Lynx (Praha), n. s., 32/2001: 215–231. ISSN 0024–7774

Paleobiogeographical history of *Prolagus*, an European ochotonid (Lagomorpha)

Paleobiogeografická historie rodu *Prolagus*, evropské pišťuchy (Lagomorpha: Ochotonidae)

Nieves LÓPEZ-MARTÍNEZ

Department of Paleontology, Faculty of Geology, University Complutense, 28040 Madrid, Spain; lopezmar@geo.ucm.es

Received 28 June 2001

Abstract. *Prolagus* is one of the world's longest mammalian lineage, dwelling for more than 20 million years, 24 Ma if its direct ancestor *Piezodus* is taken into account, in Europe, Anatolia and northern Africa. *Prolagus* fossils form locally very rich assemblages, indicating that it was a common prey supporting food webs like modern rabbits. This ochotonid was similar to modern pikas (*Ochotona*) in their body size and shape. Both share a cladogenetic evolutionary pattern, in contrast with most lagomorphs. *Prolagus* inhabited mainly in subtropical swamp and wetland forest habitats, analogous to modern leporid *Sylvilagus palustris* from the Everglades (Florida, USA). The *Prolagus* paleodistribution had a strong latitudinal component, related to its thermophile exigencies. Its area has been deformed by the Alpine arc kinematics during Late Miocene. Before its final isolation and extinction, *Prolagus* area experimented a southern displacement, fragmentation and reduction during the Pliocene, but it coincides with the highest species richness of its history, due to endemisms. Cooler climatic conditions probably influenced the displacement of the *Prolagus* area, but it seems not to be the main reason for the retreat and final extinction of *Prolagus*, since it persists in insular populations living in a climate similar to the surrounding continents. Predation pressure probably has been one determinant factor accounting for the selective extinction of *Prolagus* mainland species around Mid/Late Pleistocene boundary. Insularity at different scales leads to population extinction, in contrast to current theoretical expectations.

INTRODUCTION

Basic, reliable data collection is the prime work to reconstruct and interpret the historical patterns of geo-biological changes. Paleontological data on taxic presence and absences, quality and quantity of fossil remains and biostratigraphic successions have been collected in Europe during more than two centuries. Although differently sampled, our continent is one of the world' richest territories for extracting information on the past evolution and forecasting trends into the future.

The study of the extinction processes, which dramatically affect the biosphere with an intensity, frequency and selectivity still largely unknown, needs qualitative and quantitative high-quality data uniquely unravelled by Paleontology. The fossil record is the only way to document the extinction patterns, and allows also to infer the main factors involved in the extinction process: genetic (lineage-dependent), ecological (environmentally driven) and biogeographical (chorological and geodynamical) factors, among others.

We resume here the paleobiogeographical history, long of more than 20 million years, of one of the most common Cainozoic European mammals, the ochotonid lagomorph *Prolagus*, represented by a huge number of fossil remains in more that 300 fossil-rich localities. Its paleodistribution regularly included Europe and Anatolia, with a relatively short-lasting incursion to North Africa. Curiously it seems never have reached Asia, their literature quoting there due to a wrong identification. This lineage represents one of the longest mammal lineage of the world, and disappeared in historical times after a period of isolation and hunter human pressure, well after the Pleistocene extinction wave. No documents of its life features remain, but its rich fossil record allows to reconstruct a part of his evolutionary strategy. The knowledge of the long-lasting *Prolagus*' fate can help to forecast other lineage destinies.

THE LAGOMORPH OCHOTONID *PROLAGUS*

The lagomorph genus *Prolagus* Pomel is represented in Europe, Anatolia and North Africa by some 22 species which lived during Neogene and Quaternary times. Its peculiarities are: a continuously-growing dentition, the lack of the third lower molar, a trilobed second lower molar and peculiar-shaped premolars, with a rounded, generally isolated anteroconid and an extra cusp (protoconulid) in the third lower premolar (p3). The closely related genus *Ptychoprolagus* Tobien from late Middle Miocene of Germany, created for some specimens representing the upper dentition only, is similar to *Prolagus* but with strong folds in the thinner parts of the enamel.

The morphology and phylogeny of *Prolagus* has been reconstructed mainly by F. Major (1899), Dawson (1969), López-Martínez (1974, 1977, 1978, 1989), López-Martínez & Thaler (1975), and Tobien (1975). All these authors interpret this lagomorph as a peculiar ochotonid (family including the modern pikas, genus *Ochotona*; Fig. 2). The main differences with their modern relatives are the lack of the third lower molar and of one dorsal vertebra. The majority of *Prolagus* species like most ochotonids are small-sized lagomorphs, around 500 g body weight.

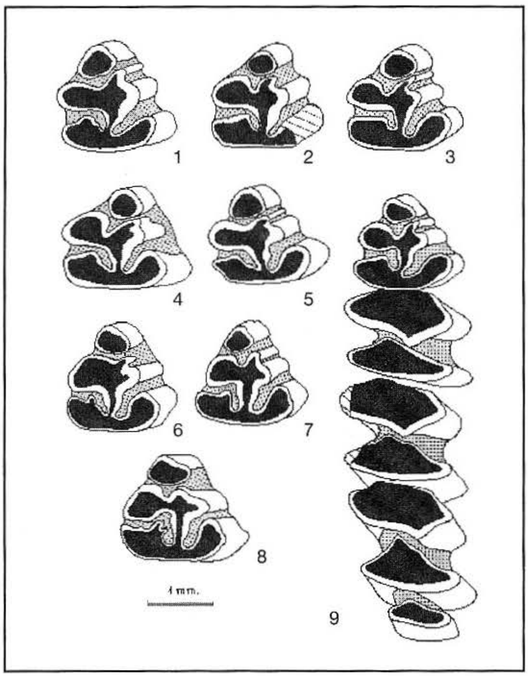
Successional stages of anagenetic lineages are clearly recognized in most Old Worlds ochotonids (Fig. 3). The genus *Piezodus* Viret, from the European Oligocene-Lowermost Miocene, is the direct ancestor of *Prolagus*, since recorded transitional populations show the transformation from *Piezodus* morphology (rooted cheek teeth, metaflexids present, lack of protoconulid in p3) into *Prolagus* morphology (lack of roots and metaflexids, presence of protoconulid) (Fig. 3). This anagenetic evolutionary pattern was extrapolated by Hürzeler (1962) to the rest of the *Prolagus* lineage. On the contrary, *Prolagus* shows several rapid radiations with a complicated cladogenetic evolutionary pattern, and most of its species are not easily connected by morphologically transitional-mosaic populations (López-Martínez 1974, 1978, 1997, Tobien 1975).

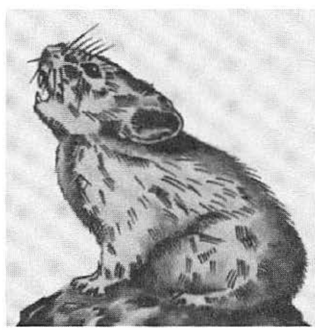
Erbaeva (1988) creates the family Prolagidae for this lineage, separate from typical ochotonids by its dental formula. However, different dental formulae exist within many mammal families, such as Palaeolagidae (even subfamilies like "Amphilaginae" Gureev in the Erbaeva's own concept (1988: 31). Therefore this feature by itself does not justify a different taxonomic rang of its own.

