The Lagomorph Fossil Record and the Origin of the European Rabbit

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Introduction

Lagomorphs are very prolific mammals with a rich fossil record, which particularly increased over the last years by washing and screening techniques for microfossil recovery. Fossil remains of lagomorphs have been extensively documented in the Old World and North America from Early Paleogene onwards (around 45 Ma). Lagomorph diversity is much larger in the fossil record than in the biosphere. Only 12 genera and about 75 lagomorph species are still living in recent times, most of them almost devoid of paleontological record. In contrast, around 75 genera and more than 230 species, most of them already extinct, are represented in the fossil record of Lagomorpha. The local faunas today rarely contain more than three sympatric lagomorphs, frequently just one or two taxa. Instead, up to eight lagomorph species coexisted in local paleofaunas. This pattern constitutes a rare case in the recorded history of organisms, since the fossil record even in well-represented groups contains a lower number of species than the biosphere. Only declining groups, such as brachiopods or perissodactyl mammals, show higher diversity in the past than in the present, which denotes that lagomorph lineages are also declining in recent times.

One of the most widespread living lagomorph species is the European rabbit *Oryctolagus cuniculus*, whose areal distribution has been greatly expanded and modified by anthropic dispersal. All living European rabbit's subspecies *O. c. cuniculus* (Germany), *O. c. algirus* (Algeria) and *O. c. huxleyii* (Madeira), have been described from apocoric localities (i.e., lying outside the primitive range of the species; Gibb 1990). Part of its ancestral (plesiocoric) area is the Iberian Peninsula, where two mitochondrial races of morphologically indistinct rabbit populations in the northeast and southeast have been distinguished, tracing back their divergence to at least 2 Ma (Branco et al. 2000). The recorded age of the species in contrast seems much younger. The oldest fossils attributed to the modern European rabbit species are around 0.5 Ma old (Middle Pleistocene, Lopez Martinez 1989; Donard 1982). Extinct species of European rabbits have been described in western European fossil

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sites (+*Oryctolagus laynensis*, 3.5 Ma; +*Oryctolagus lacosti*, 2 Ma, +*Oryctolagus burgi*, 0.3 Ma). They would allow reconstructing the history and dating the divergence of their recent relative, the European rabbit.

In this work, I present an overview of the lagomorph fossil record as a frame for evolutionary questions concerning this peculiar mammalian order, particularly for the problem of the origin and dispersal of the most widespread recent lagomorph, the European rabbit. Evolutionary biology as any other branch of biology needs paleontological data as a necessary reference for contrasting the results of different approaches (genetic, biochemical, ecological, etc.) and putting the results into their chronological and paleobiogeographical framework.

The Lagomorph Fossil Record

Most of the lagomorph fossil taxa are known mainly by their dentition, because incisors and cheek-teeth are easily preserved and recognized in fossil samples. Fortunately, these are very informative elements also widely used for modern lagomorph taxonomy, making possible the comparison between both types of data. In many cases, maxillae, jaws, and isolated postcranial material (mainly anklebones, girdles, and epiphyses of long limb bones) of fossil lagomorphs have been also identified and described. Skulls and articulated, complete skeletons are sometimes also preserved (Wood 1940; Dawson 1958; Masini 1989), and there are rare cases where soft parts, body outline, and hair are also observable (Mein et al. 1983). Since a less number of characters are available in fossils for taxonomic distinction, the fossil record shows generally a lower resolution for diversity estimates than the biosphere does. The study of lagomorph fossil remains is particularly difficult as Dawson (1967) pointed out, in part because of the conservative body plan and the large intrapopulational variability of this mammalian order.

The lagomorph fossil record contains about 78 genera and 234 species after checking 2742 fossil localities in four continents. I refer extinct taxa by a '+' preceding names. Palaeoenvironmental data have greatly increased and I do not refer here to. The record is now twice larger than in 1967 when Dawson made a first revision but has not substantially changed the main pattern with three groups of taxa: (1) gliroid mixodont mammals relatives of lagomorphs, (2) stem-lagomorphs and (3) lagomorph ascribed to both modern families.

(1) Gliroid mixodont mammals, relatives to both Lagomorpha and Rodentia, are recorded in Asia from the late Paleocene to the Oligocene (58–30 Ma ago);
(2) Stem-lagomorphs, the basal group of primitive lagomorphs, appeared in Asia around late Eocene times (about 45 Ma), spread into North America and Europe and persisted until the late Miocene (about 10 Ma); and,
(3) Living families Ochotonidae and Leporidae differentiated respectively in Asia and North America in Late Eocene–Early Oligocene (around 33–35 Ma ago).

