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A Messinian *Prolagus* from Capo di Fiume Quarry (Palena, Abruzzo, Central Italy)

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ABSTRACT – *Prolagus* is reported for the first time from Messinian beds of the Maiella Mountains. Its occurrence is testified by an incomplete, articulated skeleton. The general aspect of the fossil, its dimensions and proportions and the geographical proximity to the Gargano area, where rich collections of *Prolagus* remains were found in a recent past, are suggestive of a tentative attribution to *P. apricenicus* Mazza. The find repropose the intriguing problem of the relationships of these Abruzzo-Apulian representatives with other Italian and European species and of the date and way of immigration into the area.

RIASSUNTO – [Il *Prolagus* messiniano della cava di Capo di Fiume (Palena, Abruzzo, Italia Centrale)] – *Prolagus* è segnalato per la prima volta da livelli messiniani dei Monti della Maiella. La sua presenza è testimoniata da uno scheletro incompleto ed articolato. L'aspetto generale del fossile, le sue dimensioni e proporzioni e la vicinanza geografica all'area garganica, dove sono state rinvenute abbondanti quantità di resti di *Prolagus* in un recente passato, suggeriscono una probabile attribuzione a *P. apricenicus* Mazza. Il reperto ripropone l'interessante problema delle relazioni di questi rappresentanti abruzzo-pugliesi con altre specie italiane ed europee e dell'età e via di migrazione nell'area.

FOREWORD (P. Mazza)

Recently, one of us (E. Di C.) found an incomplete, articulated *Prolagus* skeleton in a quarry about 3 kms south of Palena, near the Capo di Fiume springs, along the Aventino stream (Text-fig. 1). Celebrated for its rich collections of beautiful fossil fish, the local sequence was studied in detail by Carboni *et al.* (1992). The discovery led to a necessary revision of the most significant Miocene representatives of *Prolagus* from Italy.

Lopez Martinez (1974a, b; 1977; 1978) and Lopez Martinez & Thaler (1975) contributed substantially to our knowledge of the western European *Prolagus* populations. These Authors held as valid 12 species referable to the genus *Prolagus*, namely *P. vasconiensis* Viret 1930; *P. tobieni* Lopez 1977; *P. schnaitheimensis* Tobien 1975; *P. oeningensis* (König 1825); *P. major* Lopez 1977; *P. crusafonti* Lopez 1975; *P. michauxi* Lopez 1975; *P. calpensis* Major 1905; *P. sardus* (Wagner 1825); *P. bilobus* Heller 1936; *P. figaro* Lopez 1975; *P. ibericus* Lopez 1975; and one to the genus *Ptychoprolagus*, *P. forsthartensis* Tobien 1975.

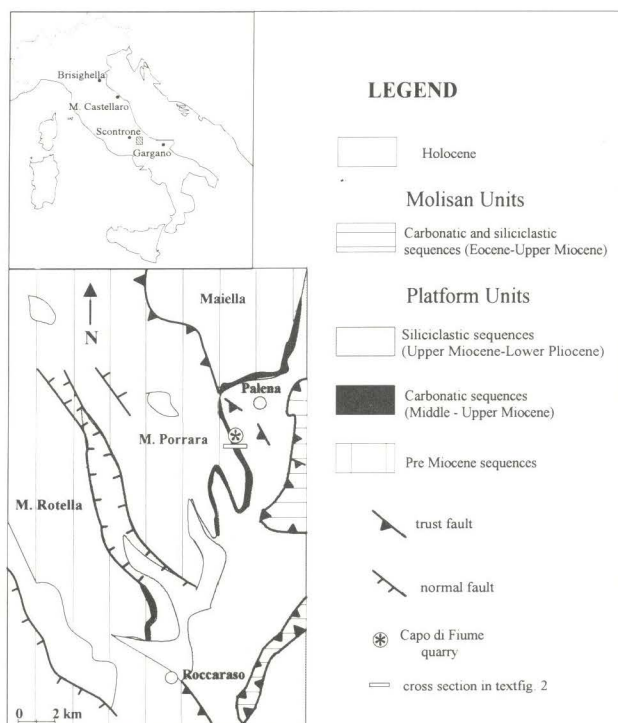
The finds from Italy are infrequent, but sometimes exceptionally abundant. Leaving aside the already mentioned *P. sardus* and *P. figaro* both reported from Sardinia, Forsyth Major (1899) reported *Prolagus* remains, but without figuring them, from the lignites of Casino, near Siena and

established a new species on them, *P. elsanus*. Since the specimens went lost, Lopez Martinez *et al.* (1975) considered the species invalid. In 1970, Berzi established the species *P. savagei* on a right mandible, a maxillary and few isolated teeth from Cascina Arondelli, a Villafranchian locality near Villafranca d'Asti, Piedmont. Lopez Martinez & Thaler (1975, p. 852) considered also this species invalid because «...fondée sur une anomalie de fossilisation», without any further explanation. Slightly later, Azzaroli (1977) observed that, since Lopez Martinez & Thaler (1975) failed to specify with which valid species should *P. savagei* be synonym, the species must be resumed.

Fondi (1970) referred to *P. sardus* few remains from karst fissure fillings from the area of Rosia, in the Montagnola Senese, near Siena.

In the late '80s, Mazza (1987) established two species, *P. apricenicus* and *P. imperialis*, on specimens from karst fissure fillings from the Gargano promontory.

