscape.

Charcoal analysis (Cockin & Furestier, 2009) agrees with our interpretation. The assemblages collected in different late Neolithic structures indicates a mixed oak woodland (deciduous *Quercus* and *Quercus ilex* being dominant) together with xerophilous plants and trees more or less typical of a riparian vegetation.

The second excavation in which *R. olivetorum* shells were found is Chemin de l'Herbous (Fig. 2), only 200 m west of Chemin de Barjols and close to the A8 motorway as well (Donelly & Furestier, 2009). Three sediment samples from the same early Bronze Age soil (1900–1800 yr BC) were analysed. *R. olivetorum* was found in two of them.

One can note the importance of freshwater species (Table 4), mainly of temporary habitats (*Galba truncatula*, *Gyraulus crista*, *Anisus spirorbis*). Some marsh species are present (*Carychium minimum*, *Vertigo antivertigo*, *Vertigo angustior*, *Oxyloma elegans*) together with hygrophilous ones (*Vallonia pulchella*, *Vertigo pygmaea*, *Succinella oblonga*). Thus a damp marshy environment is indicated.

Xerophilous open ground species are abundant (*Monacha* spp., *Candidula rugosiuscula*) and, contrary to late Neolithic assemblages at Chemin de Barjols, true Mediterranean species are represented: *Cochlicella barbara*, *Trochoidea elegans*, *Cernuella virgata*). Conversely, woodland or shade-loving species are very scarce: some

Table 3 Chemin de Barjols, Saint-Maximin-la-Sainte-Baume (Var, France). Late Neolithic molluscan assemblages with *Retinella olivetorum*.

Type of archaeological structure	Pit or silo				Silo			
Stratigraphic unit	1190		1200		1194			
Sample	129	130	131	132	120	121	122	123
Volume sieved (litres)	3	1	1	1	1	1	1	1
Pomatias elegans (Müller 1774)	9	*		1	2	*	*	*
Granopupa granum (Draparnaud 1801)		1						
Vallonia costata (Müller 1774)	76	18	35	5				1
Acanthinula aculeata (Müller 1774)	3							
Truncatellina callicratis (Scacchi 1833)	2	3	4	7	10	4	3	12
Jaminia quadridens (Müller 1774)	2				1	2	2	
Merdigera obscura (Müller 1774)	2	1						
Cecilioides acicula (Müller 1774)	129	30	72	40	94	57	7	21
Punctum pygmaeum (Draparnaud 1801)	20	5	7					
Vitrinidae sp. indet.	1		1					
Retinella olivetorum (Gmelin 1791)	102	13	13	5	4	2	3	1
Oxychilus sp.	1	4		2	2	1	1	1
Mediterranea hydatina (Rossmässler 1838)	3		1	1	2	1	1	2
Monacha cartusiana (Müller 1774)					1	1	1	1
Monacha cantiana (Montagu 1803)	3	1		2		1	1	2
Candidula rugosiuscula (Michaud 1831)	31	1	13	8	15	20	18	11
Candidula gigaxii (Pfeiffer 1850)					1		1	1
Cepaea sp. cf. *C. nemoralis* (Linnaeus 1758)					1	1		
Minimum number of individuals:	384	77	146	71	133	90	38	53
Number of taxa:	14	11	8	9	11	11	11	11

* = Non-apical and non-apertural fragments only.

fragments of *Pomatias elegans* shells, only one specimen of *Acanthinula aculeata*, *Punctum pygmaeum* and several Clausilids.

Retinella olivetorum is present although woodland seems to have been more open with more or less damp grassland. Charcoal analysis however indicates mixed oak woodland around the site, in which *Quercus ilex* was dominant, together with various mesophilous trees.

A living population of R. olivetorum *near Aix-en-Provence* The discovery of *R. olivetorum* in late Holocene deposits at Saint-Maximin-la-Sainte-Baume encouraged us to make additional efforts to find a living population where we had found two empty shells, about ten years earlier (1999). A colony was located in November 2008 in wet weather.

Ten samples were sent to Dr. Marco Bodon for anatomical examination and comparison with Italian specimens. Only three were adults. The genital tract is similar to *R. olivetorum* however with slight differences in the proximal penis. In future, more populations will need to be studied to determine the status in terms of species and subspecies of *R. olivetorum* agg. in Italy, and their precise relation with the French population (Bodon, pers. com.). Shell diameters for these adult snails were between 21.0 and 22.5 mm. The average diameter of twenty empty shells was 24.7 mm.

This living population is located near the village of Trets (Bouches-du-Rhône), i.e. 22 km east from Aix-en-Provence and only 16 km westward from the Holocene sites at Saint-Maximin-la-Sainte-Baume (Fig. 2). It is almost restricted to the riparian vegetation along Vallat de Bourgaille (N43 26.278; E5 43.362; 320 m asl), a small stream on the northern slope of Mont Olympe (height 819 m asl). The conjunction of a particular geological setting (calcareous tufa on partly siliceous substrates) with abundant water makes this area unique.