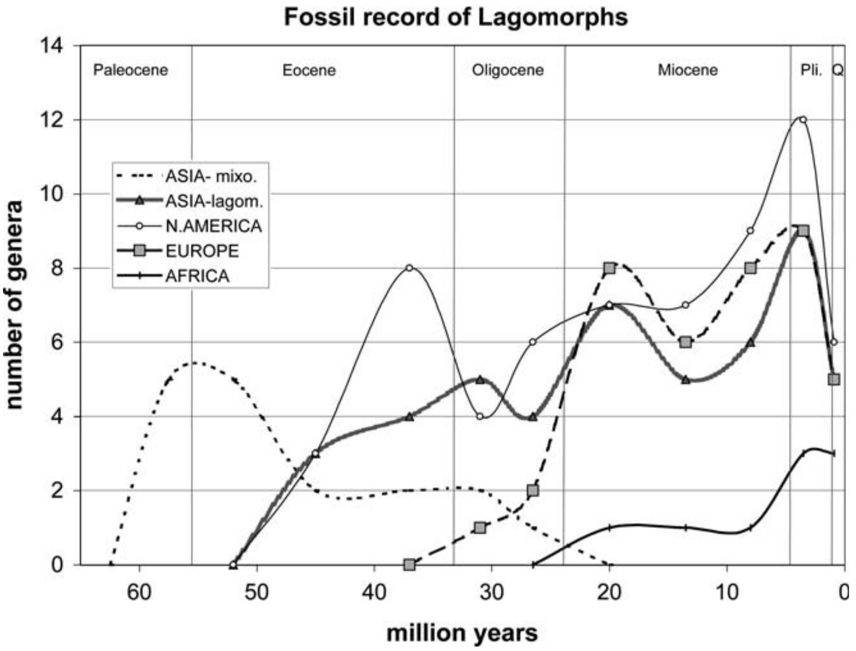

Fig. 1 Pattern of diversity of the lagomorph fossil record and their relatives, the gliroid mixodonts, during the Cenozoic era. Number of genera in four continents is plotted against age at the mid-point of the geological periods

The overall pattern of lagomorph fossil diversity is shown in Fig. 1, with the rise and fall of gliroid mixodonts in Paleocene–Early Eocene times, followed by a rapid spreading of stem-lagomorphs in Asia and North America, replaced later by the modern lagomorph families, which colonized Europe and subsequently, Africa. They underwent an important radiation around Pliocene times (5 Ma ago) and suffered a severe decline in Quaternary times, mostly in the Holartic region (Northern Hemisphere).

Origins of Lagomorphs

Several criteria indicate that Asia is the ancestral area of the order Lagomorpha:

- the oldest unambiguous, true lagomorphs (+*Lushilagus*) occur in China in Middle Eocene (around 45 Ma);
- lagomorphs in general, and stem-lagomorphs in particular, reached their higher diversity in this continent;
- the origin of lagomorphs has been related with the Asiatic mixodonts (order Mixodontia, Sych 1971). This endemic order of mammals bearing

a mosaic of characters of rodents and lagomorph, lived in Asia mainly during late Palaeocene to Oligocene (about 58 to 30 Ma). One of its families (Mimotonidae) has been proposed as the sister group of Lagomorpha (Li and Ting 1985, 1993).
- the order Rodentia, an alleged sister group of Lagomorpha and Mimotonidae, is also related to the mixodont family Eurymylidae and made their earliest appearance in Asia.

Only two families (Mimotonidae and Eurymylidae), 12 genera and about 20 mixodont species are known by now, but their fossil quality, number, and observations are currently rapidly increasing (e.g., Dashzeveg and Russell 1988; Meng et al. 2003; Asher et al. 2005).

The morphological similarities shared by mixodonts, lagomorphs, and rodents lead many authors to include all of them in the Glires superorder. Particularly, small mimotonids (+*Mimotona wana*) share a number of synapomorphies with true lagomorphs (dental roots of upper cheek-teeth within the orbit, peculiar zygoma with external fossa and ventral tubercle, large incisive foramen, grooved anterior upper incisor; Li and Ting 1993). However, the phylogenetic relationships of mixodonts are not stable. Mimotonids cluster either with Lagomorpha (clade Duplicidentata) or with other mixodonts; eurymylids group either with Rodentia (clade Rodentiamorpha) or with Duplicidentata (Averianov 1994; Meng et al. 2003; Asher et al. 2005). The order Rodentia appeared highly differentiated in North America and Asia in late Paleocene, more than 10 million years before the first well-characterized lagomorph.

Some authors interpret the basal lagomorph evolution as a smooth transitional gradation between mixodonts and primitive lagomorphs. However, a direct ancestral-descendent relationship between them is unlikely, because most mixodonts show highly specialized features and larger size in relation to primitive lagomorphs (Sych 1971; Lopez-Martinez 1985; Dashzeveg and Russell 1988; Averianov 1994). Differences concern dental and skeletal features. Primitive true lagomorphs have strongly developed premolars with a labial root, week third molars, open folds in upper premolars, upper molars with a central cusp surrounded by a crescent valley, weak hypocone closely attached to protocone, and narrow and elongated tarsals with a transversal calcaneal canal and a calcaneous-fibular joint. Mimotonids and other mixodonts instead have much reduced or even loss premolars with a closed central basin surrounded by a high cingulum and two labial roots; well-developed third molars much larger than other molars, a central basin in upper molars with strong hypocone well-detached from the protocone and short and widened, primitive tarsal bones. The ratio of third molar length clearly separates both groups (Fig. 2).