In 1983, Dr. Lorenzo Sorbini, director of the Museum of Natural History of Verona, found a fairly complete, inarticulated skeleton in the lower levels of the Gessoso-Solfifera Formation, in the area of Monte Castellaro, near Pesaro. Other *Prolagus* remains were recovered in the late '80s in karst fissure fillings of the Gessoso-Solfifera Formation at Monticino quarry, Brisighella, near Faenza. In 1989



Text-fig. 1 - Index map of the Capo di Fiume quarry. The small map of Italy shows the main Miocene localities with *Prolagus*.

Masini chose the Monte Castellaro specimen as holotype of a new species, called *P. sorbinii* in honour of the discoverer. In the same paper Masini tentatively attributed the Brisighella finds to this new species. He also supposed a possible relationship between *P. sorbinii* and *P. savagei*, which should form a separate lineage from that of *P. crusafonti* - *P. michauxi* - *P. calpensis*.

Writing in 1990, Rook and Masini reported the occurrence of two fragmental *Prolagus* mandibles, a left one and a right one, from two Upper Valdarno localities, La Solava and L'Inferno, respectively. The Authors called the left mandible *Prolagus* sp., while they attributed the right one to what they called the «*michauxi-calpensis/savagei*» morphological group. They also added a brief synoptical list of the main Italian finds and reported a personal communication by B. Engesser, who informed of the occurrence of *Prolagus* sp. also in the Baccinello V3 fauna.

GEOLOGICAL SETTING OF THE CAPO DI Fiume QUARRY (G. Aruta)

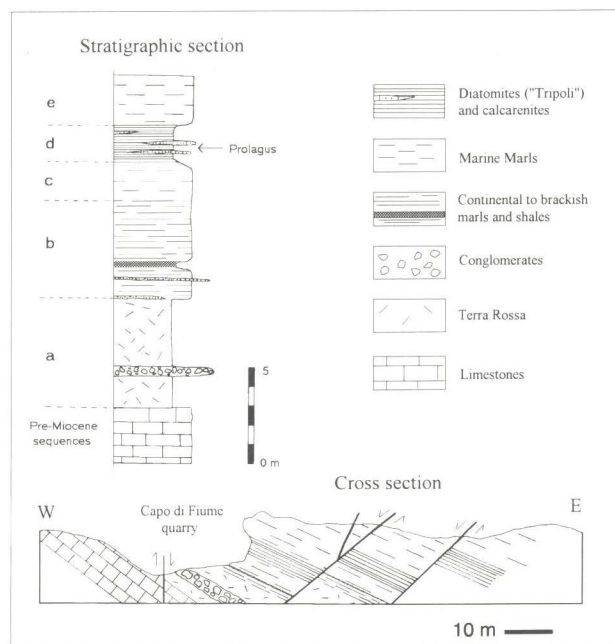
The Capo di Fiume quarry is located in the Miocene cover of the Pora Mountain structure, which belongs to an external domain of the Adriatic

area (cf. Inner Apulian Platform of Patacca *et al.*, 1993). The pre-Miocene sequence consists of over 1000 m of Upper Cretaceous restricted shelf limestones, partially covered by Upper Cretaceous to Eocene distal ramp calcarenites. The Miocene sequence unconformably lays on the Cretaceous and Eocene terms. It is composed, from the bottom to top, by Middle-Upper Miocene neritic limestones and Upper Messinian lagoonal and neritic shales and turbidite shales and sandstones (Patacca *et al.* 1993) (Fig. 1).

The Capo di Fiume Miocene sequence was studied in detail by Carboni *et al.* (1992). On the basis of this and of other investigations (Aruta & Rea, 1988; Bellatalla, 1988-1993) and of a preliminary survey made in collaboration with E. Patacca and P. Scandone, the following lithologic terms have been recognized, from the bottom upwards (Text-fig. 2):

a) about 8 m of Terra rossa, interbedded with a discontinuous level of eluvial limestone conglomerates. The lower boundary, with the substratum (which consists of light brown Upper Cretaceous calcilutites), is unclear; although faulted now, we believe it was originally stratigraphical;

b) continental to brackish deposits (Carboni *et al.*, 1992). This interval includes, from the base upwards, about 150 cms of marls, interbedded with pebbly beds, containing plant and gastropod



Text-fig. 2 - The Capo di Fiume quarry sequence and schematic geological section of the Capo di Fiume quarry. For a detailed description of the a-e intervals see text.

remains; about 70 cms of peaty shales with continental gastropod remains; about 3 m of marls rich in bivalves, microgastropods, ostracods and rare planktic foraminifers;

c) marine deposits including 1.5 m thick marls rich in mollusk remains (*Cardites*, *Ostrea*) and few gastropods. Benthic forams occur, inclusive of the Lower Messinian *Bulimina echinata* (Patacca & Scandone, pers. comm.);

d) alternated laminae of diatomites and marls called «Tripoli» by Carboni *et al.* (1992). The marly levels bear rich amounts of plant and fish remains. Trough cross-laminated calcarenite lenses occur. The Tripoli are lagoon sediments; the calcarenite lenses may be interpreted as fluvial or (according to Patacca & Scandone, pers. comm.) tidal channel deposits. At least three levels of calcarenite lenses occur: the *Prolagus* skeleton lay over the lowest. This interval is about 2 m thick;

e) dark marls and marly limestones containing bivalves, gastropods, siliceous sponge spicules and rare forams. The facies seems suggestive of a restricted marine environment. The section is 3-4 m thick.

Carboni *et al.* (1992) described a following portion represented by a rhythmic alternation of Tripoli and marine marls. Field observations led us to the conclusion that the alternation may have been caused by extensional tectonics affecting the lower levels.

