Palaeobiogeographical observations on Villafranchian continental molluscs of Italy

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In this paper the palaeobiogeographical affinities of Villafranchian continental molluscan faunas of Italy are examined. The best known Early Villafranchian (= Middle Pliocene) assemblages come from the Piedmont Basin which delivered a rich malacofauna dominated by archaic pulmonates, studied a hundred years ago by Sacco. New sampling in this basin by the authors of this paper have permitted to find some other palaeobiogeographically interesting taxa. Many taxa indicate strong affinities with west-European basins (France, western Germany). In central Italy, recent findings in deposits of the Tiberino Basin (Umbria) have pointed out a good number of Early Villafranchian pulmonate species common to the Piedmont Basin and some endemic aquatic prosobranchs. A different palaeobiogeographical history arises from the analysis of an Early Villafranchian fauna collected in western Sardinia. A strong affinity with Balearic and Iberian regions is evidenced. Molluscan assemblages of Middle Villafranchian (= Late Pliocene) age in Italy are poorly known. Late Villafranchian (= Early Pleistocene) continental molluscs come from many localities of northern and central Italy. The best studied faunas are those of the basins of Valdarno, Valdichiana and the Tiberino (western side of central Italy). In these basins the assemblages are dominated by endemic aquatic prosobranchs but some elements with western or east-European affinities are also present.
Numerous Early Villafranchian genera and species of pulmonates are lacking in the sediments of Late Villafranchian age. Probably they became extinct in coincidence with the onset of the first large ice sheet on the Northern Hemisphere, at the Gauss/Matuyama-boundary (c. 2.6 Ma BP). Late Villafranchian pulmonates are represented mostly by modern species, whereas archaic elements are dominant among the mostly endemic prosobranchs of this age. These last-mentioned elements do not cross the Early/Middle Pleistocene boundary (c. 0.8 Ma BP), i.e. they do not survive the first strong climatic crisis of the Quaternary. On the whole it results that since the beginning of the Middle Pleistocene clear modern features are shown by the continental molluscan faunas of Italy, both at genus and at species level.
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Contents

Introduction

A picture of the distribution of Italian continental molluscs during the Villafranchian was given by one of the authors of this paper in a previous work (Esu, 1982). We summarise here some of the palaeobiogeographical conclusions.

Northwestern Italy, and principally the Piedmont Basin, was considered a part of a biogeographic 'province' of western Europe during the Early Villafranchian. For central Italy the information was inadequate during this time, whereas Sardinia showed a link with the Franco-Iberian-Balearic area.

As far as the Early Pleistocene is concerned, northern Italy offered scarce elements, in particular one species from the Leffe Basin (Lombardy) which it has in common with western France. Central Italy shows a rather clear picture, even if somewhat complex: the fauna is characterised by an endemic group of species accompanied by both eastern and west-European ones.

From a biostratigraphic point of view both Early and Late Villafranchian sequences are characterised by good markers.

In the meanwhile, the authors of the present paper collected new data for a better comprehension of the palaeobiogeographical relationships of the Plio-Pleistocene continental molluscan faunas of Italy.

Some general stratigraphical observations, however, are necessary before the palaeobiogeography can be discussed.

The subdivision of the marine Pliocene has undergone some revisions in the last years. Recently Rio et al. (1991) proposed three stages, Zanclean, Piacenzian and an 'unnamed' Late Pliocene one, yet without stratotype. According to this scheme, the upper boundary of the Piacenzian Stage coincides with the Gauss/Matuyama Boundary and with the onset of the first large ice sheet on the Northern Hemisphere. Such a proposal, which envisages a new stage above the Piacenzian, seems to be valid for correlation purposes with Italian continental sequences. In fact, the deposits of Villafranca d'Asti (Piedmont), which yielded the well-known vertebrates of the Triversa Faunal Unit (Azzaroli, 1977), correlate with the Piacenzian (c. 3 Ma BP), whereas the age of the deposits containing the Montopoli Faunal Unit is dated as close to the G/M Boundary, that is at the top of the Piacenzian so proposed (for more information see Azzaroli et al., 1988). In other words, if we accept the proposal of Rio et al. (1991), the Early Villafranchian, as defined by Azzaroli (1977), is the equivalent of the Middle Pliocene.

Early Villafranchian
Piedmont Basin

Lower Villafranchian deposits are broadly spread in Piedmont, viz. near Fossano (Cuneo District), Villafranca d'Asti (Asti District) and Tassarolo (Alessandria District) (Fig. 1). They delivered abundant assemblages of continental molluscs whereas vertebrates come principally from Villafranca d'Asti, the typical locality of the Triversa F.U. (= Faunal Unit), correlated with the Piacenzian Stage and dating around 3 Ma BP (Azzaroli et al., 1988). The position of the deposits of Tassarolo and Fossano is not so exactly defined because of the scarcity of vertebrate remains and also because the assemblages of molluscs have only few species in common with Villafranca d'Asti. It is therefore not easy to establish biostratigraphic correlations and the differences in malacological composition among the assemblages collected in the three sites may be due to environmental differences, rather than to chronological ones. For this reason we prefer to discuss the Piedmont fauna as a whole.