A soft-anatomy preserving *Prolagus* specimen has been figured by Mein et al. (1983) (Fig. 4). Its overall proportions, ear shape and lack of tail are similar to living *Ochotona*. This confirms the close relationships of both genera, already signalled by the study of the hard anatomy. Both share also highly diversified, rapid cladogenetic radiations, which are relatively rare evolutionary features among ochotonids (and Lagomorpha in general; only *Lepus*, *Hypolagus* and *Sylvilagus* among Leporidae show a similar cladogenetic pattern).

THE *PROLAGUS* FOSSIL RECORD

Fossils from *Prolagus* and other lagomorphs are in some localities extraordinarily abundant, which makes them able to be detected in spite of their rather small size. The high local abundance of European ochotonids from Late Oligocene onwards indicates that they must have played a very important role as basal preys for many larger and smaller predator species, either mammals or birds, like modern rabbits and hares in Mediterranean and steppe environments. This is noteworthy that, since its appearance at least in Europe, the same mammalian order seems to have supported terrestrial vertebrate food webs, as a basal prey for carnivores.





Figs 1, 2. Fig. 1. Lower cheek teeth of *Prolagus*. Left, *P. vasconiensis* (1–4), *P. tobieni* (5–9), lower right p3 and tooth row. Lower Miocene, Aragón Spain (from López-Martínez 1984). Above right, *P. sardus*, lower left p3 (about 2 mm length). Pleistocene, Castiglione 3, Middle Pleistocene Corse France, from Pereira and Salotti, unpublished (see Salotti et al. 1997). Fig. 2 (below right). Modern *Ochotona princeps*, redrawn after Erbaeva (1988).

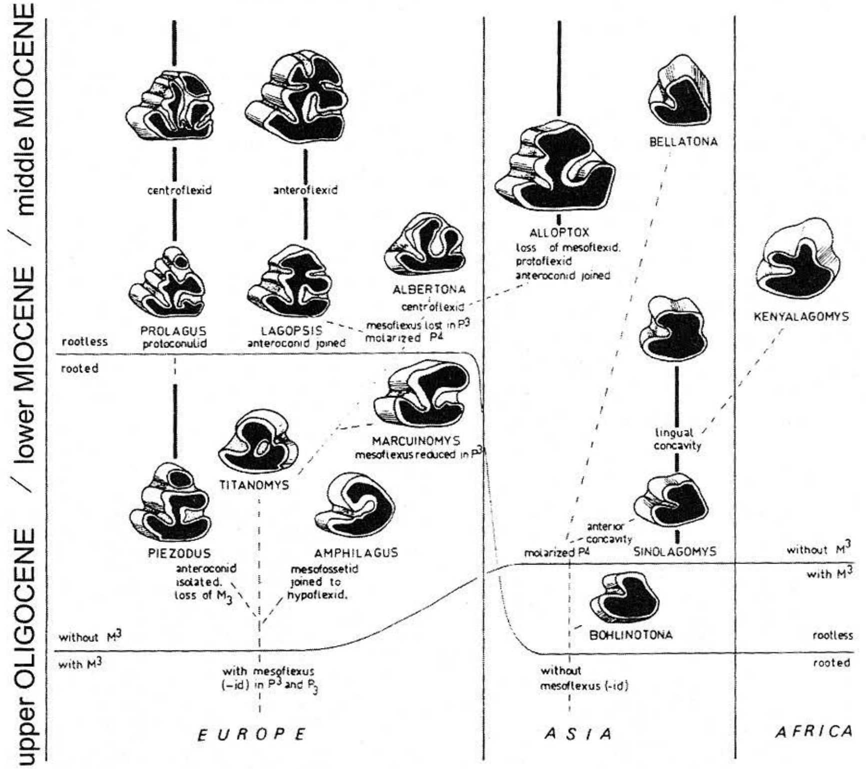


Fig. 3. Succession of Old World ochotonid lineages (from LÓPEZ-MARTÍNEZ 1986)

A large number of fossils belonging to *Prolagus* lineage has been collected in more than three hundred localities from Europe, Anatolia and North Africa. It is represented by two-dimensionally-preserved articulated skeletons, some of them with the imprints of the soft parts, and three-dimensionally-preserved isolated skulls, mandibles, post-cranial skeletal bones and fragments, as well as isolated teeth. CUVIER (1833: Pl. 174) correctly identified, described and figured the first *Prolagus* findings from the Gibraltar karstic breccias conserved in Campbell' collection (Fig. 5).

In biogeographical studies, the sampling effort must be very high, because in each locality at every moment the absence of a taxon is as significant data as its presence. The insufficient sampling makes hardy reliable the paleobiogeographical studies of large organisms. However, after the pioneering works of HIBBARD in North America and FREUDENTHAL, THALER and De BRUIJN in Europe, the introduction of washing and sieving technical procedures in microvertebrate paleontology greatly improved micromammal fossil recovery. Therefore, we have a rich fossil record allowing to reconstruct the biogeographical distribution of *Prolagus* with relative reliability. Nowadays it is possible to document not only the former presence of the lineage in the localities with well-represented fossil assemblages, but also to discard its presence in many fossil-rich localities devoid of *Prolagus* fossils.

About 22 species are distinguished in the *Prolagus* lineage:

P. oeningensis (König, 1825) (late-Middle Miocene, Germany); *P. sardus* (Wagner, 1829) (Pleistocene, Sardinia); *P. calpensis* F. Major, 1905 (Pliocene, Gibraltar); *P. vasconiensis* Viret, 1930 (Early Miocene, France); *P. bilobus* Heller, 1936 (Pliocene, Germany); *P. crusafonti* López-Martínez, 1975 (Late Miocene, Spain); *P. michauxi* López-Martínez, 1975 (Pliocene, France); *P. ibericus* López-Martínez, 1975 (Pliocene, Spain); *P. figaro* López-Martínez, 1975 (Pliocene, Sardinia); *P. depereti* (López-Martínez, 1975) (Pliocene, France) (described as subspecies of *P. figaro*); *P. schnaitheimensis* Tobien, 1975 (early-Middle Miocene, Germany); *Ptychoprolagus forsthartensis* Tobien, 1975 (late-Middle Miocene, Germany); *P. tobieni* López-Martínez, 1977 (late-Middle Miocene, Spain); *P. major* López-Martínez, 1977 (late-Middle Miocene, Spain); *P. praevasconiensis* Ringeade, 1978 (Early Miocene, France); *P. apricenicus* and *P. imperialis* Mazza, 1987 (Pliocene ?, Gargano, Italy); *P. sorbini* Massini, 1989 (Latest Miocene, Italy) (? synonymy of *P. michauxi*, see Cavallo et al. 1993); *P. aguilari* López-Martínez, 1997 (early Middle Miocene, France); *P. fortis* (López-Martínez et Sesé, 1990) (Early Miocene, Spain) (described as subspecies of *P. vasconiensis*; Murelaga et al., in prep.); *P. caucasicus* Averianov et Tesakov, 1998