The sequence is overlapped by some tens of meters of allochthonous marly clays which pass upwards to distal siltite-marly turbidites. The transition between these two terms is marked by Upper Messinian tuffs (Bellatalla, 1993).

THE CAPO DI FIUME *PROLAGUS* (P. Mazza & M. Rustioni)

The specimen was found in laminated marls slightly overlying the *Bulimina echinata* FOD. For this reason, the fossil is dated to the earliest pre-evaporitic Messinian and therefore correlates with the earliest part of the MN 13 Mammal Faunal Zone (last part of the Turolian of the mammalian biochronology).

The skeleton is about 18 cms long, from head to tail, and lies on its right side (Text-fig. 3, 4). The skull, axial skeleton, and stylopodial bones are still preserved, while the distal parts of the limbs are missing. The skull is shattered. It is fairly elongated, especially in the snout. The mandibles have massive horizontal rami and the ascending rami are slender and incline gently backwards. The digastric areas are well developed.

The mouth is practically closed, which prevents any possible view of the teeth.

The apparent dimensions are the following: gross length of the skull (snout-nuchal crest): about 46 mm; gross length of the mandible: about 30 mm; gross height of the horizontal ramus: about 9.5 mm; gross length of the scapula: about 35 mm; width across the distal condyles of the femur: about 8.5 mm.

The Capo di Fiume *Prolagus* skeleton shows the characters of Weigelt's (1989) «water carcasses»: passive position, similar to the natural posture; the limbs hanging slack, especially the rear ones; the mouth just slightly open. The skeleton is surrounded by a dark-coloured halo, probably the carbon residue of the soft tissues and of the hair. Incidentally, it is worth noting that the specimen lies in the same position as the Miocene mammals from the Oeningen Molasse described and figured by Meyer (1854).

It is known that preservation of an animal carcass is enhanced under water than under subaerial conditions. Few hours after death, the intestinal and putrefactive gases inflate the carcasses and make them resurface, unless fish or other aquatic predators do not tear them apart before. The bloated carcasses drift away carried by currents until they reach a shore. If they stay long in the water they keep decomposing, scattering their bones along the way. The first elements to detach are the distal limb bones and often also the mandibles. In well oxygenated, flowing water and most of all in presence of decomposing cellulose the carcasses are completely skeletonized in few months. Conversely, in still, anoxic water soft tissues are longer preserved.

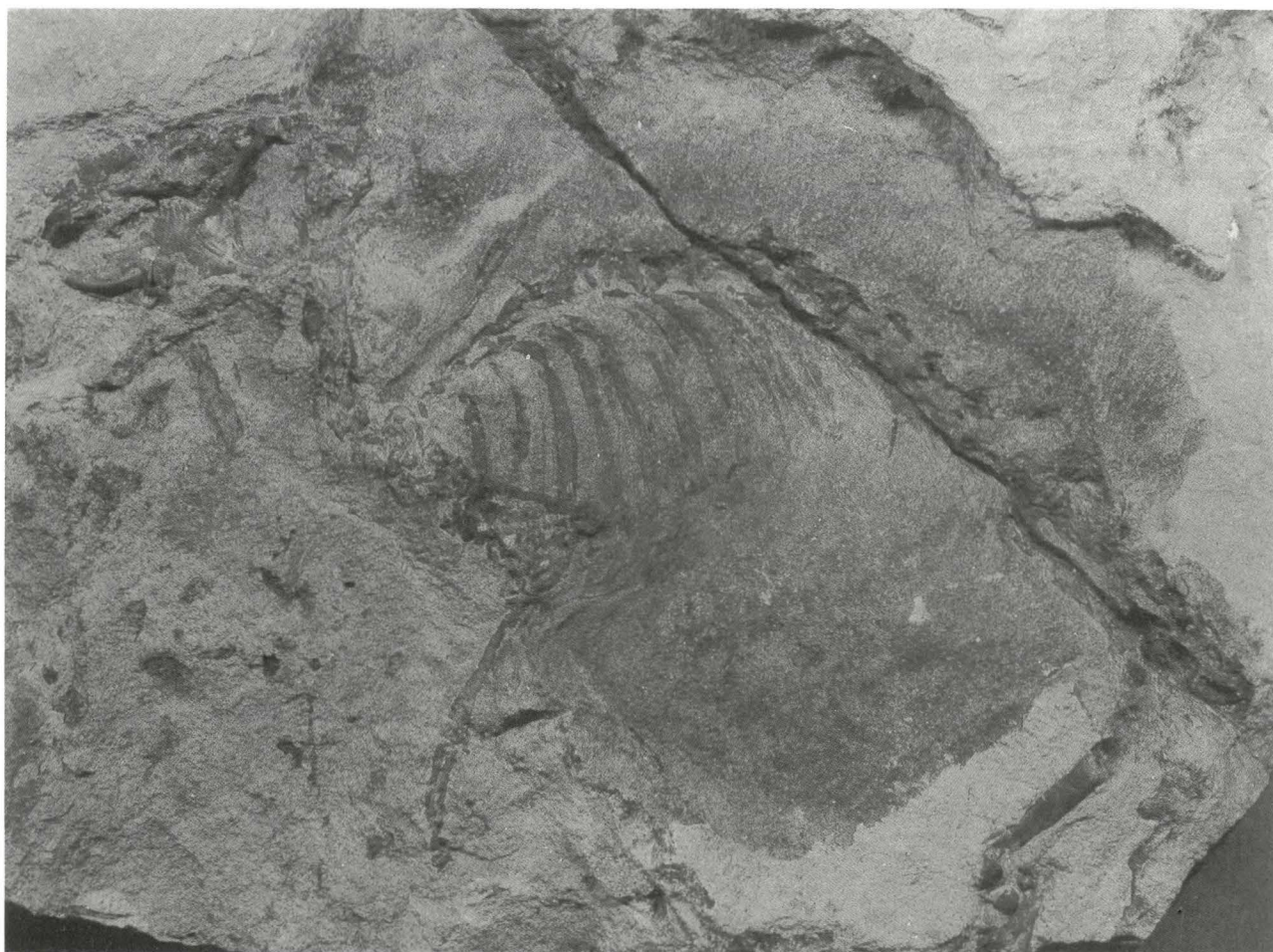
In the light of this information the Capo di Fiume *Prolagus* seems to have floated for quite a while in still or slightly flowing anoxic waters, as attested by the loss of the distal limb bones and by the prolonged preservation of the soft tissues.