This fauna is rich in genera and species and was firstly studied and broadly described by Sacco (1884, 1885, 1886, 1887, 1888). Unfortunately most of the original material was lost. In this century, various authors reconsidered Sacco's species. A first general review was made by Wenz (1923-30); single species were then examined by many other students (Esu, Girotti, Giusti, Manganelli, Nordsieck, Schlickum, Strauch, Truc; for references see caption of Table 3). The authors of the present paper collected near Villafranca d'Asti some species not mentioned by Sacco. The following species are considered: *Viviparus pollonerae* Sacco, 1884; *Nystia lenoiri* Schlickum, 1968; *Emmericia pliocenica* (Sacco, 1885); *Carychium pseudotetrodon* Strauch, 1977; *Lymnaea bucciniformis* Sacco, 1886; *Negulus villafranchianus* (Sacco, 1887); *Leiostyla (Leiostyla) capellinii* (Sacco, 1885); *Gastrocopta (Albinula) acuminata fossanensis* (Sacco, 1885); *Gastrocopta (Vertigopsis) dehmi* Schlickum & Strauch, 1979; *Pagodulina bellardii* (Sacco, 1884); *Acanthinula paronae* (Sacco, 1887); *Eostrobilops patuliformis* (Sacco, 1885); *Janulus angustiumbilicatus* (Sacco, 1885); *Discus lateumbilicatus* (Sacco, 1885); *Discus pantanellii* (Sacco, 1886); *Retinella (Riedeliella)* (?) *jourdani* (Michaud, 1862); *Triptychia emyphila* Sacco, 1885; *Triptychia mastodontophila* (Sismonda, 1851); *Serrulella* ? *decemplicata* (Sacco, 1885); *Laminifera (Laminiplicata) villafranchiana* Sacco, 1886; *Polloneria pliocenica* (Sacco, 1885); *Cochlodina* ? *prolaminata* (Sacco, 1888); *Clausilia* ? *portisi* Sacco, 1885; *Hygromia carinatissima* (Sacco, 1885); *Protodrepanostoma plioauriculatum* (Sacco, 1888); *Eobania vermicularia vermicularia* (Michelotti, 1840); *Mesodontopsis chaixi* (Michaud, 1855) and *Schlickumia bottinii* (Sacco, 1884). Some other species described by Sacco are taxonomically problematic and have been omitted.

At genus (or subgenus) level, the fauna is characterised by an extinct European stock, going back at least to the Early Cenozoic (Table 1). Another ancient stock is extinct in Europe, but still living elsewhere (Table 2).

Among extinct genera the triptychiid *Triptychia* and the helicid *Protodrepanostoma* have a European distribution whilst the hydrobiid *Nystia*, the clausiliid *Serrulella*, the helicid *Mesodontopsis* (considered to be a subgenus of *Tropidomphalus* Pilsbry by Lueger, 1981), and the zonitid subgenus *Retinella (Riedeliella)* are found in western and central Europe and the helicid genus *Schlickumia* in western Europe (Spain, France, Italy). Another subgenus, the clausiliid *Laminifera (Laminiplicata)* is known only in France and Italy. The clausiliid genus *Polloneria* is endemic of the Piedmont Basin (for

references see Table 1).

Among the genera that are extinct in Europe but living elsewhere, the vertiginid *Negulus* is an East African genus, the strobilopsid *Eostrobilops* is still living in East Asia, the zonitid *Janulus* is a Macaronesian genus whilst the chondrinid subgenera *Gastrocopta (Albinula)* and *Gastrocopta (Vertigopsis)* are Nearctic (and partly Neotropical the second one) but with extensive fossil record in the Palaearctic region (for references see Table 2).

Many of these genera and subgenera disappear in Europe at the end of the Early Villafranchian. Undoubtedly, the inadequate fossil record may in part explain these extinctions but we can also find other reasons. The most consistent is given by the first great glaciation on the Northern Hemisphere, recognised near the G/M boundary at 2.6 Ma BP (Rio et al., 1991; Zijderveld et al., 1991). This event, followed by xeric conditions in the northwestern Mediterranean region (Bertoldi et al., 1989), could have caused the extinction in Europe not only of the mentioned genera and subgenera but also of many species of other genera.

The presence of one subgenus and, possibly, one genus living in western Europe

GENERA AND SUBGENERA	STRATIGRAPHIC DISTRIBUTION	GEOGRAPHIC DISTRIBUTION	REFERENCES
Nystia Tournouer	? Palaeocene to Middle or Late Pliocene	C and W Europe	11
Retinella (Riedeliella) Schlickum & Strauch	Pliocene	C and W Europe	5, 7
Triptychia Sandberger	Late Oligocene to Middle or Late Pliocene	Europe	1, 3, 9
Serrulella Nordsieck	Early Miocene to Middle or Late Pliocene	C and W Europe	5, 7
Laminifera (Laminiplicata) Nordsieck	Middle and (?) Late Pliocene	France, Italy	6, 8
Polloneria Sacco	Middle Pliocene	Italy	8
Protodrepanostoma Germain	Early Oligocene to Middle or Late Pliocene	Europe	10
Mesodontopsis Pilsbry	Late Miocene to Middle or Late Pliocene	C and W Europe	4, 10
Schlickumia Truc	Late Miocene to Middle or Late Pliocene	W Europe	2, 10

Table 1. Distribution of extinct genera and subgenera found in Early Villafranchian deposits of the Piedmont Basin. The attribution of many fossiliferous layers outside of Italy to Early Villafranchian (= Middle Pliocene) or to the Middle Villafranchian (= Late Pliocene) must be defined.

1: Zilch, 1959-60; 2: Truc, 1971a; 3: Truc, 1972; 4: Schlickum & Strauch, 1973; 5: Schlickum & Strauch, 1975; 6: Nordsieck, 1978; 7: Riedel, 1980; 8: Nordsieck, 1981; 9: Nordsieck, 1982; 10: Nordsieck, 1986; 11: Esu & Girotti, in prep.

GENERA AND SUBGENERA	STRATIGRAPHIC DISTRIBUTION Europe	Elsewhere	GEOGRAPHIC DISTRIBUTION	REFERENCES
Negulus O. Boettger	Eocene to Middle or Late Pliocene	-	E Africa	2
Gastrocopta (Albinula) Sterki	Middle Oligocene to Early Pleistocene	Oligocene to Recent (N. America) Middle Oligocene to Pliocene (Asia)	E and C North America	3, 4, 5, 7, 8, 11
Gastrocopta (Vertigopsis) Sterki	Late Miocene to Early Pleistocene	Late Pliocene to Recent (North America)	N and C America	4, 6, 9
Eostrobilops Pilsbry	Late Oligocene to Middle or Late Pliocene	-	E Asia	2, 12
Janulus Lowe	Late Oligocene to Middle or Late Pliocene	? Pleistocene (Madeira)	Madeira, Canary	1, 10

Table 2. Distribution of genera and subgenera found in Early Villafranchian sediments of the Piedmont Basin, extinct in Europe but living elsewhere. The attribution of many fossiliferous layers outside of Italy to Early Villafranchian (= Middle Pliocene) or to Middle Villafranchian (= Late Pliocene) must be defined.