True lagomorphs appear in late Middle Eocene, around 15 million years after their late Paleocene closest relative mixodont +*Mimotona* (Fig. 3). A gap exists during the early Eocene between the earliest lagomorphs and their sister group (ghost lineage). Up to now, the taxa from this epoch (+*Aktashmys*, +*Gomphos*) appear less related to lagomorphs than the oldest mimotonids

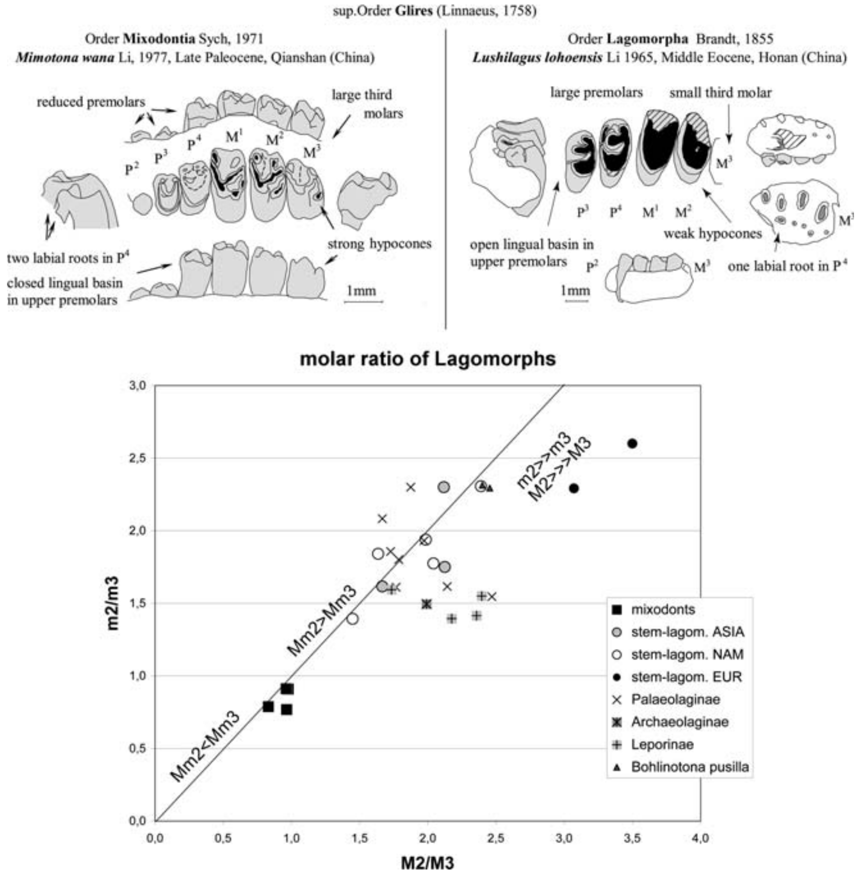

Fig. 2 Distinctive features between mixodonts and true lagomorphs. The scatter diagram represents the length ratio of the third molars against the second molars in mixodonts and different lagomorph groups

from the Palaeocene, and the same occurs with mixodont gliroids from late Eocene and Oligocene (+*Tsaganolagus*, +*Hypsimylus*, +*Mimolagus*). The origin of Lagomorpha may be hidden in this chronological gap (Fig. 3).

The Fossil Record of Stem-Lagomorphs

Traditionally, the systematics of fossil lagomorphs placed all primitive extinct taxa into the extant families Leporidae and Ochotonidae. However, primitive lagomorphs do not share diagnostic, derived characters with the modern families and can be easily distinguished from them. Here we name stem lagomorphs the *plesion* or paraphyletic group of primitive true

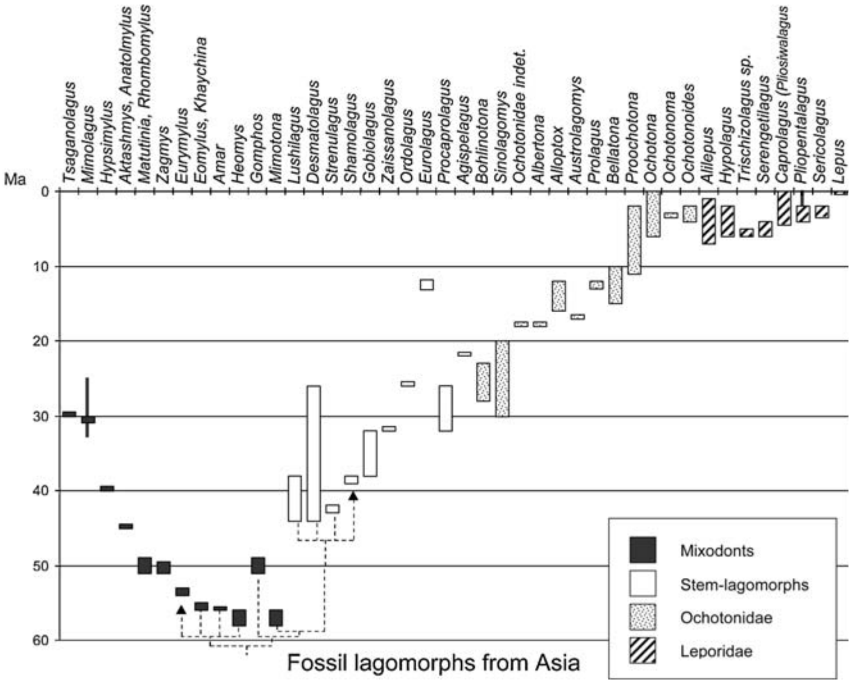

Fig. 3 The fossil record of mixodonts and lagomorphs in Asia. The phylogenetic relationships between both groups is indicated at the base of the chronobiogram, revealing a gap of 15 million years (ghost lineage) between the first lagomorphs and their closest mixodont relative, *Mimotona*

lagomorphs (+*Lushilagus*, +*Shamolagus*, +*Gobiolagus*, +*Procaprolagus*, +*Mytonolagus*, +*Megalagus*, +*Eurolagus*, +*Gripholagomys*) included by some authors in the families 'Palaeolagidae' and 'Amphilagidae'.