RELATIONSHIPS WITH OTHER ITALIAN *PROLAGUS* REPRESENTATIVES

The discovery of a *Prolagus* skeleton in an area so close to the Gargano promontory, where a number of karst fissure fillings yielded large amounts of *Prolagus* specimens in a recent past, called for a more detailed assessment of the phyletic relationships of the Italian representatives of the genus.

Unfortunately, at the moment the fossil can be determined only with broad approximation.

The general size and proportions of the specimen and the morphology of the mandibles are



Text-fig. 3 - *Prolagus* cf. *Prolagus apricenicus* from Messinian of Capo di Fiume quarry. Left lateral view of the skeleton. Natural size.

suggestive of *P. apricenicus*, to which the Capo di Fiume skeleton is tentatively referred (Pls. 1, 2). Such an attribution may be also consistent with the geographical proximity of the Capo di Fiume area to the Gargano promontory.

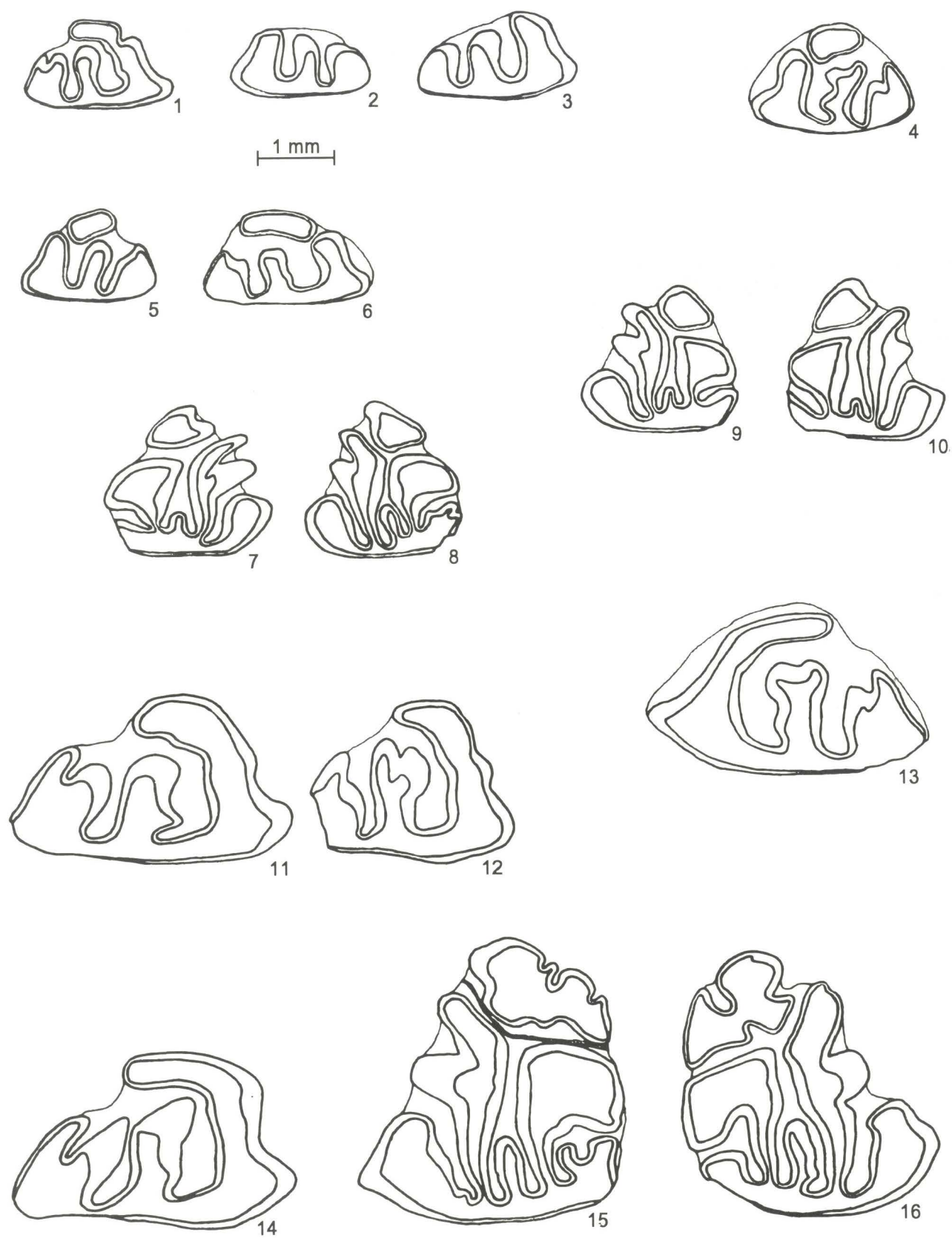
P. apricenicus still retains a certain number of plesiomorphic characters. Those which seem to be the oldest Gargano representatives are relatively small-sized, have a very reduced premolar foramen

at level of the hypocone of the fourth upper premolar, and have a primitive second upper premolar with hypercone, lagicone and postcone rounded and about equally developed, or with a rounded or elongated precone, without a mesial hyperlophe connecting it with the hypercone, and a third lower premolar with roundish to lozenge shaped anteroconid and with a crochet present in over 90% of the individuals. In the fissure fillings