1: Girard, 1892; 2: Zilch, 1959-60; 3: Steklov, 1966; 4: Taylor, 1966; 5: Steklov & Chytovich, 1967; 6: La Rocque, 1970; 7: Prisjazhnjuk et al:, 1975; 8: Prisjazhnjuk, 1978; 9: Schlickum, 1978; 10: Riedel, 1980; 11: Stworzewicz, 1981; 12: Manganelli et al., 1989. For *Janulus* see also Waldén (1983).

but absent from Italy is also interesting. The pupillid *Leiostyla (Leiostyla)* presents a west-European, Maghrebian, Macaronesian distribution (Manganelli et al., 1990; Pokrysko & Waldén, 1992). The arionid genus *Geomalacus* is also present in the Piedmont Basin after Sacco (1885) with the species *Geomalacus pliocenicus* Sacco, 1885. The genus is now living in Ireland and on the Iberian Peninsula (Wiktor & Parejo, 1989). However, the classification of fossil slugs is very difficult and Sacco himself was very doubtful about the attribution of this form.

Considering now the Piedmont fauna at species level, we observe that many of the extinct species are endemic (see Table 3), whereas some others are also found in the Middle and/or Late Pliocene of central Italy (see next chapter). Some species are known in deposits of Early or Middle Villafranchian age of France: *N. lenoiri, C. pseudotetrodon, H. carinatissima, M. chaixi,* of western Germany: *V. pollonerae, L. bucciniformis, G. (A.) acuminata fossanensis, D. lateumbilicatus, D. pantanellii,* or from both areas: *G. (V.) dehmi* and perhaps *R. (R.) jourdani* (for references see Table 3). *N. villafranchianus* is found in central Italy and in Sardinia. Three species range up to the Late Villafranchian: *L. bucciniformis, G. (V.) dehmi* and *E. v. vermicularia* (Esu & Girotti, 1991; Puisségur, 1984; Tuccimei, 1889). For the last species references are given by Tuccimei (1889) for deposits that he holds as Pliocene but which the present authors consider to be Early Pleistocene in age (unpublished data).

SPECIES	Piedmont	Umbria (1)	Umbria (2)	Sardinia	Rest Italy	France	Germany	Austria	REFERENCES
Hydrocena (Hydrocena) dubrueilliana	-	x	-	-	-	x*	-	-	8, 14, u.d.
Viviparus pollonerae	x	-	-	-	-	-	x	-	1, 15
Nystia lenoiri	x	-	-	-	-	x	-	-	6, 23
Emmericia pliocenica	o	-	-	-	-	-	-	-	2, 23
Emmericia sp. n.	-	-	o	-	-	-	-	-	23
Prososthenia sp. n.	-	-	o	-	-	-	-	-	22
Carychium pseudotetrodon	x	x	-	-	-	x	-	-	12, 22, u.d.
Lymnaea bucciniformis	x	-	-	-	+	-	x	-	3, 15, 22
Negulus villafranchianus	x	x	-	x	-	-	-	-	13, 22
Leiostyla capellinii	o	-	-	-	-	-	-	-	2, 8, 21
Leiostyla gottschicki	-	x	-	-	-	-	m	m	21, 22
Gastrocopta (A.) a. fossanensis	x	x	-	-	-	-	x	-	2, 5, 15, 22
Gastrocopta (V.) dehmi	x	x	-	-	-	x°	x	-	15, 18, u.d.
Pagodulina bellardii	o	-	-	-	-	-	-	-	1, 5
Acanthinula paronae	o	-	-	-	-	-	-	-	4, 5, 9
Eostrobilops aloisii	-	o	-	-	-	-	-	-	20
Eostrobilops patuliformis	o	-	-	-	-	-	-	-	2, 5, 20
Janulus angustiumbilicatus	o	-	-	-	-	-	-	-	2, 5
Discus lateumbilicatus	x	-	-	-	-	-	x	-	2, 16
Discus pantanellii	x	-	-	-	-	-	x	-	3, 16
Triptychia emyphila	o	-	-	-	-	-	-	-	2, 5, 11
Triptychia mastodontophila	o	-	-	-	-	-	-	-	1, 2, 5, 11
Serrulella? decemplicata	o	-	-	-	-	-	-	-	2, 17
Laminifera (Laminipl.) villafranchiana	x	x	-	-	-	-	-	-	3, 17, 22
Polloneria pliocenica	o	-	-	-	-	-	-	-	2, 17
Cochlodina? prolaminata	o	-	-	-	-	-	-	-	4, 17
Clausilia? portisi	o	-	-	-	-	-	-	-	2, 17
Hygromia carinatissima	x	-	-	-	-	x	-	-	2, 7
Protodrepanostoma plioauriculatum	o	-	-	-	-	-	-	-	4, 19
Eobania vermicularia vermicularia	x	-	-	-	x°	-	-	-	1, 5
Mesodontopsis chaixi	x	-	-	-	x	x*	-	-	8, 10, 19
Schlickumia bottinii	o	-	-	-	-	-	-	-	1, 7

Table 3. Distribution of extinct species found in Early Villafranchian sediments of the Piedmont Basin and Umbria. A species of *Retinella (Riedeliella)*, probably identical with *R. (R.) jourdani* of France and W. Germany, is also present in the Piedmont Basin. Some other species described by Sacco are taxonomically more problematic and have been omitted.

(1) Dunarobba; (2) Todi.

o = endemic species; x* = also in Early Pliocene; x° = also in Early Pleistocene; + = Early Pleistocene; m = Miocene.