In August 1989 a wildfire started very near this point in which 5000 ha were burned, mainly *Pinus halepensis* woodland and *Erica scoparia*

Table 4 Chemin d'Herbous, Saint-Maximin-la-Sainte-Baume (Var). Bronze Age molluscan assemblages with *Retinella olivetorum*.

Stratigraphic Unit	2079	2979	2004/J
Sample	<i>	370	223
Land Mollusca			
Pomatias elegans (Müller 1774)	*	*	3
Carychium minimum Müller 1774	4		2
Cochlicopa lubrica agg.	3	2	2
Pupilla bigranata (Rossmässler 1839)	14	6	1
Vallonia costata (Müller 1774)	18	133	4
Vallonia pulchella (Müller 1774)	95	228	105
Acanthinula aculeata (Müller 1774)		1	
Vertigo antivertigo (Draparnaud 1801)	10		2
Vertigo pygmaea (Draparnaud 1801)	36	38	26
Vertigo angustior Jeffreys 1830		1	
Clausilia rugosa (Draparnaud 1801)	1		1
Clausiliidae sp. indet.		4	
Succinella oblonga (Draparnaud 1801)	60	36	42
Oxyloma elegans (Risso 1826)	4	1	6
Punctum pygmaeum (Draparnaud 1801)		10	
Retinella olivetorum (Gmelin 1791)		16	8
Small limacid shells	6	2	5
Cochlicella barbara (Linnaeus 1758)	1	1	
Monacha cartusiana (Müller 1774)	55	76	87
Monacha cantiana (Montagu 1803)	8	11	
Trochoidea elegans (Gmelin 1791)			1
Candidula rugosiuscula (Michaud 1831)	98	163	124
Candidula gigaxii (Pfeiffer 1850)			3
Xerosecta cespitum (Draparnaud 1801)		1	1
Cernuella virgata (Da Costa 1778)			2
Cepaea sp. cf. *C. nemoralis* (Linnaeus 1758)	5	5	*
Freshwater Mollusca			
Bithynia tentaculata (Linnaeus 1758)	3		8
Galba truncatula (Müller 1774)	64	27	38
Stagnicola fuscus (Pfeiffer 1821)	1		5
Radix balthica (Linnaeus 1758)			1
Anisus spirorbis (Linnaeus 1758)	36	11	27
Gyraulus crista (Linnaeus 1758)	4	10	38
Minimum number of individuals:	527	784	543
Number of taxa:	22	23	26

* = Non-apical and non-apertural fragments only.

maquis. Aerial photographs show that six years after the disturbance the landscape was very altered. Almost everywhere the interfluves were covered with a low-growing secondary vegetation, garrigue or dry grassland, but the substrate remained visible here and there. Woodland or isolated trees were only preserved along the thalwegs and particularly in the Vallat de Bourgaille in which *R. olivetorum* is living. This is partly because, prior to the fire, the vegetation in the thalweg was mainly composed of deciduous trees while pine trees and scrubs were dominant on the interfluves. Nowadays, although vegetation has grown significantly, the limits of the fire are still visible.

In the Vallat de Bourgaille numerous *R. olivetorum* are living in leaf litter along the banks of the stream. The dense and diversified vegetation is mainly composed of deciduous oaks (*Quercus pubescens* Wild.). Leaving the thalweg the vegeta-

Table 5 Vallat de Bourgaille, Trets (Bouches-du-Rhône). Recent assemblage with *Retinella olivetorum* from a litter sample (c.10 litres) collected within riparian vegetation.

Land Mollusca	
Cochlostoma patulum (Draparnaud 1801)	2
Pomatias elegans (Müller 1774)	147
Carychium tridentatum (Risso 1826)	1
Vallonia costata (Müller 1774)	2
Acanthinula aculeata (Müller 1774)	199
Granaria variabilis (Draparnaud 1801)	3
Solatopupa similis (Bruguière 1792)	2
Abida polyodon (Draparnaud 1801)	9
Chondrina avenacea (Bruguière 1792)	1
*Columella edentul*a (Draparnaud 1805)	8
Truncatellina sp.	1
Vertigo pygmaea (Draparnaud 1801)	2
Clausiliidae sp. indet.	1
Punctum pygmaeum (Draparnaud 1801)	212
Vitrea contracta (Westerlund 1871)	108
Euconulus cf. *Euconulus fulvus* (Müller 1774)	152
Oxychilus draparnaudi (Beck 1837)	23
Retinella olivetorum (Gmelin 1791)	39
Zonites algirus (Linnaeus 1758)	2
Monacha cantiana (Montagu 1803)	16
Ciliella ciliata (Hartmann 1821)	6
Xeropicta derbentina (Krynicki 1836)	2
Xerotricha conspurcata (Draparnaud 1801)/ *Microxeromagna lowei* (Potiez & Michaud 1835)	3
Candidula rugosiuscula (Michaud 1831)	5
Xerosecta cespitum (Draparnaud 1801)	1
Cepaea nemoralis (Linnaeus 1758)	1
Cornu aspersum (Müller 1774)	1
Helix lucorum Linnaeus 1758	2
Freshwater Mollusca	
Galba truncatula (Müller 1774)	9
Pisidium sp.	2