Stem lagomorphs have relatively low-crowned rooted cheek-teeth with a complicated dental pattern bearing persistent folds and cusps. In the upper cheek-teeth, the arrangement of cusps shows a peculiar central one (whose homology with that of other mammals has been extensively debated), surrounded by a crescentic, curved valley. The upper cheek-teeth are highly asymmetric; their crowns are higher in the lingual side and curves laterally as the lingual root grows more than the labial ones (see Fig. 4). A tubercle in the maxillary bone containing the dental roots enters the orbit. The long-lasting milk teeth are large. The third molars are highly reduced compared to mixodonts, but relatively large compared to Leporidae or Ochotonidae. The lower cheek-teeth show a conspicuous third lobe (hypoconulid), which disappears later with wearing. Their highly characteristic first lower premolar has a small, narrow trigonid and lacks an anteroconid. The skull and skeletal features show highly derived, diagnostic states (in zygoma, orbits, bony palate, vertebrae, tibia and tarsals; see Lopez-Martinez 1985). The size is generally small; exceptionally, some of them reached a large size (+*Megalagus*, +*Gymnesicolagus*).

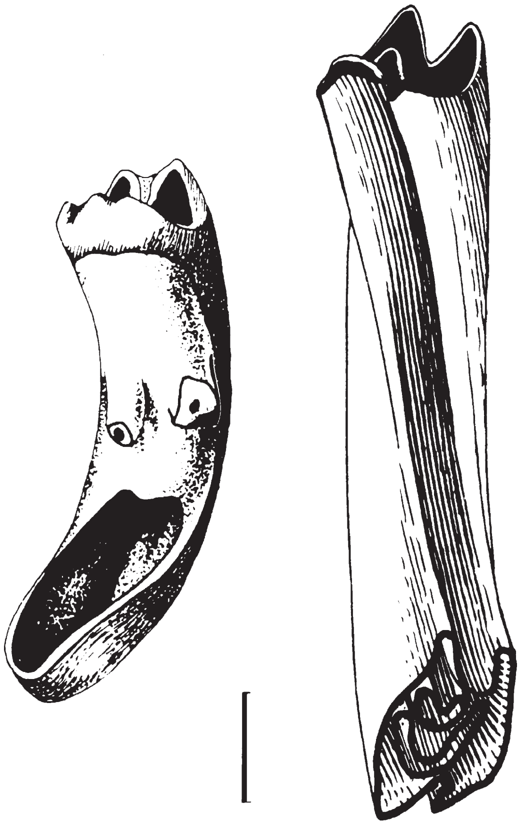

Fig. 4 Hypsodonty in upper cheek-teeth of stem-lagomorphs (*left*) compared to fossil lagomorphs related to the modern family Ochotonidae (*right*)

Well-characterized stem lagomorphs first appeared in Asia (+*Lushilagus*, +*Strenulagus*, +*Shamolagus*, +*Gobiolagus*, +*Desmatolagus*, etc.) in Middle Eocene (about 45 Ma ago) and afterwards in North America (+*Mytonolagus*, +*Tachylagus*, +*Procaprolagus*) in the late Eocene (about 43 Ma, Fig. 5). By the latest Eocene and early Oligocene (36–30 Ma), the group shows a rapid diversification (+*Megalagus*, +*Desmatolagus*, +*Ordolagus*, +*Agispelagus*, +*Zaissanolagus*) and try the invasion of Europe with low success (+"*Shamolagus*" *franconicus*, +*Desmatolagus* sp.). Only at the end of the Oligocene (about 25 Ma ago) a new wave of immigrants successfully colonizes Europe (+*Amphilagus*, +*Piezodus*), already differentiated as primitive ochotonids.

Some stem lagomorphs persisted after the appearance of well-differentiated leporids and ochotonids in Early Oligocene, a golden epoch of lagomorph diversity where up to eight lagomorph taxa in Asia and four in North America are recorded in sympatry. During the Miocene they spread into the Northern Hemisphere (+*Megalagus*, +*Gripholagomys*, +*Russellagus*, +?*Desmatolagus*, +*Eurolagus*, +"*Amphilagus*"...) and became completely extinct by late Miocene