1: Sacco, 1884; 2: Sacco, 1885; 3: Sacco, 1886; 4: Sacco, 1888; 5: Wenz, 1923-30; 6: Schlickum, 1968; 7: Truc, 1971a; 8: Truc, 1971b; 9: Schlickum & Truc, 1972; 10: Schlickum & Strauch, 1973; 11: Nordsieck, 1974; 12: Strauch, 1977; 13: Esu, 1978; 14: Schlickum, 1979; 15: Schlickum & Strauch, 1979; 16: Schlickum & Geissert, 1980; 17: Nordsieck, 1981; 18: Puisségur, 1984; 19: Nordsieck, 1986; 20: Manganelli et al., 1989; 21: Manganelli et al., 1990; 22: Esu & Girotti, 1991; 23: Esu & Girotti, in prep.; u.d. = unpublished data.

A few species known from the Piedmont Basin have been signaled at other localities but their systematic attribution is wrong or dubious. *E. pliocenica* has been signaled at Mollon (France) (Depéret, 1894) but the taxon found at this locality is a new species of *Emmericia* (Truc, 1971b; Esu & Girotti, in prep.). After Schlickum & Strauch (1979) a lymnaeid found at Szentes (Hungary) and described by Halaváts (1888) as *Lymnaea (Acella) longa* belongs to *L. bucciniformis*; after Krolopp (1980) this Hungarian taxon is a synonym of *Lymnaea stagnalis* (L., 1758) and we agree with this statement. A limacid from Fossano has been classified as *Limax fossilis* Sacco, 1885 by Sacco (1885). To this species some remains from the Pliocene of France (Grangeon & Jodot, 1956) and of Germany (Schlickum & Strauch, 1979, as *Limax* sp. 2 = *L. fossilis*) have been ascribed. The difficulties in classifying fossil limacids at species level make all these attributions very dubious. Also, the affinities of some other species found at Frechen and/or Fortuna (western Germany), including species of the Piedmont Basin (Schlickum & Strauch, 1979), are very dubious. Some clausiliids of the Piedmont Basin have been signaled at Pliocene sites of France but are now considered to be endemic (Truc, 1972; Nordsieck, 1974, 1978, 1981, 1982).

Central Italy

Scanty data are available for central Italy and, in addition, there is uncertainty about the chronostratigraphic position of some outcrops.

Early or Middle Villafranchian assemblages are known from three localities: the first one is Pieve Fosciana in the Tuscan Castiglione di Garfagnana Basin (Lucca District), the second and third ones are Dunarobba and Todi (Perugia District) in the Umbrian Tiberino Basin (Fig. 1).

The fauna of Pieve Fosciana is rather poor, containing some extant species and three extinct species: the helicid *Mesodontopsis chaixi*, a Pliocene species of west-European distribution, the helicid *Eobania v. vermicularia* and the oleacinid *Palaeoglandina lunensis* (d'Ancona, 1867), which became extinct in the Early Pleistocene, being known only from a few Italian localities. As already stated for Piedmont, *Mesodontopsis* is an extinct genus, as is *Palaeoglandina*, which has a European distribution, ranging from Palaeocene to Early Pleistocene. Fossil mammals of Pieve Fosciana are correlated by Azzaroli (1977) with the Triversa F.U.

Dunarobba is a site well-known for the 'fossil wood' of coniferae. Here, two assemblages of continental molluscs are known (Esu & Girotti, 1991), the former from the sediments which buried the trunks and the latter from the sedimentary coating which adheres to the single trunks, in their fissures and in their hollow interiors. The material is still under investigation, but nevertheless we can state that the former assemblage is composed by Late Villafranchian species of the Tiberino Basin (Esu & Girotti, 1975), whereas the latter one shows astonishing similarities with the Piedmont fauna as listed in Table 3 (living species omitted). The chronostratigraphic attribution for the last one, is Early Villafranchian, but there is not reference to any mammalian F.U. However, the possibilities of the survival of this assemblage as a relict association during the Late Villafranchian cannot be excluded. In fact, the presence of the Tertiary discoglossid genus *Latonia* (Anura, Amphibia), in a rich association of vertebrates of latest Villafranchian age at Pietrafitta (Umbria), indicates the