EXPLANATION OF PLATE 1

- Figs. 1-10 - *Prolagus apricenicus* from the Gargano fissure fillings: 1) Holotype, right P²; 2) Paratype, left P²; 3) Paratype, right P²; 4) Paratype, left P²; 5) Paratype, left P²; 6) Paratype, right P₃; 7) Paratype, left P₃; 8) Paratype, right P₃; 9) Paratype, right P₃; 10) Paratype, left P₃.
- Figs. 11-16 - *Prolagus imperialis* from the Gargano fissure fillings: 11) Holotype, right P²; 12) Paratype, right P²; 13) Paratype, left P²; 14) Paratype, right P²; 15) Paratype, left P₃; 16) Paratype, right P₃.

All figures from Mazza (1987).





Text-fig. 4 - *Prolagus* cf. *P. apricenicus* from Messinian of Capo di Fiume quarry. Particular of the skull. x 2.

which are supposed to be progressively more recent, the size of the individuals steadily increases and the teeth add several apomorphies.

The plesiomorphies shown by *P. apricenicus* are shared also by *P. oeningensis* König, a Middle Miocene representative known in Spain, France, Germany and Turkey. The similarities are such that the most primitive *P. apricenicus* specimens might be easily accommodated in *P. oeningensis*.

P. cf. P. apricenicus from Capo di Fiume, *P. sorbinii* from Monte Castellaro, the advanced representatives of *P. apricenicus* and *P. imperialis* from Gargano (Pls. 1-2) and *P. cf. P. sorbinii* from Brisighella are stratigraphically distributed from the pre-evaporitic to the evaporitic and post-evaporitic Messinian. Although grossly contemporaneous, these Late Miocene Italian ochotonids seem to belong to two separate stocks.

While the Abruzzo-Apulian representatives manifestly stem out directly from *P. oeningensis*, the Marchean-Emilian forms bear cranial and overall jaw characters that denounce a derivation from the more advanced *P. crusafonti*.

P. crusafonti is a small-sized representative. It has a slender skull with elongated snout, a broad premolar foramen, located at the level of P4/, and mandibles with massive horizontal rami. It still bears a primitive second upper premolar and in its third lower premolar the anteroconid is rounded and about the size of the metaconid. The crochet is generally present.

Like in *P. crusafonti* the type specimen of *P. sorbinii* from Monte Castellaro has an elongated, slender snout and a wide premolar foramen, placed approximately in the same position. The horizontal rami of the mandible are massive as well. The dentition, on the other hand, is more advanced. P2/ has a fairly developed mesial hyperloph. In the third lower premolar the anteroconid is as large as the metaconid, but it is elongated. The crochet is wanting. The Monte Castellaro specimen is slightly larger than *P. crusafonti*. The *Prolagus* teeth from Monticino quarry were rightfully referred to *P. cf. P. sorbinii* by Masini (1989) for the many affinities shared with the Monte Castellaro specimen.

Also the Villafranchian *P. savagei* shares a number of dental affinities with *P. sorbinii*. The only significant difference is that the anteroconid of the third lower premolar may be indented, a feature never observed, at least until now, in *P. sorbinii*.

On the contrary, a number of cranial, mandibular and dental differences separate *P. sorbinii* from the coeval *P. michauxi*. The skull of the latter species is short and sturdy. Its premolar foramen is very broad and opens between P4/ and M1/. Its mandible is slender, with elongated ascending rami, quite more inclined backwards than in *P. sorbinii* and *P. savagei*. *P. michauxi* has advanced second upper premolars, with arcuated para- and metaflexi. Its third lower premolar bears an elongated, lozenge-shaped and fairly indented anteroconid and a rather

well developed crochet. *P. michauxi* and *P. sorbinii* have overlapping sizes.

P. calpensis and *P. michauxi* share many cranial, jaw and dental characters. *P. calpensis* has lost the crochet in the third lower premolar.

By and large we agree with Masini (1989) in separating the *P. sorbinii* - *P. savagei* clade from the *P. crusafonti* - *P. michauxi* - *P. calpensis* lineage; however, in our view *P. sorbinii* did not derive from *P. oeningensis*, rather from its direct descendant *P. crusafonti*. Two separate lines therefore seem to have arisen from *P. crusafonti* during the Late Miocene: one leading to *P. michauxi*, the other to *P. sorbinii*.

Three different clades have been seen so far, the one of *P. apricenicus* - *P. imperialis*, that of *P. sorbinii* - *P. savagei* and that of *P. michauxi* - *P. calpensis*. The first apparently originated from a deme of a southward migrating *P. oeningensis* population, established in the Abruzzo-Apulian area, perhaps early during the Miocene. By the early-middle Late Miocene a branch of a *P. crusafonti* population settled in northern and central Italy, giving rise to the *P. sorbinii* - *P. savagei* stock, which seems to have been rather widespread in Italy from the Late Miocene at least up to the whole Early Pleistocene. The third clade was started by *P. michauxi*, approximately coeval to *P. sorbinii*, which gave rise to a new southward migrating wave towards Anatolia.