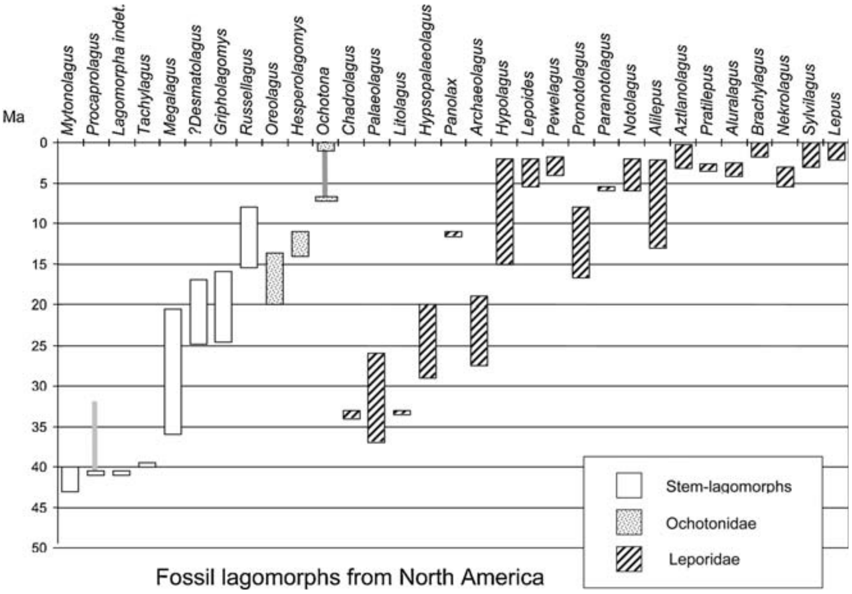

Fig. 5 Chronobiogram of the lagomorph fossil record in North America

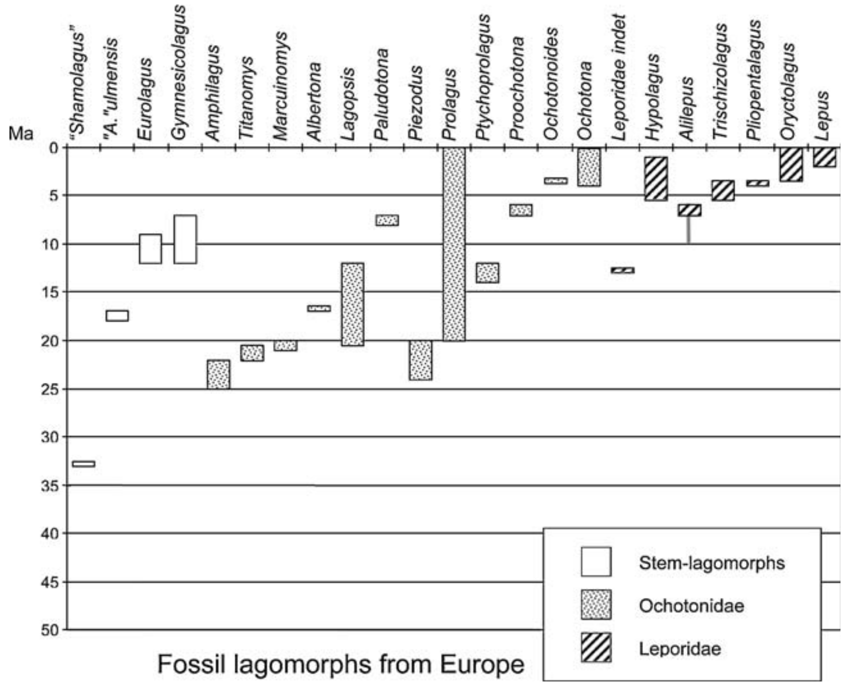

Fig. 6 Chronobiogram of the lagomorph fossil record in Europe

times. One of the largest and latest surviving stem lagomorphs was the highly modified +*Gymnesicolagus*, extinct about 7 Ma ago in the Balearic Islands (Fig. 6).

Many authors include the stem lagomorphs in the family Leporidae because they share a primitive dental formula (2/1 i, 0/0 c, 3/2 p and 3/3 m). However, this is a primitive feature of the order, and natural groups or clades must instead be defined by shared derived features. Thus stem-lagomorphs are an outgroup for Ochotonidae and Leporidae (McKenna 1982). Primitive members of the modern lagomorph families have common derived features not shared by stem lagomorphs, such as rootless adult teeth, loss of the crescentic valleys in early wear stages, permanent hypostriae that do not close up with wear, and simplified, very reduced third molars. The origin of the lagomorph modern families is related to the stem-lagomorph genus +*Desmatolagus*, recorded in early Oligocene (33 Ma) of northern continents and attributed either to Ochotonidae or Leporidae by authors. Some species of this genus are closer to the Asiatic Oligocene Ochotonidae (+*Bohlinotona,* +*Sinolagomys*), but the first true leporids appeared and spread in North America (+*Palaeolagus,* +*Chadrolagus*), phylogenetically related to the stem-lagomorph +*Mytonolagus* (Gawne 1978). Therefore, the derived features shared by both modern lagomorph families were probably independently attained in each continent from different ancestors.

The Fossil Record of ochotonids

The way ochotonids obtained the total hypsodonty of the upper cheek-teeth is different from that of the leporids, which strength the hypothesis of an independent origin of both families. Ochotonids produce continuous-growing cheek-teeth by a strong torsion of the shafts, rejecting the buccal roots and cusps towards the exterior of the maxilla (Fig. 4). The curved labial roots of the upper cheek-teeth are contained in a convex maxillary tubercle connected to the zygoma. They lose the upper third molar (M3) and reduce the lower third molar to a single lobe. Trigonids and talonids are permanently isolated. The palate shows a conspicuous premolar foramen. These features are probably derived, while the non-molarized upper premolars, the basicranial horizontal profile and the presence of two mental foramina in the jaw are probably primitive features.