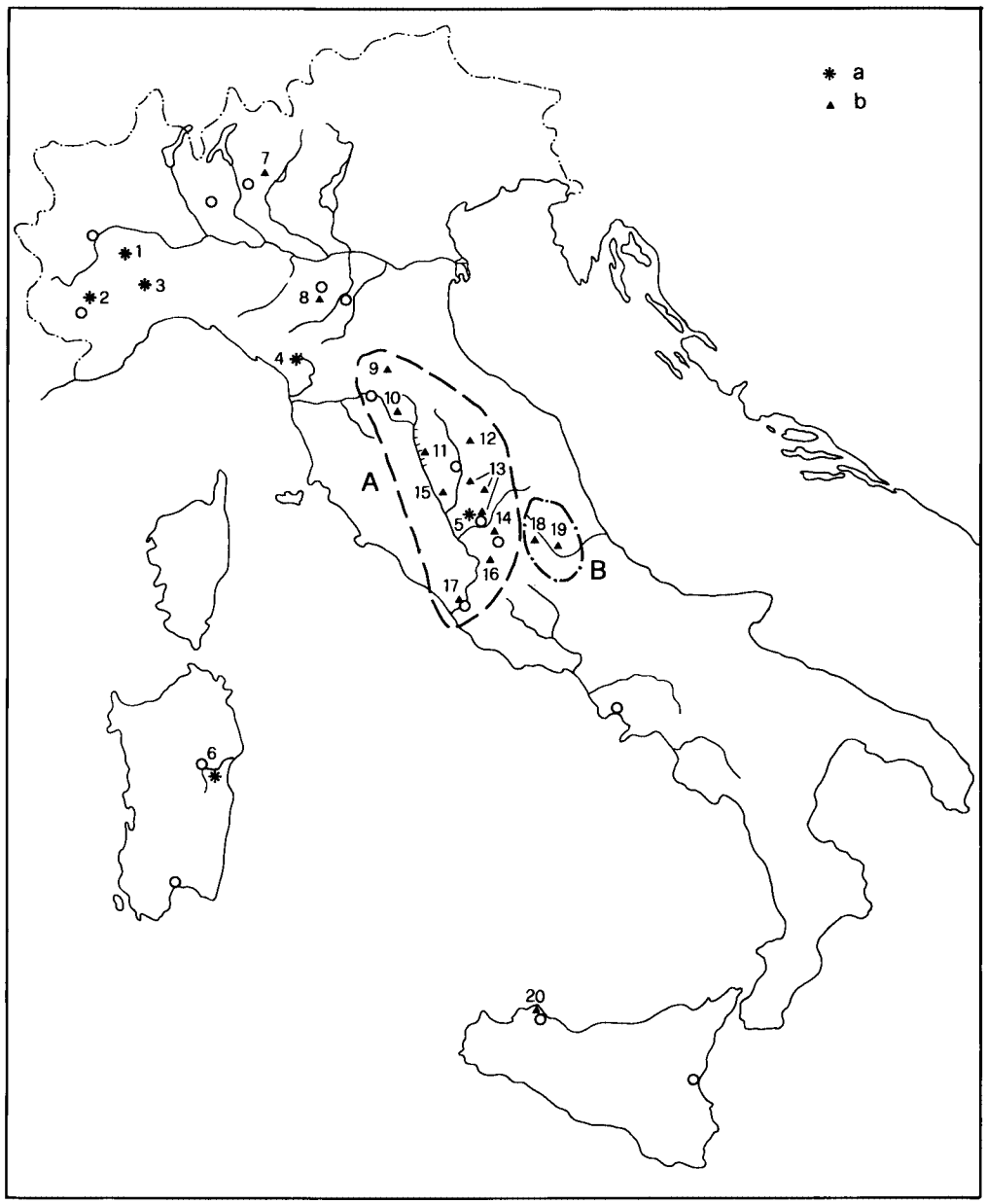

Fig. 1. Villafranchian fossiliferous localities of Italy with continental malacofaunas. a = Early Villafranchian; b = Late Villafranchian. 1: Villafranca d'Asti; 2: Fossano; 3: Tassarolo; 4: Pieve Fosciana; 5: Todi, Dunarobba; 6: Nuraghe Su Casteddu; 7: Leffe; 8: Crostolo; 9: Mugello; 10: Valdarno Superiore; 11: Valdichiana; 12: Gubbio; 13: the Tiberino, Tavernelle; 14: Rieti; 15: Chiani- Tevere; 16: Valli Sabine; 17: Monte Mario; 18: L'Aquila; 19: Fossa - San Demetrio dei Vestini; 20: Monte Pellegrino. 15, 16 and 17 = Continental strata in marine Lower Pleistocene sequences. A = Basins of the Tyrrhenian side of central Italy with a great number of endemic aquatic prosobranchs (Late Villafranchian); B = Basins of the Adriatic side of central Italy without endemic elements (Late Villafranchian).

possibilities of survival of some Pliocene elements in the basins of central Italy during the Early Pleistocene. The last occurrence of *Latonia* outside the Tiberino Basin is at Triversa (Piedmont Basin) (Kotsakis & Faraone, in press).

The species in common with the Piedmont Basin are *Carychium pseudotetrodon*, *Negulus villafranchianus*, *Gastrocopta (Albinula) acuminata fossanensis*, *Gastrocopta (Vertigopsis) dehmi*, and *Laminifera (Laminiplicata) villafranchiana*. The pupillid *Leiostyla gottschicki* (Wenz, 1922) is known only from the Sarmatian of Germany and Austria. The strobilopsid *Eostrobilops aloisii* Manganelli, delle Cave & Giusti, 1989 must be considered an endemic species for the moment, pending a comparison with the very similar *Eostrobilops patuliformis* (Sacco, 1885) of Piedmont. The hydrocenid *Hydrocena (Hydrocena) dubrueilliana* (Paladhile, 1873) is found also in the French Pliocene. The living species of the subgenus *Hydrocena (Hydrocena)* are very broadly distributed in Macaronesia, South Africa, South and East Asia and on some Pacific islands, with a relict species in Dalmatia (Wenz, 1938-44) (for other references see Table 3).

Two prosobranchs, a new *Emmericia* and a new *Prososthenia*, still under investigation, come from the lacustrine clays of the Toppetti quarry at Todi; an endemic character is postulated for both species. Some species of *Prososthenia* are recorded from different localities of Tuscany in 'Pliocene' layers but the stratigraphic position of these layers is very uncertain (Esu, 1982).

Southern Italy

Remains of prosobranchs like *Melanoides* or *Prososthenia* are found in Middle (?) Pliocene brackish deposits at Catanzaro (Calabria) and Benevento (Campania) but the material has not yet been studied.

Sardinia

A rich continental molluscan fauna was collected from the Nuraghe Su Casteddu Formation, near Dorgali (Nuoro District) (Fig. 1). The assemblage is referred to the Early Villafranchian by Esu & Kotsakis (1985). Unfortunately, the fossiliferous level is now submerged as a result of the damming of the Cedrino river.

Twenty-one species were recognised (Esu, 1978). From the biogeographical point of view it is possible to distinguish three groups of species (Esu, 1978; Esu & Kotsakis, 1985): a) endemic species like *Cochlostoma sardoum* Westerlund, 1890, *Hypnophila* aff. *H.bisacchiae* Giusti, 1970, *Hypnophila girottii* Esu, 1978, *Testacella (Testacelloides) gestroi* Issel, 1873, and perhaps *Oxychilus* sp. n. ?; b) species with Franco-Iberian affinities like *Tudorella ferruginea* (de Lamarck, 1822), *Planorbarius thiollieri* (Michaud, 1855), *Oestophora* aff. *O. kuiperi* Gasull, 1966; c) species with European affinities like *Negulus villafranchianus* (Sacco, 1887), *Vallonia pulchella* (Müller, 1774), *Lauria cylindracea* (da Costa, 1778), *Truncatellina callicratis* (Sacchi, 1883), *Chondrina avenacea* (Bruguière, 1792), *Punctum pygmaeum* (Draparnaud, 1801), and *Discus ruderatus* (Studer, 1820).