The lack of any evidence of colonization by *P. michauxi* supports the hypothesis that the Abruzzo-Apulian area was completely isolated from other nearby mainlands during the Late Miocene.

STRUCTURAL AND PALEOGEOGRAPHICAL EVOLUTION (G. Aruta)

Porrara Mountain is connected to the North with Morrone Mountain and both form a slab which thrust over the Maiella group moving eastwards presumably after the Early Pliocene. The overthrust partly disrupted Molisan units already settled, in Late Miocene-Early Pliocene times, over the Porrara and Maiella Units (Patacca *et al.*, 1991). To the South the Maiella and Porrara structure is overlapped by the Molisan and Sannite nappes coming from inner domains (Patacca *et al.*, 1991; Crostella, 1967).

A paleogeographical reconstruction of the Gargano, Porrara, Pesaro and Faenza area is tempted below on the basis of the present stratigraphical and structural knowledge (Argnani *et al.*, 1991; Centamore *et al.*, 1991; Patacca & Scandone, 1989; Patacca *et al.*, 1991; Lavecchia *et al.*, 1989; Menichetti *et al.*, 1991; Sgrosso, 1986).

At least until the Late Messinian, the Porrara, Maiella and Gargano carbonatic structures made part of the Adriatic foreland. These areas were structural highs probably connected to one another since the Mesozoic and were likely more extended than they are today: they are overlain by the Apennine chain at South, but they were probably connected with Mount Alpi which crops out from a tectonic window through the Apennine sheets in Basilicata (Patacca *et al.*, 1993; Sgrosso, 1986). Towards the North both Maiella Mountains and Gargano are bounded by increasingly deeper facies; however, extensive Meso-Cenozoic structural highs, characterized by restricted platform facies and covered by Messinian to Pleistocene sequences, are present off Ancona (Argnani *et al.*, 1991).

Inwards (presently towards the West) the Porrara-Maiella structural highs were bordered by basinal to slope facies (Molisan Basin and M. Genzana) (Sgrosso, 1986, Patacca *et al.*, 1989) at least since the Middle Mesozoic. The deep-sea sedimentation persisted up to the Late Messinian with foredeep turbidite facies.

Apart from those occurring off Ancona and Bagnolo, the platform facies of the Southern Apennine passed to the Upper Mesozoic-Cenozoic Umbrian-Marchean-Romagna Scaglia deep-sea facies along the complex Ancona-Anzio structural line (Castellarin *et al.*, 1982). Turbidites are reported during the Messinian in the Laga foredeep, which stretched Northwest of Maiella Mountain (Centamore *et al.*, 1991).

Wide-scale geological evidence therefore attests to the existence of an extensive intracratonic basin since the Mesozoic (Scaglia to Schlier basin of Marche and Northern Abruzzo, Mount. Genzana and Molise basins) and of a foredeep, during the Messinian, which bounded to the West the platform areas of Porrara, Maiella and Gargano, still undisturbed at least until the Early Pliocene.

The geodynamic setting of the Umbro-Marchean areas differs considerably. They were seat of pelagic sedimentation during the Mesozoic and of foredeep turbidite sedimentation from the Middle Miocene. During the Late Tortonian-Messinian the turbidite deep-sea areas (Marnoso-Arenacea and Urbana, Serraspina and Camerino sandstones) were progressively interested, from the inner areas outwards, by slope and bathyal sedimentation (San Polo Marls, Gessoso Solifera lowest marls). According to several authors these sediments are perhaps linked with piggy back basins (Patacca *et al.*, 1990, 1991), located along the front of the chain, originated by the enucleation of the Perugia massives (Lavecchia *et al.*, 1989). During the Messinian the foredeep areas

shifted South-Eastwards (Laga Basin) where deep-sea conditions persisted also during the evaporitic phase. The Faenza and Pesaro areas probably were structural highs during the Messinian and were separated from the Maiella and Gargano by deep-sea areas.

DISCUSSION

(P. Mazza, M. Rustioni, G. Aruta & E. Di Carlo)

According to De Giuli, Masini & Valleri (1987) Ochotonids, along with Erinaceids, Glirids and Cervoids, colonized the Gargano area during the Early Miocene, while *Cricetus*, *Microtia* and *Eliomys*, possibly accompanied by *Apodemus*, made their entrance during the Messinian. The Pliocene sea-level rise then disrupted the Gargano area forming an archipelago isolated from the surrounding mainland areas. This induced a very rapid endemization of the micromammals. A limited exchange between the islands of the archipelago seems testified by the sudden appearance, in the records of the several fissure fillings, of forms of conflicting size and evolutionary degree [De Giuli & Torre (1984a, b), De Giuli, Masini, Torre & Valleri (1984, 1985, 1986), De Giuli, Masini & Torre (1985a, b; 1986), De Giuli, Masini, Torre & Boddi (1985) and Mazza (1986a, b, 1987)].

In 1990, a rich fossiliferous site was found at Scontrone (L'Aquila) (Rustioni *et al.*, 1992; Patacca pers. comm., 1994). The macromammals from this locality, which are contained in Early Tortonian marine calcarenites, are very similar to the ones that were recovered from the Gargano fissure fillings (Freudenthal, 1971, 1976; Ballmann, 1976; Leinders, 1983; Willemsen, 1983) accompanied by *Prolagus*, *Microtia* and other rodents. Unfortunately, no micromammals have been found until now at Scontrone. Particularly significant are the artiodactyls, which seem to be holdovers of very primitive ruminant stocks, possibly immigrated from Asia through eastern Europe. Multidisciplinary observations point to the Late Oligocene - Early Miocene as the most probable time of immigration of the Scontrone fauna (Patacca pers. comm., 1994). The primitiveness of the community suggests that it was

likely isolated from any other fauna since.