Ochotonids first appeared in central Asia during the Oligocene (+*Sinolagomys,* +*Bohlinotona*). Their origin is close to the small-sized species of +*Desmatolagus*. At the end of this period they spread to Europe (25 Ma ago, Fig. 6), where a local radiation of tropical ochotonids swarmed until recent times (+*Titanomys,* +*Marcuinomys,* +*Albertona,* +*Lagopsis,* +*Piezodus,* +*Prolagus*, etc.). Ochotonids entered North America (+*Oreolagus,* +*Hesperolagomys*), Africa (+*Austrolagomys*) and India (Ochotonidae indet.) by the Early Miocene, around 18 Ma ago (Fig. 7), while +*Alloptox* and

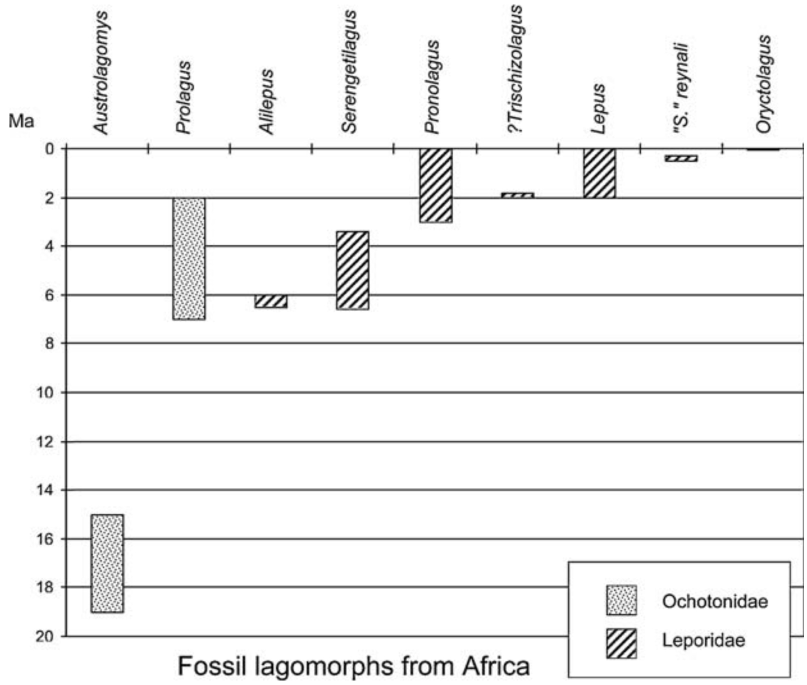

Fig. 7 Chronobiogram of the lagomorph fossil record in Africa

+*Bellatona* replaced the primitive Ochotonids in Asia during the Miocene. Most of them were extinct by the late Miocene, the only survivor being +*Prolagus* in Europe (Russian authors consider it a different family, 'Prolagidae'). It entered in NW Africa at the end of Miocene (6 Ma ago), but finally its last species (+*P. sardus*) became extinct in Corsica and Sardinia few hundreds years ago.

A new wave of Ochotonids (+*Proochotona*, +*Ochotonoides*, +*Ochotonoma* and *Ochotona*) formed in Asia in Mio-Pliocene and spread in Northern Hemisphere where *Ochotona* persist today, except in Europe where they became extinct. The fossil record of the modern genus *Ochotona* documents many extinct Pliocene and Pleistocene species: about 12 species disappeared in Asia (e.g., +*Ochotona lagreli*, +*Ochotona antiqua*, +*Ochotona transcaucasica*, +*Ochotona niewanica* and +*Ochotona tologolica* among others), three in Europe (+*Ochotona polonica*, +*Ochotona valerotae* and +*Ochotona horaceki*) and two in North America (+*Ochotona spanglei* and +*Ochotona whartoni*). In contrast, most of the living *Ochotona* species (around 22–26) have a poor fossil record restricted to the last few thousand years (*Ochotona erythrotis*, *Ochotona princeps*, *Ochotona pusilla*, *Ochotona thibetana*). Thus, the diversity turnover of modern pikas seems relatively as high as in other quaternary specious micromammals like arvicolid rodents although lagomorphs are poorer than rodents in diversity and abundance, either in the fossil record or the biosphere.

The Fossil Record of leporids

In contrast to ochotonids, leporids obtained the total hypsodonty of the cheek-teeth by straightening the crown shafts. Their roots locate in a vertical tubercle entering the orbit separated from the zygoma. Upper premolars are molarized and the upper third molar (M3) is preserved but reduced to a single lobe. Trigonids and talonids have lingual connections and the mandible has a single mental foramen. The skull has a basicranial angle of near 30°. These features are probably derived, while the presence of a bilobed lower third molar is a primitive feature. Other apparently primitive traits, such as the premolar foramen extremely reduced or absent and the uniserial incisor enamel could in fact be secondary acquisitions.

The family Leporidae is divided into three subfamilies: Palaeolaginae, Archaeolaginae and Leporinae according to the lower p3 pattern (Dice 1929; Wood 1940). Palaeolaginae p3 is hour-glass-shaped (trigonid and talonid connected by a central narrow isthmus). Archaeolaginae p3 has trigonid and talonid connected by a large lingual isthmus, which is the primitive pattern for most stem lagomorphs (Fig. 8). Leporinae p3 has trigonid and talonid