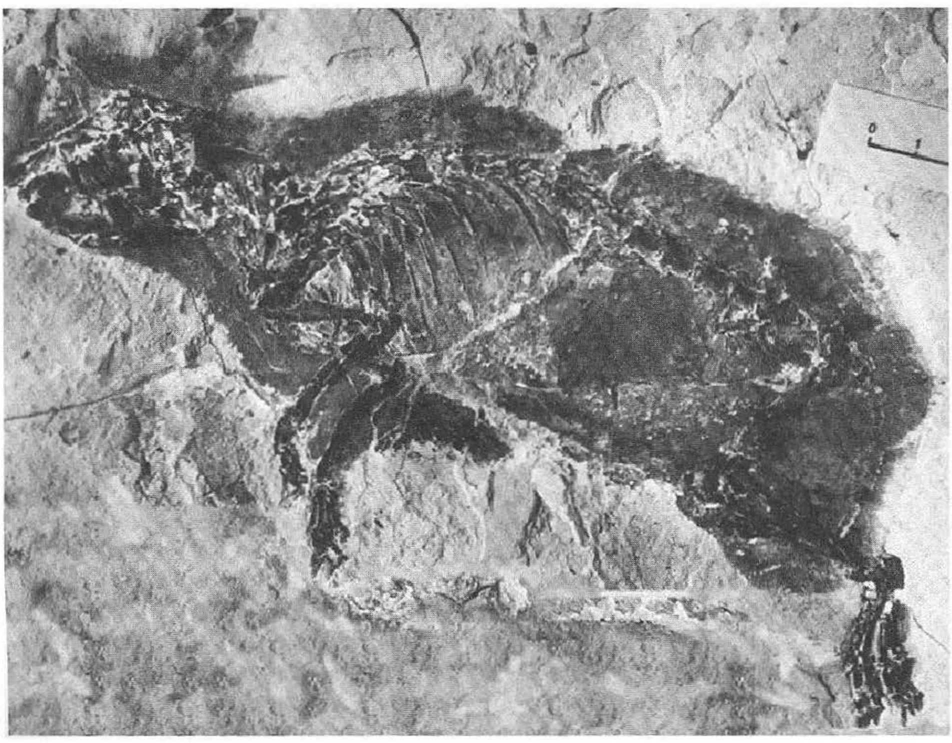


Fig. 4. *Prolagus crusafonti* from Late Miocene at Andance (France). After Mein et al. (1983).

Tab. 1. Percent of localities with *Prolagus* present and absent. Geographical distribution

region	N Africa	SW Europe	NC Europe	E Europe + Anatolia	total localities
Prolagus present	44	67	44	32	173
Prolagus absent	56	33	56	68	143
total localities	18	161	85	41	320
No. of species	1	19–20	7	7	22–23

(Pliocene, Russia); *Prolagus* sp. A, open name in LÓPEZ-MARTÍNEZ (1989) (Middle Pleistocene, Spain).

Our data base include 320 well-documented fossil localities from Europe, Anatolia and North Africa. In the following, we have considered as *Prolagus*-dwelling sites those having yielded rich assemblages of young and adult specimens, as well as those containing one or more almost complete, articulated skeletons. Poor assemblages containing isolated *Prolagus* tooth or mandibles are considered as distribution areas of *Prolagus* and/or its possible predators, producing sedimentary sinks of pellets and scattered remains, indicative of *Prolagus* living less than 50 km far from there. Some sites have been detected as having yielded a taphonomic mixed assemblage of probably reworked fossils (older, reworked fossils together with resedimented elements of a younger assemblage), and also poorly sampled, mixed introgressive deposits (e. g., from successive erosion and deposition episodes in karstic pouches). When detected and correctly dated, these mixed assemblages are also useful as indicative of populations living near the site at different periods.

THE PALEOENVIRONMENTS OF *PROLAGUS*

The open lands (savannah, steppe, alpine prairie, Mediterranean shrub, chaparral and desert biomes) are the favourite habitats of extant lagomorphs. Modern pikas (*Ochotona*) uniquely dwell in open rocky mountainous habitats. Forest-dwelling lagomorphs are rare (*Nesolagus*, *Sylvilagus*), and very few species are known to inhabit riparian or aquatic habitats (*Sylvilagus aquaticus*, *S. palustris*). If we extrapolate this actualistic scheme to the past, it seems likely to infer an open landscape habitat for most of the extinct lagomorphs like the *Prolagus* species. However, the European Miocene climate reconstructions and paleofloras seem mainly indicate a relatively humid, warm, forested habitat for *Prolagus*.

Prolagus (*P. schnaitheimensis*, *P. forsthartensis*, *P. oeningensis*) abundantly appears in lacustrine limestones and coal seams of the Bohemian basins (Czech Republic), ranging in age from Lower to Middle Miocene. The paleoenvironmental studies of these sites lead to reconstruct a highly covered woodland environment around coal-producing swamp forests. Plant megafossils indicate a flora formed by wet subtropical elements with some highly thermophile components. Different swamp cypresses dominates (Taxodiaceae), together with other deciduous-leaves trees, evergreen trees (Pinaceae, palms and Lauraceae), epiphyte lianas and many genera of aquatic and riparian plants (FEJFAR & KVAČEK 1993). This landscape reminds that of the modern paludal Everglades from Florida, home of *Sylvilagus aquaticus*, *S. palustris* and other wetland-linked lagomorphs.

In the Upper Miocene lacustrine diatomite and volcanic deposits from Andance (France), where soft-parts of organisms have been preserved, *Prolagus* (*P. crusafonti*) co-occurs with wet subtropical plants from a coastal swamp and mixed forest as well. There were many aquatic plants (*Ceratophyllum*, *Cirsium*, *Sparganium*, etc.) and Taxodiaceae swamp trees, as well as riparian trees (*Populus*, *Salix*, *Liquidambar*) and other subtropical trees living in less waterlogged soils (*Zelkova*, *Platanus*, Lauraceae, *Cinnamomun*, *Smilax*, *Carya*, *Parrotia*, Juglandaceae, *Castanea* and varied conifers), covered by varied epiphytic lianas, ferns and mosses (MEIN et al. 1983, DEMARQ et al. 1989). This humid environment was supposedly surrounded by drier open prairies, occupied by grazing antelopes and equids. *Prolagus* is the most frequent and best preserved mammal in the diatomite deposits. Probably driven by the actualistic model of modern lagomorphs, found mostly in open habitats (see above), the authors infer that the Andance *Prolagus* inhabited open clears within the woodland around the lake. However, forest clears are particularly not a natural habitat, and modern forest mammals are hardly specialised in such places. *Prolagus* could instead be a forest-dweller or even a peri-aquatic riparian pika, similarly to the two modern paludal species of the American leporid *Sylvilagus*.