P. apricenicus and the Capo di Fiume *Prolagus* possibly derive from a *P. oeningensis* deme which colonized the Abruzzo-Apulian area during the radiation of the latter towards Anatolia through the Balcans, an event that seems to have occurred in the course of the Middle Miocene, on the basis of the literature (Lopez Martinez & Thaler, 1975; Lopez Martinez, 1978). However, this opens a puzzling problem. Since there is no evidence of any corridor connecting the Abruzzo-Apulian area with the Balcans during the Middle Miocene, standing the present geological and stratigraphical information (Patacca pers. comm., 1994), the only possible moments for the colonization by the micromammals are either that supposed for the Scontrone macromammals, the Late Oligocene - Early Miocene, or the Early Messinian, when wide-scale regressions occurred.

Another debated problem is the age of the Gargano *Prolagus*-bearing karstic fissure fillings. The reconstruction of the evolutionary events that are supposed to have occurred between the end of the Miocene and the beginning of the Pliocene made by De Giuli & Torre (1984), De Giuli, Masini, Torre & Valleri (1984, 1985), De Giuli, Masini & Torre (1986), De Giuli, Masini & Valleri (1987) and Mazza (1986a, b, 1987) is convincing, but it should perhaps be slightly shifted backwards in time. According to Patacca and Scandone (pers. comm., 1993) the Late Miocene marine regression reached its climax during, or at the very end of, the preevaporitic Messinian, while during the evaporitic phase there was a remarkable positive eustatic reversal, which explains the deposition of thick sheets of evaporites and of turbidite sequences in several parts of the Mediterranean basin. Moreover, extensional tectonics added their effects along the Adriatic side of the Apennine, locally increasing the sea-level rise. In the light of this, the marine transgression, responsible for the elimination of the previous corridors, should be dated to the Late Messinian and not to the Early Pliocene.

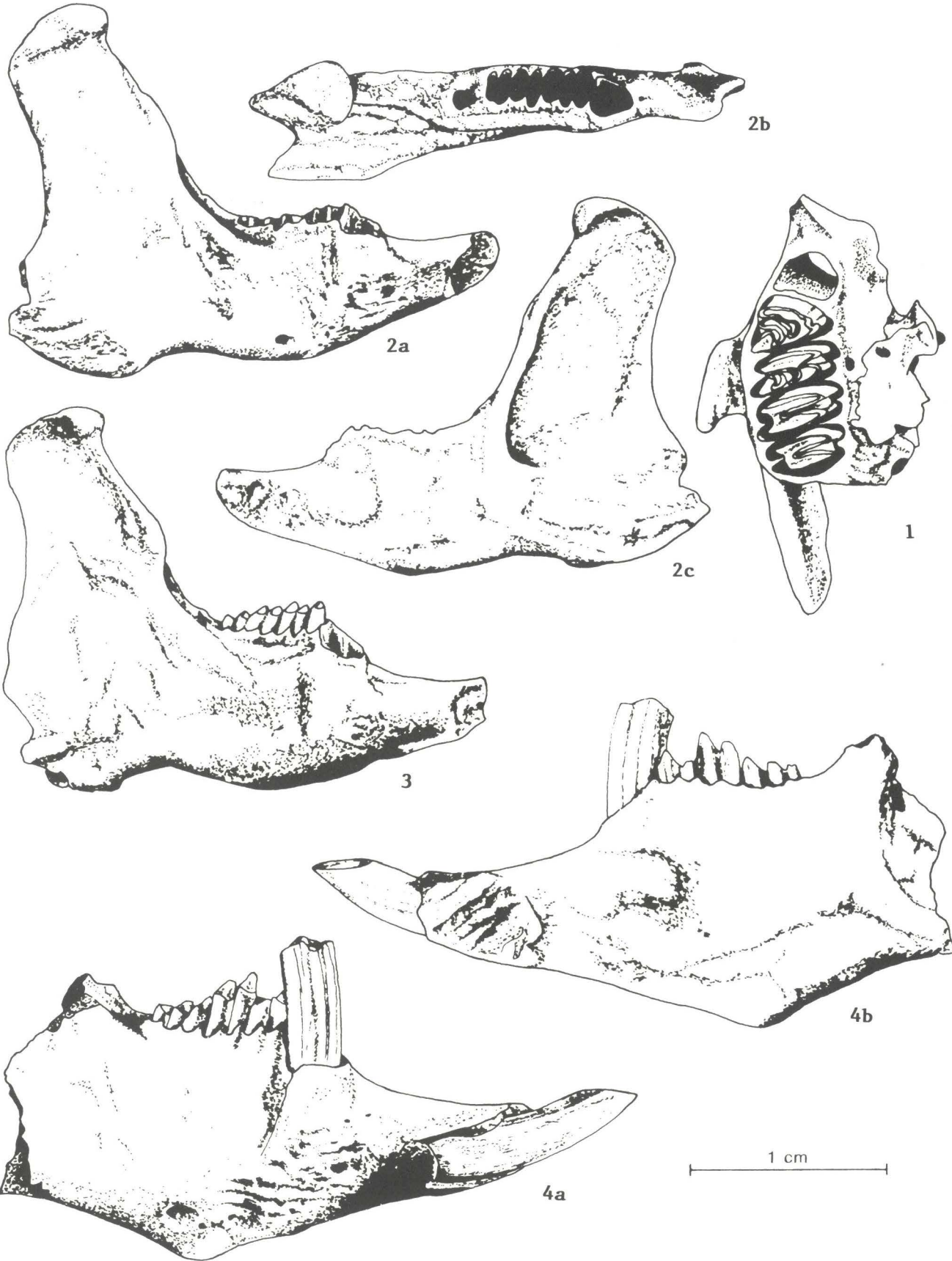
D'Alessandro *et al.* (1979) dated a layer of neritic calcarenites («Calcareniti di Adrano»), which the

EXPLANATION OF PLATE 2

Figs. 1-3 - *Prolagus apricenicus* from the Gargano fissure fillings: 1) Right maxillary, ventral view; 2a-c) right mandible, lateral, dorsal and medial view; 3) right mandible, lateral view.