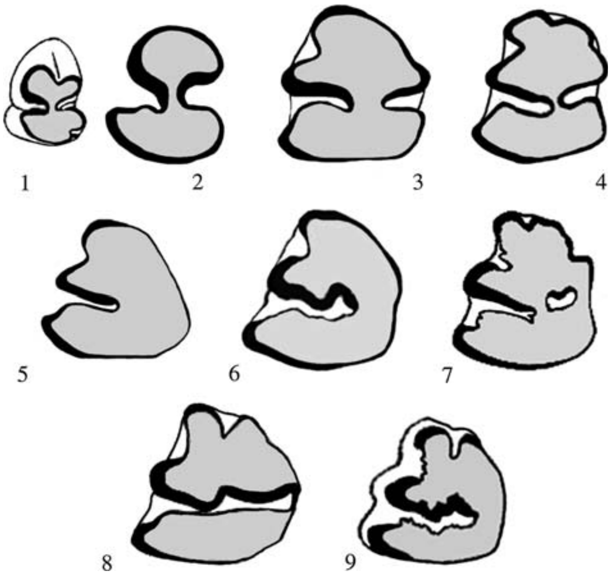

Fig. 8 Pattern of the leporid p3, one of the most distinctive morphological features of lagomorphs. *Upper row* palaeolagine-types. *Middle row* archaeolagine-types. *Lower row* leporine-types. Transitions are observed between palaeolagine and archaeolagine types and between archeolagine +*Nekrolagus* or +*Aluralagus* types and leporine type, but not between palaeolagine and leporine types *1* young +*Palaeolagus* (+*P.haydeni*). *2* adult +*Palaeolagus* (+*P. haydeni*). *3* +*Alilepus* (+*A. annectens*). *4* +*Trischizolagus* (+*T. dumitrescuae*). *5* +*Hypolagus*. *6* +*Aluralagus*. *7* +*Nekrolagus*. *8 Lepus*. *9 Sylvilagus* (+*S. hibbardi*). Redrawn from Wood (1940), White (1991) and different works by Daxner, Fejfar, Qiu, Radulescu and Sampson

connected by a narrow lingual isthmus like other lower cheek-teeth. Based on current phylogenetic hypotheses, authors include some Palaeolaginae in the Leporinae subfamily (Dawson 1958; White 1991; Voorhies and Timperley 1997), but as a consequence systematics became unstable and lacks subfamilial diagnostic characters.

The first Palaeolaginae leporids (+*Paleolagus*, +*Chadrolagus,* +*Litolagus,* +*Hypsopalaeolagus*) related to the stem lagomorph +*Mytonolagus* appeared and diversified in the latest Eocene (38 Ma ago) in North America, the homeland of the Leporidae (Fig. 5). Palaeolaginae are particularly abundant in the Western Interior during the Oligocene, when they attain the molarization of P3-P4 and add an anteroconid to p3. Later on, some Palaeolaginae leporids (+*Panolax*) coexisted with their sister group Archaeolaginae (+*Archaeolagus,* +*Hypolagus,* +*Lepoides,* +*Pewelagus*) documented from Miocene to Pleistocene (23–0.3 Ma). Archaeolaginae already loss almost all primitive cusps and valleys in early stages of tooth wear, and their p3 adds an anteroexternal fold. +*Hypolagus* is the most prolific and widespread archeolagine in North America, where 12 species are known from Middle Miocene to Pliocene (15–2 Ma). It spreads in Eurasia (5 species in Asia, 3 species in Europe) in latest Miocene and subsisted in Sicily Island until the Pleistocene. Rare leporid findings are recorded in Europe since Middle Miocene (about 13 Ma ago), but they do not settle definitely there until the latest Miocene, a case similar to the first European lagomorph invasion.

The history of Leporinae can be traced back to their putative common ancestor +*Alilepus*, known in North America from late Miocene to late Pliocene (10–2 Ma) and spreading in the Old World around 7 Ma ago where subsisted until Early Pleistocene. Its origin has been related to the genus +*Pronotolagus* from middle to upper Miocene (16–8 Ma), characterized by a four-folded p3 probably derived from primitive Archaeolaginae or advanced Palaeolaginae. Both +*Pronotolagus* and +*Alilepus* show a palaeolagine-type p3 but have been classified as Leporinae based on their phylogenetic relationships with their successors. Between 16 and 6 Ma there are few fossils attributed to Leporinae (Voorhies and Timperley 1997). In contrast, a remarkable diversity burst explodes in the Pliocene, when more than 16 new leporid genera appeared. Among them are the Leporinae +*Aluralagus*, +*Aztlanolagus*, +*Nekrolagus,* +*Notolagus*, +*Paranotolagus*, +*Pratilepus,* +*Trischizolagus* (Figs. 3, 5, 6 and 7), and the largest lagomorph, a giant +*Alilepus* relative recorded from Minorca Island. Local diversity is also remarkable; up to seven coexisting lagomorph taxa are cited in a single Pliocene local assemblage from North America. All these Pliocene leporids became extinct by late Pleistocene or Holocene times.

Living leporids with a palaeolagine-type p3, which appear as a natural group in some molecular phylogenies, are poorly represented in the fossil record. Among them, the Japanese *Pentalagus* is the only one with a fossil relative, +*Pliopentalagus* from the European and Asiatic Pliocene. It assesses the refugee status of the surviving insular Amami rabbit. From the remaining palaeolagine-like living taxa (*Bunolagus, Pronolagus,* and *Romerolagus*), only *Pronolagus* has been documented by fossil remains from South African Plio-Pleistocene.