PROLAGUS ECOLOGICAL PALEOBIOGEOGRAPHY

The hypothesis of *Prolagus* as a generally thermophile wetland dweller can be supported by comparing its relative abundance in two south-western European successions, Spain

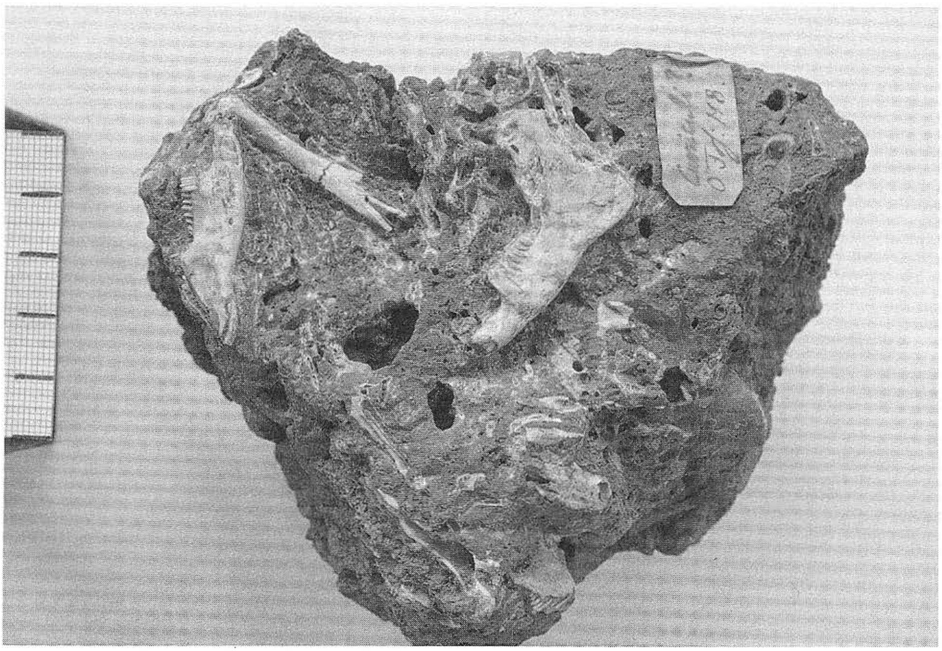


Fig. 5. *Prolagus calpensis* from Gibraltar, figured by CUVIER (1833).

Tab. 2. Percent of localities with *Prolagus* present. Chronological and geographical distribution

region	N Africa	SW Europa	NC Europa	E Europa + Anatolia	No. of localities	No. of species
Lower Miocene	0	62	100	0	16	6
low Middle Miocene	0	57	100	0	46	5
up Middle Miocene	0	75	91	100	27	4
Upper Miocene	0	89	60	50	43	1
Uppermost Miocene	67	88	50	25	27	3
Pliocene	75	80	9	28	76	9
Pleistocene	50	50	0	0	65	4
Holocene	0	39	0	0	20	1

and France (Fig. 6). *Prolagus*' preferred distribution in relation with *Lagopsis*, the other abundant European ochotonid (Fig. 4) is clearly biased towards higher latitudes. Their latitudinal segregation is strongly increased during the two arid periods detected in the European Early and Middle Miocene. The first one is recorded in Lower Miocene deposits (Biozone Z, Late Ramblian), and it coincides with relatively lower temperatures (Van der MEULEN & DAAMS 1992). The second arid period occurred around the Middle Miocene during the Langhian age (15–14 million years, see Van der MEULEN & DAAMS 1992), when a very warm and arid climate specially affected the peritethyan area. During this episode, where fibrous clay minerals typically formed in marginal lacustrine environments, *Prolagus* disappeared in heavily affected areas, like the Iberian southern basins (Lisbon, Madrid, Daroca, Buñol). During these dry climate periods it was replaced by the slightly larger ochotonid *Lagopsis*, but *Prolagus* subsisted in higher latitudes, less affected by the aridity wave (see Fig. 6). From its northern shelter, *Prolagus* extended into the south during relatively more humid episodes, like that of lowermost middle Miocene (Biozone A = lower Aragonian; DAAMS & Van der MEULEN 1992).

Not all the *Prolagus* species must had the same ecological requirements. For example *P. ibericus*, from the Pliocene Iberian interior highlands, or the large *Prolagus* species from the insular Gargano (MAZZA & ZAPONTE 1987), are recorded from karstic mesas inhabited by specialised arid land dwellers, such as hypsodont murid and cricetid rodents and gazelles. Even so, subtropical climate was present in these relatively arid landscapes, with seasonal rainfall assuring water maintenance in open reservoirs guaranteed by the rich karstic water resources in dolinas, pools and sinks holes.

Probably a relatively arid, open subtropical landscape was also present in lowland localities with *Prolagus* from Latest Miocene and Pliocene of Southern and Eastern Europe and Anatolia (Spain, Italy, Greece, Turkey, Caucasus) and Pleistocene of Central Europe (Hungary), inhabited by camels and ostriches. But *Prolagus* could dwell there in locally wet areas, such as the finimiocene Pesaro coastal swamp in Italy, and the Maramena wet forest in Greece. The presence of *Prolagus* in the finimiocene tropical rainforest of Salobreña (Spain), together with diverse sub-Saharan rainforest rodents, shows its affinities for warm-wet woodland habitats.

THE *PROLAGUS* PALEODISTRIBUTION

According to the fossil documents collecting the richest and best studied Late Cenozoic fossil-bearing localities from Europe and surrounding areas, two maps of *Prolagus* paleodistribution have been elaborated, one for the Miocene (20 to 8 million years ago, Fig. 7) and other for the latest Cenozoic (8 Ma. to present, Fig. 8). Both maps represent two paleogeographic reconstructions, one by DERCOURT et al. (1993) for Tortonian age (Late Miocene, around 9 Ma) and the other by RÖGL (1998) for Messinian age (Latest Miocene, around 7 Ma).

These two maps also offers an image of the conflicting interpretations given by authors for the complicated paleogeographical frame of the area during the Cenozoic, strongly affected by the alpine orogenic belt dynamics. Realistically, accurate agreed maps of successive snapshots for short periods can hardly be expected for the moment. The quoted authors offer a good viewpoint of the main paleogeographical features of the area during the Late Cenozoic, which can be summarized as follows:

(1) a general retreat of the platform realms, gradually and stepwise increasing the sharpness of the shores and the topographic gradients.

(2) an increased isolation of the Tethys remaining seaway, progressively fragmented and cut from the Atlantic ocean. Its complete closing and subsequent evaporitic precipitation, during a relatively short time, is one of the most important Old World paleogeographic event (the Messinian salinity crisis).

(3) an increase of the emerged land area and progressive sea retreat, by lowering sea level due to polar icecaps formation and general uplift due to multiple plate collisions.

(4) a generally more continuous land masses, due to integrative collision of former continental microplate islands. Exceptions were the opening of the Lion' Gulf plus rotation of the Thyrrenian block, and the collapse of the Betic-Rifean and Aegean blocks.

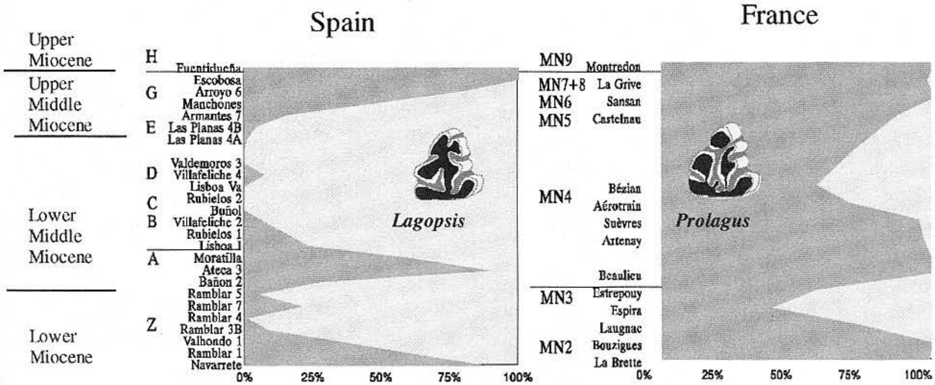


Fig. 6. Relative abundance of *Prolagus* and *Lagopsis* (Ochotonidae, Lagomorpha), in two well-dated successions from Spain and France during Early to early Late Miocene. A latitudinal component is clearly observed, *Prolagus* being relatively more abundant in northern regions. This climatic signal is related to relative humidity (Van der MEULEN & DAAMS 1992). Humid periods are signalled by *Prolagus* incursions in southern regions.