Fig. 4 - *Prolagus imperialis* from the Gargano fissure fillings: 4a-b) Right mandible, lateral and medial view.

All figures from Mazza (1987).



Authors correlate with that capping the karstic fissure fillings of the Apricena quarries, from which rich amounts of *Prolagus apricenicus* and *P. imperialis* remains were collected, to the Late Tortonian for the occurrence of *Neogloboquadrina acostaensis*, *N. pseudopachyderma*, *Globorotalia tumida plesiotumida* and *G. suterae*. Nonetheless, Lower Pliocene sediments do occur in the area, as detected by Valleri (1984) in a section exposed in the Erba quarry, near Apricena. D'Alessandro *et al.* (1979) confirmed the occurrence of Pliocene sediments, but added that they lay disconformably over the Mesozoic and Miocene sequences (Ricchetti *et al.*, 1992).

A generic attribution of the Gargano fissure fillings to the Tortonian would be consistent with the date suggested by Freudenthal (1971, 1976), who referred the vertebrates from the karst fissure sediments of Apricena quarries to the Vallesian-Turolian, and would make the Gargano community approximately contemporaneous to the very similar one from Scontrone. However, it somewhat contrasts with the age and evolutionary degree of the Capo di Fiume specimen, which is Early Messinian in age, but quite primitive. In Gargano, primitive *Prolagus* representatives actually seem to survive, in progressively slighter numbers though, until later times, together with more advanced forms, as attested by Mazza's (1986a, b; 1987) observations. Another possibility, however, is that the Capo di Fiume area was separated from the Gargano soon after the Middle Miocene colonization and that its environmental and ecological conditions remained practically unaltered for a longer span than in Gargano.

By and large, the degree of evolution of *P. apricenicus* seems to exclude a Late Miocene immigration, unless one does not admit a case of evolutionary regression and homoplasy with *P. oeningensis*. However, there is still another possibility.

In the light of Freudenthal's (1985) more recent observations, the micromammals are supposed to have colonized the Gargano in an age that «may be equal to, or somewhat older than, the age of the Crevillente faunas» (pag. 62). Freudenthal observed that there are strict similarities between some distinctive components of the two faunas, such as between, respectively, *Cricetulodon* sp. and *C. fahlbuschi*; *Cricetus* sp. and *Hattomys* sp., from the Gargano, and *C. kormosi*, from Crevillente; *Apodemus* sp. and *Apodemus* cf. *primaevus*; and that *Stephanomys* from Crevillente is the most probable ancestor of *Microtia*. For reasons explained above, if the micromammals actually colonized the Gargano area in the Messinian, this has happened at its beginning. The primitiveness of the *Prolagus* immigrant

may then be explained supposing that it derived from some holdover *P. oeningensis* enclave that may have survived, practically unaltered, in the Balcan area.

CONCLUDING REMARKS

The scenario that comes out from the combined information from Scontrone, Capo di Fiume and Gargano suggests the following reconstructions.

Macromammals presumably made their entrance in the area by the Late Oligocene-Early Miocene, as already suggested by De Giuli *et al.* (1987) and as apparently confirmed by the Scontrone fossil community. On the contrary, the micromammals may have arrived in two or three following migratory waves or all at the same time.

De Giuli *et al.* (1987) believed that the Ochotonids, Erinaceids and Glirids may have accompanied the Artiodactyls, making their entrance during the Early Miocene. The evolutionary degrees of *Prolagus*, however, seems to exclude a pre-Middle Miocene arrival and suggests to slightly post-date this first micromammal event; on the other hand the Ochotonids would represent the result of a following invasion.

In the hypothesis that all the micromammals arrived during the Messinian, one must imagine a Balcan *P. oeningensis* holdover which came in along with *Cricetulodon*, *Cricetus*, *Apodemus*, *Microtia* and the glirids.

These two different views lead to conflicting evolutionary conclusions.

The environment seems to have maintained warm and humid, with rather thick forests dominating the Abruzzo-Apulian landscapes, for the whole time spanning the Middle-early Late Miocene interval. Between the latest Tortonian and the earliest Messinian the environmental conditions seem to have drastically modified.

If *P. oeningensis* was an early colonizer it would have given rise gradually to *P. apricenicus*, because of the prolonged uniformity of the environmental conditions. On the other hand, should the arrival of *P. oeningensis* be dated to the Early Messinian, the evolution of *P. apricenicus* would result quite accelerated, since the time for such event would be quite more restricted and the environmental conditions such to induce the rapid endemization of the original *P. oeningensis/apricenicus* population, manifested by a progressive increase of variability and size.

Whatever the case, new morphotypes, which tended to displace the original ones, increasingly appeared within the *Prolagus* population. The larger-

sized and more specialized *P. imperialis* thus appeared. The most advanced representatives of the two species share marked dental affinities with later insular forms, the Corse-Sardinian *P. figaro* and *P. sardus*; this is a good proof of the isolation and endemization of the Gargano representatives.

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