The ancestors of the endemic species may have entered the island during the Messinian 'salinity crisis', but a different biogeographical history could be supposed for many of them as well, for instance for the cochlicopid *Hypnophila*, as a result of a

vicariant event (see Pielou, 1979) due to the detachment of the Sardinian-Corsican microplate(s) from the Pyrenaic margin during the Middle Oligocene and the consequent opening of the Balearic Basin. In fact this genus is still living on the Pyrenees (Giusti & Manganelli, 1984; Esu & Kotsakis, 1985 with bibliography).

The species with western affinities seem to have entered Sardinia during the Messinian. The pomatiasid *Tudorella ferruginea* is similar to *T. baudoni* (Michaud, 1862) from the French Pliocene and may descend from a Late Miocene species of this area (Esu, 1978, 1986). *T. ferruginea* is extant and also found as a fossil on the Balearic Islands and only as a fossil on Ibiza (Quaternary) and Sardinia (Early and Middle Pliocene) (Esu, 1986). The helicid *Oestophora* has presently an Iberian-Maghrebian distribution. *O. kuiperi*, which is nearest to the species from the Nuraghe Su Casteddu Formation, lives on the Iberian Peninsula. *P. thiollieri* ranges from Late Miocene to Middle Pliocene on the Iberian Peninsula and from Early to Middle Pliocene in France; some records from Greece and Turkey need to be verified.

Species with European affinities could have entered Sardinia during the Messinian and, by passive transport, also in Pliocene times. On Sardinia, in Piedmont and in Umbria, in fact, *N. villafranchianus* is not older than Early Villafranchian, and in the Ruscinian the genus is recorded from western Europe by other species; so the Italian species entered Sardinia by passive transport during the Early Villafranchian.

Middle Villafranchian

At a few localities of central Italy remains of vertebrates of Middle Villafranchian have been collected. In these localities (the Tiberino Basin/Umbria, Sacco River Valley/southern Latium) continental molluscs are also present but they have not yet been studied (Segre, 1982; Kotsakis, 1986; Basilici, 1992; unpublished data).

Late Villafranchian

Northern Italy

The Late Villafranchian assemblage of the Leffe Basin (Bergamo District, Lombardy; Esu & Girotti, 1991), contains, besides some biostratigraphically and biogeographically non significant species, a west-European one, *Valvata chalinei* Schlickum & Puisségur, 1978, an extinct valvatid recorded only from the Early and Late Villafranchian of France (Esu, 1983).

Some assemblages, found along the Crostolo River (Reggio Emilia District, Emilia) and mentioned in Esu & Girotti (1991), are characterised by a high percentage of modern terrestrial pulmonates. The modern character of Early Pleistocene terrestrial pulmonates is recognised also in the other Italian basins. We register an almost complete renewal in consequence of the drastic extinctions of Pliocene pulmonates linked with the 2.6 Ma BP glacial event. Among the Early Villafranchian forms of the Piedmont Basin, only the freshwater species *Lymnaea bucciniformis* survives up to the Late Villafranchian and is present in the molluscan assemblages of the Crostolo. Among the prosobranchs two species are of particular interest, an endemic Italian Late Villafranchian viviparid, *Viviparus ampullaceus* (Bronn, 1831) and an hydrobiid of the genus *Lithoglyphus* (probably a new species). This last form was found by the

authors in the Crostolo and Stirone sections in continental sediments alternating with marine ones. *Lithoglyphus* presently is a mainly central-eastern European genus and as a fossil it characterises the Quaternary warm phases of central and eastern Europe (Ložek, 1964). But it is also known from the Early Pleistocene of The Netherlands and East Anglia (Gibbard et al., 1991).

Central Italy

The intramontane basins of central Italy yielded numerous molluscan assemblages of fluvial, fluvio-lacustrine and marshy environments, which are widely spread (de Stefani, 1876-80; Esu & Girotti, 1975 with bibliography). The present drainage of the areas occupied by these intramontane sedimentary basins seems to reflect an heritage of Early Pleistocene palaeogeographic patterns in which two types of assemblages differentiated.

In fact, the areas of the Pleistocene basins of Mugello (Tuscany), Valdarno superiore (Tuscany), Val di Chiana (Tuscany, Umbria), Gubbio (Umbria), the Tiberino and Tavernelle (Umbria), Rieti (Latium) are cut by drainage systems flowing towards the Tyrrhenian Sea, whereas rivers flowing towards the Adriatic Sea erode the Pleistocene basins of L'Aquila (Scoppito/Madonna della Strada, L'Aquila District, Abruzzi) and Conca di Fossa - San Demetrio dei Vestini (L'Aquila District, Abruzzi). Actually, the assemblages of the basins on the Tyrrhenian side are characterised by a high number of endemic and/or archaic species, which became extinct at the end of the Late Villafranchian (Esu & Girotti, 1991). On the other hand, the assemblages of the basins on the Adriatic side bear biostratigraphically and biogeographically insignificant species, without endemisms or extinct species, both among prosobranchs and pulmonates (unpublished data). We can therefore observe a correspondence between the Early Pleistocene palaeogeography, already differentiated on the Tyrrhenian and Adriatic sides, and the palaeobiogeography of the continental molluscs differentiated in the mentioned two types of assemblages (Fig. 1).

Considerations on the assemblages of the eastern slope of the Apennines are here omitted, but we will try to depict the Tyrrhenian ones, with their endemic and archaic character. The following are the most characteristic species: *Theodoxus (Neritaea) groyanus* (de Férussac, 1825), *Viviparus ampullaceus* (Bronn, 1831), *V. belluccii* de Stefani, 1880, *Valvata anconae* de Stefani, 1877, *V. interposita* de Stefani, 1880, *Stephania bronni* (d'Ancona, 1867), *Prososthenia etrusca* (de Stefani, 1880), *P. meneghianiana* (de Stefani, 1874), *P. oblonga* (Bronn, 1831), *P. ovata* (Bronn, 1831), *Tournouerina belnensis* (Delafont & Depéret, 1893), *Tanousia lithoglyphoides* (Girotti, 1972), *Neumayria priscillae* Girotti, 1972, *Micromelania (Goniochilus) zitteli* (Schwartz von Mohrenstern, 1864), *Emmericia umbra* de Stefani, 1877, *Melanoides curvicosta* (Deshayes, 1832), *Melanopsis affinis* de Férussac, 1823, *Lymnaea bucciniformis* Sacco, 1886, *Ancylus parmophorus* de Stefani, 1880, *Palaeoglandina lunensis* (d'Ancona, 1867), *Eobania vermicularia vermicularia* (Michelotti, 1840), *Campylaea fabarensis* (Tuccimei, 1889), *Unio pillae* de Stefani, 1884, and *Anodonta bronni* d'Ancona, 1867.