(5) a shortening of the crust, and corresponding decrease of the general available surface for the biosphere spread in the area. This general decreasing area was compensate with more land surface due to orogenic uplift and valley erosion, making a more rough landscape.

The two compound maps of the *Prolagus* paleodistribution resume in a rather general view the overall pattern of its chorological changes. The boundary between the two time periods represented in both maps, around the Tortonian/Messinian boundary, has been chosen as being a turning point in the paleobiogeographical evolution for the entire peritethyan biota. The first map (Fig. 7) shows the Tortonian transgressive episode flooding a large extent of the formerly emerged platforms. The second map (Fig. 8) represents a further minor transgression at a relatively lower sea level after drying of the former platforms, just before the total isolation of the Tethyan remains and the Messinian salinity crisis.

(a) The Miocene Prolagus *paleodistribution*

The first 12 million years long period of *Prolagus* evolution are summarized in a single map at the risk of information loss, for the shake of simplicity and clarity (Fig. 7). A more detailed time series showing the changing *Prolagus* distribution is shown in Fig. 9. The changes are expressed as percent of localities occupied by *Prolagus* in relation with the total localities available for that period. Data are separated into four regions:

– Southwest Europe, SWE (Iberian peninsula, southern France and subalpine Italy),
– Northcentral Europe, NCE (north-central France, Germany, Switzerland, Austria, Poland, Czech Republic, Slovakia and Hungary),
– Eastern Europe and Anatolia, EEA (the Balkans, Belaus, Ukraine, Russia and Turkey),
– North Africa, NA (Morocco, Algeria, Tunisia, Libya).

Some peritethyan regions are poor in or devoid of paleontological data for this period (NW Europe, NW Iberia, north Africa, eastern Europe). The highest data density concentrates in rich and well explored Miocene basins in SWE and NCE for the entire period, and EEA for late Middle Miocene to Pliocene. Ancient insular areas are detected in Middle Miocene Balearic Islands and Late Miocene of Italy (Toscana, Gargano), however *Prolagus* was only present in one of them (Gargano, see below).

The Miocene *Prolagus* paleodistribution area draws a rough latitudinal band stretching in an East-West direction, which clearly bends as an arc around the Alpine region (Fig. 7). The radial axis of this arc coincides with the Rhine grabben. This paleodistribution strongly indicates the bending movement suffered by the European continent as a whole, the eastern and western ends approaching southwards and towards each other. Formerly, the *Prolagus* area central section was probably aligned with the eastern and western sections, at a similar latitudinal position. The Alps Range would have a pivotal position, in the centre of this arching movement. Its northward push direction of its thrusting stacking tectonics must be one of the reasons for the northward displacement of the *Prolagus* area central section.

Some trends appear in the paleobiogeographical changes of*Prolagus* along the Miocene in Europe (Fig. 9). Its frequency decreases in NCE, passing gradually from 100% in Early Miocene to 60% in Late Miocene. At the same time it increases in SWE, passing from around 60% in Early Miocene to near 90% localities in Late Miocene. The behaviour of *Prolagus* in EEA may be compared to that in NCE, except for a higher density in EEA during the Pliocene. The *Prolagus* apparently sudden entry there during Middle Miocene is probably an effect of the poor fossil record from this region during Early and early-Middle Miocene (only a single rich locality is well known).

During the Middle/Late Miocene boundary, an extinction wave affected all Ochotonid lineages: *Lagopsis*, *Eurolagus*, *Ptychoprolagus* and three *Prolagus* species were extinct. A single rapid spreading new *Prolagus* species survived, *P. crusafonti*, the lineage being then at the lowest specific richness level of its history (Fig. 9). During 4 Ma, the single species *P. crusafonti* is the only representive of the genus, from about 11 to 8 million years ago. Its homogeneous distribution and stability contrasts with its high morphological variability (López-Martínez 1988). The new species occupies the same area that its relative, formerly widespread *P. oeningensis*, which seems to be its direct ancestor. This total replacement of *P. oeningensis* by *P. crusafonti* along its entire area seems not have been preceded by a previous bottleneck process. Nevertheless, to be sure we need more continuous records of rich, successive populations in distant localities across the Middle/Late Miocene boundary.

Part of the southern boundary of the Miocene *Prolagus* paleodistribution is located across the mid Iberian Peninsula. It stretched from east to west with a sensible latitudinal compo-

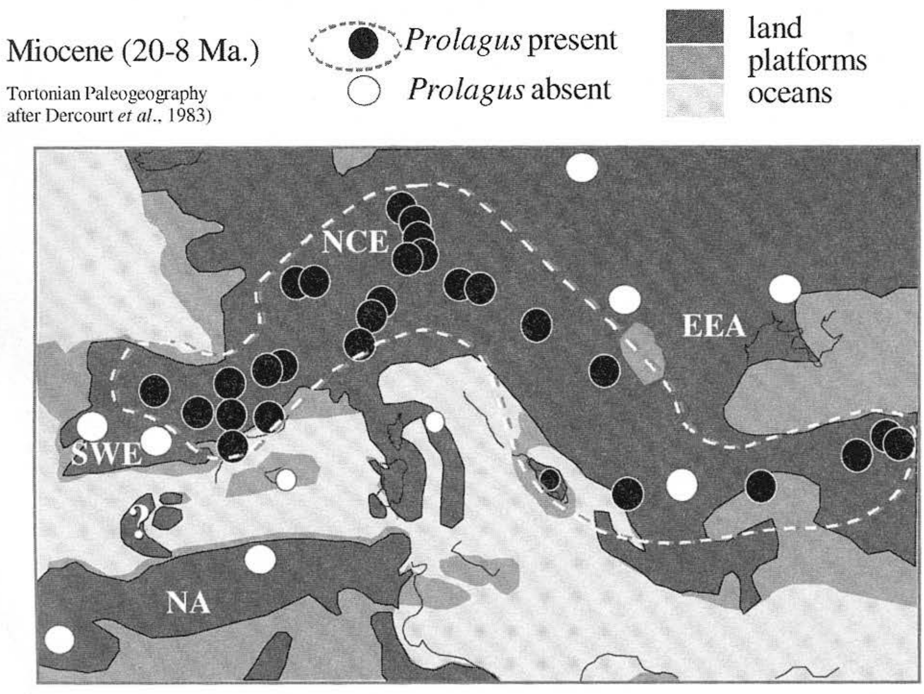


Fig. 7. Map of Miocene *Prolagus* paleodistribution. Insular species of Lagomorphs are represented by smaller circles. EEA: eastern Europe and Anatolia. NA: northern Africa. NCE: northern and central Europe. SWE: southern and western Europe.

nent. This frontier fluctuated northwards and southwards during the Early to Middle Miocene, apparently linked among other factors to the changing climatic conditions (see above, Fig. 6). A similar Neogene fluctuation of the boundary between Paleartic and Ethiopic bioprovinces has been detected by PICKFORD & MORALES (1994).