tion becomes more or less open and xerophilous (high and low secondary vegetation dominated by *Erica* spp. and sprinkled with young pines and oaks).

We have taken a sample of about 10 litres of leaf litter in Vallat de Bourgaille, on the banks of the stream, at the point the population of *R. olivetorum* seemed to be important. A list of species is given in Table 5. The dominant ecological group includes shade-loving species living in leaf litter of woodland habitats. Most of them are frequent in Mediterranean deciduous or mixed oak woodland in Provence (*Pomatias elegans*, *Cepaea nemoralis*, *Zonites algirus*, *Cornu aspersum*, *Helix lucorum*, *Monacha cantiana*, *Oxychilus draparnaudi*, *Acanthinula aculeata*, *Punctum pygmaeum*, *Abida polyodon*, *Vallonia costata*). Some others are more typical of moist woodland (*Ciliella ciliata*, *Columella edentula*, *Carychium tridentatum*, *Euconulus* cf. *E. fulvus*). The presence of occasional freshwater molluscs (*Pisidium* sp., *Galba truncatula*) is due to stream floods. The remaining species were probably brought there by running waters from surrounding maquis, garrigue and grassland on both sides of the thalweg (*Candidula rugosiuscula*, *Xerosecta cespitum*, *Microxeromagna armillata* / *Xerotricha conspurcata*, *Xeropicta derbentina*, *Cochlostoma patulum*, *Chondrina avenacea*, *Granaria variabilis*, *Solatopupa similis*).

Some *R. olivetorum* can also be found in the maquis and garrigue close to the thalweg, together with open ground species like *Xerosecta cespitum*. This shows a relative tolerance of *R. olivetorum* for open habitats.

The living population of *R. olivetorum* is very restricted to the thalweg of Vallat de Bourgaille at an altitude between 310 and 340 m asl. Further researches around this site and in several other similar valleys in the area were unsuccessful.

The presence of *Helix lucorum* in Vallat de Bourgaille (in woodland as in maquis) must be noted. In the same way *Xeropicta derbentina* is an invasive species in dry open habitats. *Helix lucorum*, which is not native to Provence, has become more and more frequent in woodlands or in orchards in the region (Brancotte, 2001; Chevallier, 1994). In Italy *H. lucorum* and *R. olivetorum* are commonly found in mixed thermophilous woodlands of Tuscany where both species are indigenous.

DISCUSSION

Fragmentation of the Eemian distribution range or Holocene introduction? Two hypothesis must be examined to explain the presence of a living population of *R . olivetorum* in Provence, about 250 km from the western boundary of its main range. The first is a possible recent introduction. The second is the fragmentation of a wider and continuous Eemian range through both the action of climate change (last glacial) and human impact (woodland clearance).

The possibility of a recent introduction (or reintroduction) cannot be excluded for the area size of the living population at Trets is very

restricted, and because *R. olivetorum* is living there with *H. lucorum*, both species having distributions which frequently overlap within their native range, for example in the Tuscan Apennines (Cianfanelli & Lori, 2007). One conceivable way for an introduction of both species might have been reforestation using imported seedlings during the 19th century or early 20th century. Nevertheless there is very little likelihood of that. Moreover, *H. lucorum* is a large species, easily visible, and known to have been introduced in the region very recently (Brancotte, 2001; Chevallier, 1994; Germain, 1930–1931).

The second hypothesis seems to us more useful. The evidence: (1) *R. olivetorum* is so common within Eemian deposits from Monaco to La Motte (Var) that it could be considered as an index fossil of this interglacial; (2) the Trets living population, very isolated, is the most westward identified occurrence of *R. olivetorum*; (3) *R. olivetorum* is present (without any *H. lucorum*) within late Neolithic and early Bronze Age deposits 16 km eastward from the site it is now living.