Among the extinct genera the hydrobiids *Prososthenia* and *Tanousia*, and the bithyniid *Neumayria* have a wide European distribution during the Neogene and Early Pleistocene. The hydrobiid *Tournouerina* is known from the Late Neogene and Early

Pleistocene of western Europe (France, The Netherlands) whilst the micromelaniid subgenus *Micromelania (Goniochilus)* has an east-European and Siberian distribution. The genus *Stephania*, of uncertain systematic position, is endemic (for references see Wenz, 1938-44; Esu & Girotti, 1975; Meijer, 1989). The living neritid subgenus *Theodoxus (Neritaea)* is now present in northeast Africa, the Near East and with a relict species in Dalmatia (Wenz, 1938-44; Schütt, 1963; Brown, 1980).

At species level we observe a great number of endemic species, some of them with a long stratigraphic range in the same area (*P. meneghiniana* and *N. priscillae* are present from the Late Miocene). A few species are signaled in Pliocene and/or Pleistocene deposits of western Europe (*T. belnensis*, *N. priscillae*), a few others in Pliocene deposits of the Balkan Peninsula or the Aegean area [*P. ovata*, *M. (G.) zitteli*, *M. curvicosta*] and *V. interposita* is signaled in Pliocene deposits of France, Slovenia and Croatia and in the Early Pleistocene of France. Some of the above-mentioned findings outside of Italy are, however, very dubious (for references see Table 4). All 24 species reported in Table 4 became extinct at the end of the Late Villafranchian.

A species now living in Asia and in North Africa (but see observations in van Damme, 1984), the corbiculid bivalve *Corbicula fluminalis* (Müller, 1774), is also present in deposits of Late Villafranchian age in the Tiberino Basin. During the Villafranchian *C. fluminalis* colonised many fluviatile environments of central and western Europe. In central Italy the species survives till Middle Pleistocene times (Esu & Girotti, 1975 with bibliography).

One should note that among the 24 extinct species, 17 are aquatic prosobranchs. The snails of this group are more regionalised (Taylor, 1988) and generally characterise the lakes with a great number of endemic species (Boss, 1978).

From a geological point of view the Villafranchian basins do not show any evidence of continuous sedimentation from Early to Middle Pleistocene. There is a break linked to tectonics, climatic and sea-level changes. Coarse sedimentation inhibited the development of the aquatic species and, in any case, the prevailing prosobranch fauna that lived in central Italy from Late Miocene to Early Pleistocene times, did not survive the onset of the Pleistocene glacial period of the Northern Hemisphere.

Sicily

In an ossiferous breccia of Monte Pellegrino (Palermo District) containing remains of an endemic insular mammalian fauna ascribed to the Late Villafranchian, a few species of terrestrial molluscs have been collected. All but one are attributed to living endemic species by de Gregorio (1887). Some other species have been collected in breccia's of the same area but unfortunately these breccia's on the slopes of Monte

Table 4. Distribution of extinct Late Villafranchian species of central Italy.

T.s. = Tyrrhenian side.

o = endemic species; ? = dubious presence; x? = cfr.

1: Esu & Girotti, 1975; 2: Schlickum & Puisségur, 1977; 3: Conti & Esu, 1981; 4: Willmann, 1981; 5: Esu, 1982; 6: Puisségur, 1984; 7: Brezigar et al., 1985/86; 8: Meijer, 1989; 9: Esu & Girotti, 1991; 10: Gibbard et al., 1991. For *N. priscillae* see also Preece (1990).

SPECIES	LATE MIOCENE			PLIOCENE						EARLY PLEISTOCENE						REFERENCES
	C. Italy (T.s.)	Romagna	Medit. area	C. Italy (T.s.)	Piedmont	France	Germany	Kos-Rhodos	Slovenia	Sicily	C. Italy (T.s.)	Emilia	France	The Netherlands		
Theodoxus (N.) groyanus	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Viviparus ampullaceus	-	-	-	-	-	-	-	-	-	-	o	o	-	-	-	9
Viviparus belluccii	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Valvata anconae	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Valvata interposita	-	-	-	-	-	?	-	-	?	-	x	-	?	-	-	1, 7
Stephania bronni	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Prososthenia etrusca	-	-	-	o	-	-	-	-	-	-	o	-	-	-	-	1
Prososthenia meneghiniana	o	o	-	o	-	-	-	-	-	-	o	-	-	-	-	1
Prososthenia oblonga	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Prososthenia ovata	-	-	-	x	-	-	-	-	?	-	x	-	-	-	-	1, 7
Tournouerina belnensis	-	-	-	-	-	x	-	-	-	-	x	-	x	x	-	3, 5, 8
Tanousia lithoglyphoides	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Neumayria priscillae	x	-	-	-	-	-	-	-	-	-	x	-	x	x	x?	1, 2, 6, 8, 10
Micromelania (G.) zitteli	-	-	-	-	-	-	-	x	-	-	x	-	-	-	-	1, 4
Emmericia umbra	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1, 5
Melanoides curvicosta	-	-	x	x	-	-	-	x	-	?	x	-	-	-	-	1, 4
Melanopsis affinis	-	-	-	?	-	-	-	-	-	-	o	-	-	-	-	1, 5
Lymnaea bucciniformis	-	-	-	-	x	-	x	-	-	-	x	x	-	-	-	3, 5, 9
Ancylus parmophorus	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	1
Palaeoglandina lunensis	-	-	-	o	-	-	-	-	-	-	o	-	-	-	-	5, 9
Eobania vermicularia vermicularia	-	-	-	o	o	-	-	-	-	-	o	-	-	-	-	5
Campylaea fabarensis	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	9
Unio pillae	-	-	-	?	-	-	-	-	-	-	o	-	-	-	-	5
Anodonta bronni	-	-	-	-	-	-	-	-	-	-	o	-	-	-	-	9