(b) the Latest Cenozoic Prolagus *paleodistribution*
An important paleogeographic event occurred at the Messinian salinity crisis, about 6 Ma ago. Around this period, the Betic-Rifean Massif, situated in an intermediate position between SWE and NA, collided into the Betic-Rifean orogen and closed the North-Betic and South-Rifean seaways. A great faunal exchange occurred then between Europe, Asia and Africa, comparable with the Great American Interchange. Carnivores, camels, tropical African rodents, monkeys and antelopes invaded Europe, while *Prolagus* and other micromammals invaded northern Africa, taking the opposite direction. Probably during this event *Prolagus* reached the Thyrrenids (Corsica and Sardinia, its last territories), but failed to occupy the Balearic, Crete, Malta, Cyprus and other future Mediterranean islands (Fig. 8).

Further during the Pliocene, the Betic-Rifean massif partly collapsed, opening a new seaway between the almost dried rests of the Tethyan basin and the Atlantic ocean through Gibraltar and the Alboran sea. The *Prolagus* paleodistribution extended then along NA

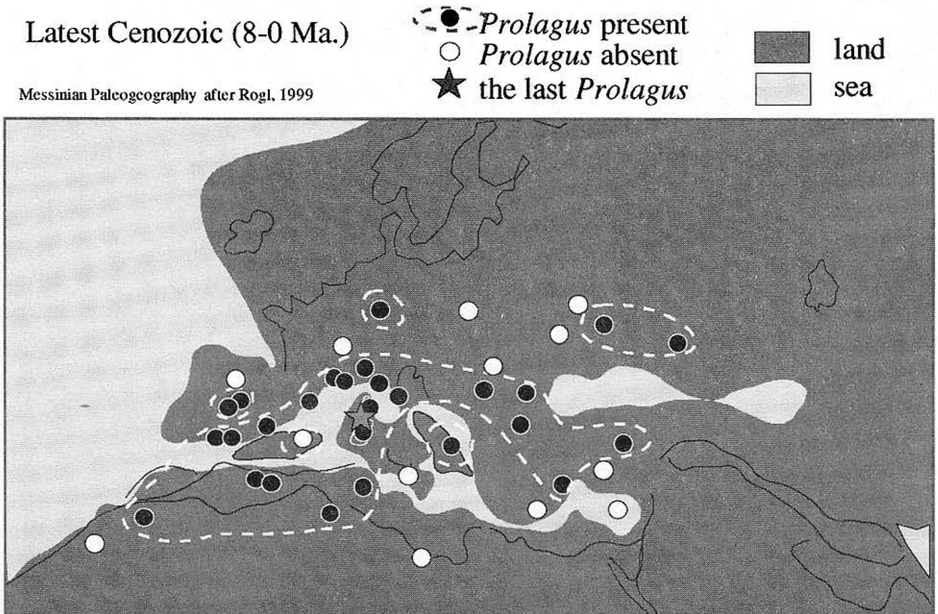


Fig. 8. Map of latest Cenozoic *Prolagus* paleodistribution; legend like Fig. 7.

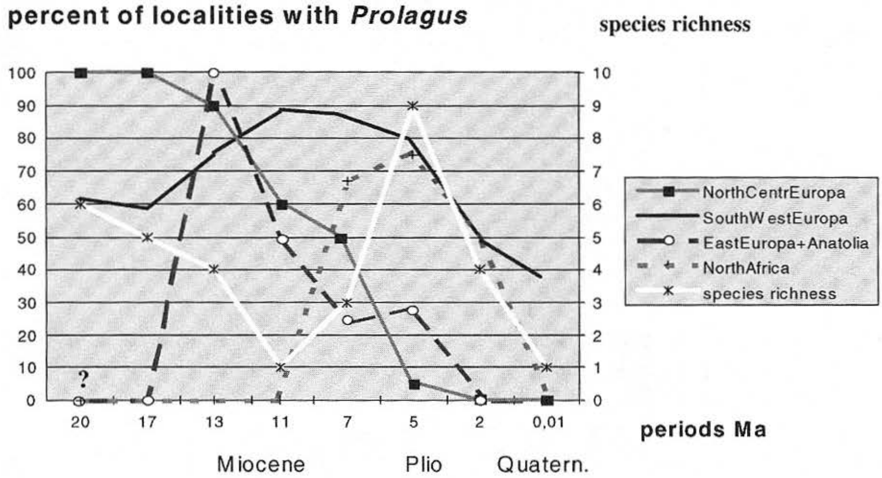


Fig. 9. Distribution chart of *Prolagus* in four Old World regions, during Neogene and Quaternary (in abscises, marked by initial period in million years). In ordinates, relative number of localities where *Prolagus* is present. Number of *Prolagus* species at each period is also indicated.

across Morocco, Algeria and Tunis, but simultaneously contracted and fragmented at its northern margin. *Prolagus* almost disappeared from NCE, the northern part of EEA and the Atlantic margin of the SWE. During the Pliocene, three marginal, isolated, endemic populations remained at the north-western (*P. ibericus*), north-central (*P. bilobus*) and north-eastern (*P. caucasicus*) margins of its formerly continuous area (Fig. 8). These three allopatric populations did not survive into the Pleistocene.

As a result of the retreat and fragmentation of the *Prolagus* area, the proportion of the *Prolagus*-bearing fossil assemblages generally decreases in all regions around 7 million years, except in NA where increases during the Pliocene and its decrease was retarded (Fig. 9). Ironically, the *Prolagus* declining Pliocene period shows also its maximum species richness, 9 species, because of the high number of endemic species (Fig. 9). During this epoch, *Prolagus* was replaced by the *Ochotona* lineage at its eastern margin area (Hungary, Moravia, Rhodes, Anatolia). This fact, together with the Leporid spread, indicate the extension of open, relatively arid landscape settings.

The southward displacement of the *Prolagus* area during the Latest Cenozoic seems linked to the beginning of the last climatic cooling phase affecting the whole planet. In northern Europe, a temperate climate substituted the subtropical climate formerly installed for tens million years. However, the warm climate (subtropical until the end of Pliocene, then Mediterranean), persisted during the Latest Cenozoic in southern Iberian and northern African regions without signs of cooling except in the highest peaks. Moreover, the Pliocene and the interglacial Pleistocene pulses were warm enough for allowing the thermophile *Prolagus* to live in Europe in favourable conditions. During the Quaternary the climate in the mainland was supposedly comparable to that existing in the Thyrrenids, where *Prolagus* subsisted until historical epoch. Therefore, the climatic conditions were not the main reasons for the retreat and final extinction of *Prolagus*. The insularity effects and other possible factors accounting for the *Prolagus* extinction will be discussed below.

THE INSULAR POPULATIONS AND THE *PROLAGUS* EXTINCTION

In spite of the relatively high proportion of known insular lagomorphs, both recent and extinct, the *Prolagus* lineage rarely inhabited true Tethyan islands along its history. The only exceptions are the Latest Miocene-Pliocene Gargano islands and the Plio-Pleistocene Thyrrenids. In contrast, other island were successfully colonized by Lagomorphs, like Baccinello in Latest Miocene, Sicily and Balears in Neogene. *Prolagus* is recorded in nowadays insular areas, such as Chios and Kos islands in EEA, but these localities were not isolated when *Prolagus* lived there during the Mio-Pliocene.

Ancient insular mammal faunas can be recognized in the fossil record by special signs: a low species richness community, few or no carnivores, small mammals became larger and the opposite, large mammals became smaller (Thaler 1973, Sondaar 1977). Insular *Prolagus* and other Ochotonids, like other micromammals, are larger than their mainland relatives. Conversely, insular leporids can behave like large mammals, becoming smaller than the mainland hares (case of the Balearic hare, see Palacios & Fernandez 1992).