Taking these facts into account, we suggest the following. During the last interglacial (Eemian) and particularly for the duration of OIS 5e, between 130 and 125 ky, a particular context (warm climate, forested landscape and mature soils) enabled *R. olivetorum* (together with other species) to expand westward from the Ligurian Apennines, at least to the locality (Trets) were it is still living. Subsequent cooling during the last glacial period led to the fragmentation of this range, some *R. olivetorum* populations being able to survive into rare refugia. The area of Montagne du Regagnas, Mont Olympe and Mont Aurélien would have included such refugia. Locally *R. olivetorum* might have spread out during the postglacial warming, jointly with mixed oak woodland. The site of Saint-Maximin corresponds to the first significant human clearance of woodland environment in the neighbourhood. Thus the living population at Trets would be the last (or one of the lastest) trace(s) of the past extension of the species. Particular features of the habitat of Vallat de Bourgaille are highly favourable: presence of a perennial stream and of rich vegetation on friable substrates, both siliceous and calcareous.

Implication for Pleistocene stratigraphy and biochronology *R. olivetorum* has often been considered an index species of the Eemian in south-eastern France (Dubar, 1984; Dubar *et al*., 2008). The present discovery of both a living population and Holocene specimens in western Provence indicates that this species could possibly be found in more recent deposits. The present observation might be applied to other species. *Ruthenica filograna* (Rossmässler 1836), present in Pleistocene deposits at Menton (Nevill, 1880), is often considered as an index species of the last interglacial in Burgundy and along the Rhône valley (Puisségur, 1976) while it might have been present in England earlier (Kerney, 1959; Kerney, 1976; Kerney, 1977). It is still living in the French Maritime Alps (Gittenberger, 1978). *Renea bourguignatiana* Nevill 1880 furnishes an extreme example. The type species of the genus *Renea*, described as one of the extinct species at Menton (Nevill, 1880), was found living, a century later, in a neighbouring site in the province of Imperia (Boeters, Gittenberger & Subai, 1989).

Consequently, care must be taken using *R. olivetorum* or *R. filograna* as biochronological markers, since their presence is not sufficient to prove the Eemian age of a deposit. In most cases studied, *R. olivetorum* and *R. filograna* are considered chronological markers because acme-zones (Birks & Birks, 1980) can be correlated with the last interglacial. Within the molluscan zonation which characterizes the Eemian in the Nice area (see above), *R. olivetorum* shows a peak frequency and abundance (acme or peak-zone) considered to be linked with the maximum of forest development during OIS 5e.

A contribution to the Pleistocene refuge hypotheses The present finding is one kind of evidence which agrees with the presumption of scattered refugia in Provence during the cold stages of the Pleistocene, besides major refugia like the Maritime Alps where a high endemism in landsnail fauna (Médail & Diadema, 2009) may suggest a high survival rate through glacial stages (Holyoak, 1989).

If the living population at Trets actually resulted from the breakup of the Eemian distribution range, the survival of the species in a locality close to the present one, but probably in a sheltered place having both a better sun exposure and humidity, may be expected. Beug (1975) and Pons (1984) suggested that some north

Mediterranean refugia could have existed at an intermediate altitude on the southern slopes of several mountains. Following that hypothesis, a glacial refugium of *R. olivetorum* might have been on the southern slope of Mont Olympe.

In any case, the presence of a suitable refugium on the bottom of the northern slope of Olympe must be precluded for there are loess and other periglacial deposits almost everywhere in this zone (Bonifay, 1961; Nicod, 1967).

Resilience to wildfires The relict population of *R. olivetorum* at Trets has thus gone through several major threats since its expansion in the Eemian interglacial. Fragmentation of its range during the last pleniglacial is identified as important. During the time it has been restricted to the small site of Vallat de Bourgaille, the population has probably undergone two major wildfires, the first in World War II (1943), and the second in 1989. The small thalweg may have acted at least twice as a refugium both for trees and snails. The recolonisation by woodland vegetation from this point since the last fire is clearly visible on successive photographs. Recolonisation by snails seems to follow. This may be the reason it was easier to find living *R. olivetorum* in 2008 than in 1999.

This provides an example of the resilience of Mediterranean land snails to wildfires (Kiss & Magnin, 2006) and the capacity of some snail species to persist in habitats of small size (Pfenninger & Bahl, 1997).

Acknowledgements

We are most grateful to Marco Bodon for the anatomical study, for the Italian distribution map (drawn using the program of Fabio Stoch) and for valuable remarks on the manuscript. Simone Cianfanelli, Ettore Bo and Folco Giusti have provided a lot of data concerning *R. olivetorum* in Italy. The manuscript benefited from comments and corrections by Folco Giusti. Thanks to Sophie Martin for support in field work, to Frédéric Médail for helpful botanical discussions, to Béatrice Prat (*Oxford Archaeology*) who entrust us for molluscan analysis of Saint-Maximin archaeological sites, to Alain Bertrand for providing *R. incerta* shells, and to Jean-Denys Strych (CÉPAM) for technical assistance.

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