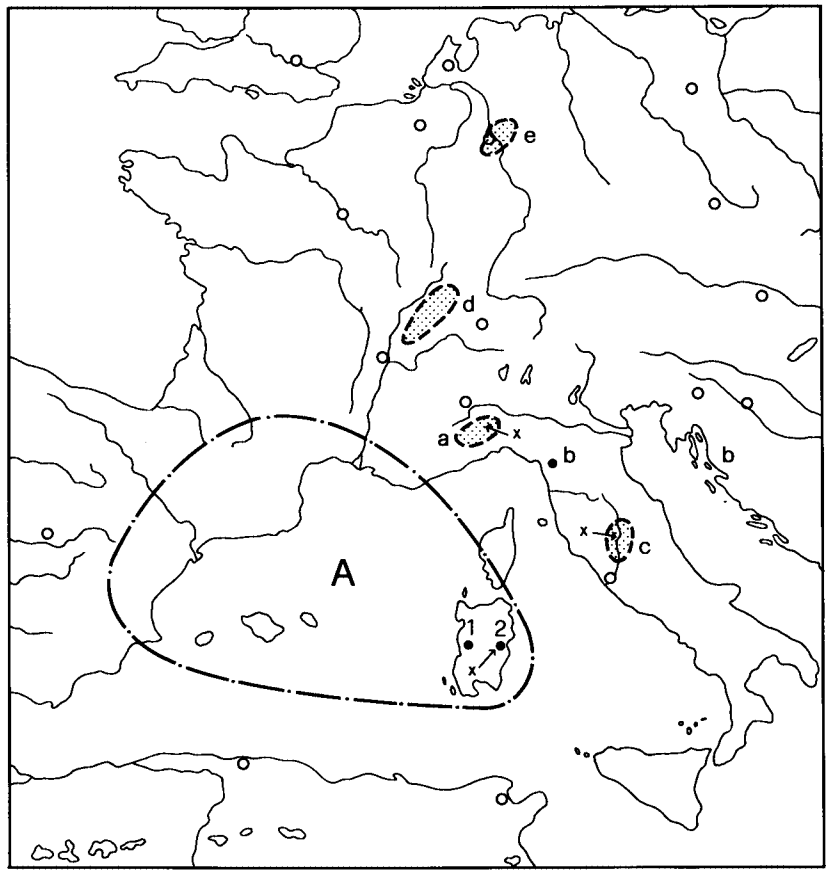

Fig. 2. Early Villafranchian continental basins with malacofaunistic affinities. a: Piedmont Basin; b: Pieve Fosciana Basin; c: the Tiberino Basin (terrestrial species); d: La Bresse Basin; e: Niederrheinische Braunkohle. A. Affinities of Sardinian Pliocene continental malacofauna. 1: Mandriola (Ruscinian); 2: Nuraghe Su Casteddu (Early Villafranchian). x = *Negulus villafranchianus*.

Pellegrino are of different ages. However, one extinct helicid is assigned to an endemic extinct subgenus, *Campylaea (Allolaemus) doderleiniana* Monterosato, 1869 (cfr. Zilch, 1959-60). The affinities of this form are uncertain. From marine beds of presumed Sicilian age from the surroundings of Palermo a species of *Melanoides* has been reported. The specific attribution of this form is uncertain (for references see Caloi et al., in press).

Conclusions

It is possible to make the following observations on the palaeobiogeography of the Villafranchian continental molluscs of Italy:

1) Rich Early Villafranchian assemblages, collected in various localities of the

Piedmont Basin, are dominated by archaic pulmonates. Many of their ancestors belong to Early Cenozoic European lineages. Some species are endemic whilst some others are found in the Rhône and the Rhine valleys. Some genera are restricted to Italy, France, and western Germany (Fig. 2).

2) In central Italy (Tyrrhenian side) the Early Villafranchian freshwater molluscs belong to endemic prosobranch species, some of which are known from deposits of Late Miocene age of the same area. Many of the terrestrial species of Dunarobba (Umbria) are the same as, or very similar to those of the Piedmont Basin (Fig. 2).

3) Most of the Pliocene species of pulmonates became extinct in coincidence with the onset of the first Late Cenozoic ice sheet on the Northern Hemisphere, at c. 2.6 Ma BP. Perhaps some of them survive as a relict assemblage in central Italy up to Middle and/or Late Villafranchian times.

4) A rich Early Villafranchian fauna from western Sardinia indicates strong Franco-Iberian affinities (Fig. 2). Some species or their ancestors colonised the island during the Late Miocene, whilst another stock has an earlier vicariant origin. A few species are transported passively during the Early Villafranchian.

5) Late Villafranchian assemblages from northern Italy (Leffe, Crostolo) are composed of modern freshwater and terrestrial pulmonates with a few extinct aquatic prosobranchs with central Italian, French or central-east-European affinities.

6) The Late Villafranchian molluscan assemblages of the basins on the Adriatic side of central Italy include only modern freshwater elements.

7) The rich Late Villafranchian malacofaunas on the Tyrrhenian side of central Italy (Mugello, Valdarno Superiore, Valdichiana, Tiberino-Tavernelle, Gubbio, Rieti) are characterised by a great number of endemic aquatic prosobranchs. Some of them are present here from the Late Miocene. A few species are known from deposits of Late Pliocene age in the eastern Aegean area, whilst some others are recorded from western Europe and/or from the Balkan Peninsula.

8) The endemic archaic elements of central Italy do not cross the Early/Middle Pleistocene boundary. From the early Middle Pleistocene the aquatic prosobranchs are almost completely renewed. From this age the Italian continental molluscs have a modern character.

9) A few Sicilian terrestrial molluscs of (?)Late Villafranchian age belong, principally, to living endemic species.

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