Both Gargano and Thyrrenid insular *Prolagus* populations produced at least two endemic species each: *P. apricenicus* and *P. imperialis* in Gargano (Mazza 1987, Mazza & Zafonte 1987), *P. figaro* and *P. sardus* in Thyrrenids (López-Martínez & Thaler 1975). Although there are some indices of the coexistence of the two sister species in each case, the frequent taphonomic mixture of karstic fissure filling deposits can be misleading. All these insular species show large size, robust skeleton and some complications in the premolar morphology. In contrast, other known cases of insular lagomorph populations show a single species only, and they tend either to simplify (*Paludotona* Dawson, *Gymnesicolagus* Mein et Adrover) or to complicate its dental morphology (modern *Pentalagus* Lyon).

The isolation time seems independent of the degree of morphological differentiation between insular and mainland populations. The modern insular leporid *Nesolagus netscheri* from Sumatra shows similar morphology that a recently discovered mainland population from Laos. In spite of the ca. 8 million years divergence time inferred by their genetic distances, they differ only by a somewhat larger interorbit (see Surridge et al., 1999). Conversely, the Pliocene Thyrrenian insular *Prolagus figaro* strongly diverged from their closest mainland *Prolagus* population (*P. depereti*) in a relatively short time (much less than 1 m.y.). The Balearic hare as well, *Lepus granatensis solisi*, has rapidly changed its shape and loss about 5% in size (was probably introduced by man less than 7000 years ago; Palacios & Fernandez 1992).

Around Middle Pleistocene epoch, all *Prolagus* species were extinct, except those from eastern and southern Iberian littoral (*Prolagus calpensis* from Barcelona, *Prolagus* sp. from Malaga) and Thyrrenian islands (*Prolagus sardus* from Corsica and Sardinia). The two species differed in size, the mainland species being around three quarters of the insular species size. Both have similar limb proportions. However, dentition size was similar, thus the insular species had a disproportionate body size in relation to teeth size.

Before the Late Pleistocene, the mainland *Prolagus* populations disappeared. The latest glacial period could bring too much a cold climate until its last refuge. Also, the littoral habitats of the last mainland *Prolagus*, may be the humid backshore of coastal forests, probably disappeared because of the arid glacial period and the increasing steep of orogenic landscapes. However, these factors as well must have affected the Thyrrenids, where *Prolagus* survived for 150,000 years more. Therefore, these factors alone cannot explain the *Prolagus* extinction. Other factors, such an increased predation pressure, must account for the selective extinction that stroked mainland and spared insular *Prolagus*.

After its isolation phase, the *Prolagus* extinction pattern is similar to that of other mammals. The fate of insular faunas is nearly predictable: the endemic, isolated mammal species shows more or less longevity, but its fatal destiny is always extinction. This regularity is just an empirical observation. We do not know cited examples of an insular mammal species successfully invading the mainland area (the continent, in case of terrestrial faunas). Conversely, there are many examples of insular species becoming extinct, not only among mammals but many other groups also. This pattern do not seem to be determined by any evolutionary constraint. In fact, the current evolutionary theory predicts the opposite, namely allopatric isolation would be a prerequisite of evolutionary change and speciation. On the contrary, in the fossil record as well as in modern world, the observed pattern is extinction comes frequently after a previous isolation phase. *Prolagus* and other extinct vertebrates repeat this pattern at different scales, since the final extinction of the last threatened insular refugees occurred in a small island butte, Tavolara (VIGNE 1988).

The extinction of the mainland endemic *Prolagus* species such as *P. ibericus*, *P. bilobus* and *P. caucasicus*, occurred probably earlier, near the Plio/Pleistocene boundary. The isolation of endemic species by geographic barriers are not a necessary factor linked to the extinction. Also endemic, either sympatric or allopatric species are prone to the extinction. This was the case for *P. schnaitheimensis* and *P. forsthartensis* (sympatric respectively with *P. vasconiensis* and *P. oeningensis*), and for the above cited allopatric species. They differentiated after the fragmentation of a former continuous distribution area, without evident geographic barriers.

CONCLUSIONS

Near 22 *Prolagus* species (Lagomorpha: Ochotonidae) inhabit Europe, Anatolia and northern Africa during more than 20 million years mainly in subtropical swamp and wetland forest habitats, analogous to modern leporid*Sylvilagus palustris* from the Everglades (Florida, USA). Although they were a common prey supporting food webs like modern rabbits, a combination of climatic change (to colder and arid conditions) and stronger predation pressure lead to its extinction, after a suite of paleogeographic changes: (1) a southern displacement of the area, (2) a fragmentation, (3) a strong reduction during the Pliocene, and 4) isolation in the Thyrrenids (Corsica and Sardinia Islands). The Pliocene areal reduction coincides with the highest species richness of the lineage history, due to endemisms.

The reasons for the retreat and final extinction of *Prolagus* include arid and cooler climatic conditions; but its selective extinction in mainland during Pleistocene was not climatically driven, since it persists in insular populations living in a climate similar to the surrounding continents. Stronger predation pressure probably has been one determinant factor, man being one of its potential predators as it has been shown in Corsica. Population isolation is a prelude of extinction, in contrast to current theoretical expectations.

SOUHRN

Rod pišťuch *Prolagus* představuje jednu z nejdelších vývojových linií v historii savců světa, která se vyvíjela v Evropě, Anatolii a severní Africe více než 20 milionů let, a pokud je do výčtu zahrnut jako přímý předek i rod *Plezodus*, tak až 24 milionů let. Fosílie jedinců rodu *Prolagus* tvoří místy velmi bohatá společenstva, která dokládají, že tato zvířata byla – podobně jako moderní králici – běžnou součástí potravních sítí. Tyto pišťuchy byly velikostí a tvarem těla podobné pišťuchám náležejícím současnému rodu *Ochotona*. Rod *Prolagus* obýval především subtropické mokřady a vlké lesy, a byl ekelogickým analogem současného králíka bažinného (*Sylvilagus palustris*), který žije v Everglades na Floridě (USA). Fosilní rozšíření rodu *Prolagus* má patrný charakter zeměpisné délky, způsobený zřejmě jeho termofilními ekologickými preferencemi. Jeho areál rozšíření byl vymezen pohybem Alpského oblouku během pozdního miocénu. Před konečnou isolací a vymřením rodu *Prolagus* se areál jeho rozšíření v průběhu pliocénu měnil a posouval na jih, fragmentoval a zmenšoval, v této době ale měl také nejvyšší druhovou bohatostí v celé své historii, která byla způsobena endemismem. Chladnější podnebí pravděpodobně ovlivnilo posuny areálu rozšíření rodu *Prolagus*, ale nezdá se, že by bylo hlavním důvodem ústupu a konečného vymření tohoto rodu. Rod *Prolagus* od té doby přežíval v ostrovních populacích žijících v podnebí podobném okolním světadílům. Určující faktor, který způsobil selektivní vymření pevninských druhů rodu *Prolagus* kolem hranice středního a pozdního pleistocénu byl zřejmě predační tlak. Fragmentace areálů rozšíření v různém měřítku tak vedla k populačnímu vymírání. Tyto závěry však neodpovídají dosavadním hypothesám.

ACKNOWLEDGEMENTS

Many thanks to Dr. Ivan HORÁČEK, Dr. Jiří MLÍKOVSKÝ and Dr. Petr BENDA for their invitation to participate in this volume in homage to Prof. Dr. Oldřich FEJFAR, and for their editorial work. The kindness and the engagement of Prof. FEJFAR with all, students, colleagues and fossils, have been proverbial. I acknowledge him in my name and that of all my students and friends who always received from him and his wife support, hospitality and rich knowledge. Among many good moments, some of us will never forgot the splendid Rohanov meeting that Prof. FEJFAR made possible. Thank you both, Oldřich and Svatuška for being always there.

REFERENCES

CAVALLO O., SEN S., RAGE J.-C. & GAUDANT J., 1993: Vertebrés Messiniens du faciès à Congeries de Ciabòt Cagna, Corneliano D'Alba (Piémont, Italie). *Riv. Piemont. Stor. Natur.*, **14**: 3–22.

CUVIER G., 1833: *Recherches sur les ossements fossiles.* Paris, 514 pp.

DAWSON M. R., 1969: Osteology of *Prolagus sardus*, a Quaternary ochotonid (Mammalia, Lagomorpha). *Palaeovertebrata*, **2**(4): 157–190.

DEMARQ G., MEIN P., BALLESIO R. & ROMAGGI J.-P., 1989: Le gisement d'Andance (Coiron, Ardèche, France) dans le Miocène supérieur de la vallée du Rhône: un essai de corrélation marin-continental. *Bull. Soc. Géol. France*, **8**(4): 797–806.

DERCOURT J., RICOV L. E. & VOIELYNCK B. (eds.), 1993: *Atlas Tethys Paleoenviromental maps.* Paris: Gauthier-Villars, 307 pp.

ERBAEVA M. A., 1988: *Late Cenozoic pikas: taxonomy, systematics, phylogeny.* Nauka, Moskva, 224 pp (in Russian).

FEJFAR O. & KVAČEK Z., 1993: Tertiary basins in Northwest Bohemia. *Excursion nr. 3 Paläon. Ges. 63 Jaherstaung, Univ. Karlova, Čes. Geol. Společ.*: 1–35.

LÓPEZ-MARTÍNEZ N., 1974: *Evolution de la lignée d'Ochotonidés Piezodus-Prolagus dans le Cénozoïque d'Europe Sud-Occidentale.* Thèse Univ. Sci. Tech. Languedoc, Académie Montpellier, 165 pp.

López-Martínez N., 1977: *Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario inferior de España*. Tesis Doct. Univ. Complutense, Madrid (unpubl.)

López-Martínez N., 1978: Cladistique et Paléontologie. Application à la phylogénie des Ochotonidés européens (Lagomorpha, Mammalia). *Bull. Soc. Géol. Fr., Paris*, **7**(20, 6): 821–830.

López-Martínez N., 1984: Los Lagomorfos (Mammalia) de la sucesión del Mioceno inferior de Calamocha (Teruel). *Col. Paleont.*, **39**: 27–44.

López-Martínez N., 1986: The Mammals of the Lower Miocene of Aliveri (Greece). V: The Ochotonid Lagomorph *Albertona balkanica* n. gen. n. sp. and its evolutionary relationships. *Proc. Konink. Nederl. Akad. Wetensch.*, **89**(2): 177–194.

López-Martínez N., 1988: Contribution à l'étude du gisement Miocène supérieur de Montredon (Hérault). Les grands mammifères. 1 – Lagomorphes. *Paleovertebrata*, **6**: 7–14.

López-Martínez N., 1989: Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario inferior de España. *Mem. Museo Paleont. Univ. Zaragoza*, **3**: 1–342.

López-Martínez N. 1997: Lignées évolutives, formes intermédiaires et évolution en mosaïque: exemple des lagomorphes européens. Pp.: 105–120. In: Aguilar J. P., Légendre S. & Michaux J. (eds.): *Actes du Congrès BiochroM'97. Mem. Trav. E.P.H.E. Inst. Montpellier*, **21**.

López-Martínez N. & Thaler L., 1975: Biogéographie, évolution et complements à la systématique du groupe d'Ochotonidés *Piezodus-Prolagus* dans le cénozoïque d'Europe Sud-Occidentale. *Bull. Soc. Géol. France, Paris*, **7**(17, 5): 850–866.

Major C. J. F., 1899: On fossil and recent Lagomorpha. *Trans. Linn. Soc. Lond.*, **7**: 433–520.

Mazza P., 1987: *Prolagus apricenicus* and *Prolagus imperialis*: two new Ochotonids (Lagomorpha, Mammalia) of the Gargano (Southern Italy). *Boll. Soc. Paleontol. Ital.*, **26**: 233–243.

Mazza P. & Zafonte F., 1987: Phyletic and ecologic considerations on the Gargano (Southern Italy) *Prolagus* (Ochot. Lagom. Mamm.). *Boll. Soc. Paleontol. Ital.*, **26**: 221–231.

Mein P., 1983: La vie en Ardèche au Miocène supérieur d'après les documents trouvés dans la carrière de la montagne d'Andance. *Nouv. Arch. Mus. Hist. Natur. Lyon*, **21**: 37–44.

Palacios F. & Fernandez J., 1992: A new subspecies of hare from Majorca (Balearic Islands). *Mammalia*, **56**: 71–85.

Pickford M. & Morales J., 1994: Biostratigraphy and Palaeobiogeography of East Africa and Iberian Peninsula. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **112**: 297–322.

Rögl D. v., 1998: Palaeogegraphic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Ann. Naturhistor. Mus. Wien*, **99A**: 279–310.

Salotti M., Bailon S., Bonifay M. F., Courtois J. Y., Dubois J. N., Ferrandini J., Ferrandini M., LaMilza J. C., Mourer-Chauviré C., Popelard J. B., Quinif Y., Réal-Testud A. M., Miniconi C., Pereira E. & Persiani C., 1997: Castiglione 3, un nuveau remplissage fossilifère d'âge Pléistocène moyen dans le karst de la région d'Oletta (Haute Corse). *C. R. Acad. Sci. Paris*, **324**(2): 67–74.

Sondaar P. Y., 1977: Insularity and its effect on mammal evolution. Pp.: 671–704. In: Hecht M. K., Goody P. C. & Hecht B. M. (eds.): *Major patterns in vertebrate evolution*. Plenum Press.

Surridge A. K., Timmins R. J., Hewitt G. M. & Bell D. J., 1999: Stripped rabbits in Southeast Asia. *Nature*, **400**: 726.

Thaler L., 1973: Nanisme et gigantisme insulaire. *La Recherche*, **37**: 741–750.

Tobien H., 1975: Zur Gebisstruktur, Systematik und Evolution der Genera *Piezodus*, *Prolagus* und *Ptychoprolagus* (Lagomorpha, Mammalia) aus einigen Vorkommen im jüngeren Tertiär Mittel- und Westeuropas. *Notizbl. Hess. Landes. Bodenforsch. Wiesbaden*, **103**: 103–186.

Van der Meulen A. J. & Daams R., 1992: Evolution of early-middle miocene rodent faunas in relation to long-term paleoenvironmental changes. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **93**: 227–253.

Vigne J. D., 1988: *Les mammifères post-glaciaires de la Corse: étude archéozoologique*. 26 suppl. Gallia Préhistoire, CNRS, 330 pp.