Most living leporids (*Oryctolagus*, *Sylvilagus*, *Caprolagus*, *Lepus*) present the leporine p3 pattern. No transitional populations are known whose p3 transformed from palaeolagine to leporine type. In contrast, two morphologically intermediate p3 types exist (Fig. 8): +*Nekrolagus*-type p3, with an enamel lake between two isthmus connecting trigonid and talonid (present in rare *Oryctolagus* and *Lepus* specimens); and +*Aluralagus*-type p3, with a rather wide single lingual isthmus (sometimes observed in *Sylvilagus*). This would confirm phylogenetic proposals suggesting an independent acquisition of the leporine p3 pattern through parallel evolution across a cladogenetic radiation (Dawson 1958; White 1991; Averianov 1999).

Among living Leporinae, *Oryctolagus* has the oldest fossil record of around 3.5 Ma (see below). Other modern Leporinae genera appeared one-half to 1 million years later (*Sylvilagus* 3 Ma ago and *Lepus* 2.5 Ma ago in North America; *Caprolagus* 3? to 1.8 Ma ago in India and Pakistan). *Nesolagus* and *Poelagus* lack fossil references. Africa and SW Asia have a poorly studied fossil record that may probably change this picture.

Like living Ochotonidae, living Leporinae are represented in the fossil record by extinct species: +*Brachylagus coloradoensis*, +*Caprolagus lapis,* +*Caprolagus (Pliosiwalagus) sivalensis*, +*O. laynensis* (Fig. 9); +*O. lacosti,* +*O. burgi*, +*Sylvilagus hibbardi*, +*Lepus terraerrubrae*, +*Lepus veter*, +*Lepus*

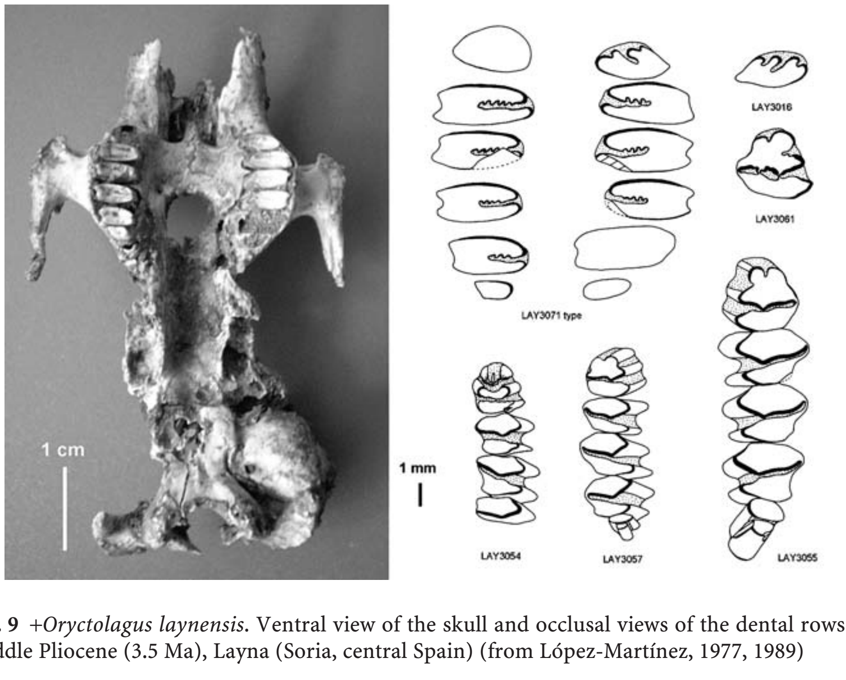

Fig. 9 +*Oryctolagus laynensis*. Ventral view of the skull and occlusal views of the dental rows. Middle Pliocene (3.5 Ma), Layna (Soria, central Spain) (from López-Martínez, 1977, 1989)

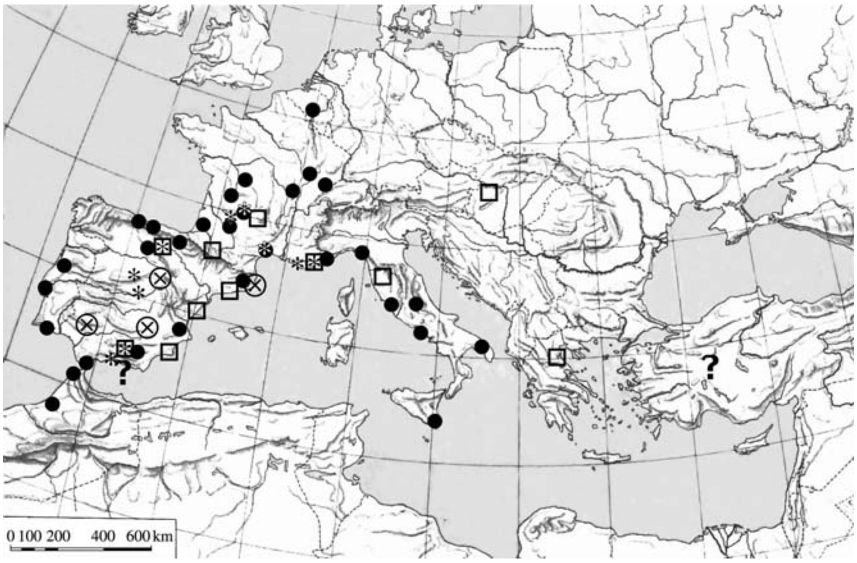

Fig. 10 Map of *Oryctolagus* fossil findings. *Crossed circles +O. laynensis*, Middle-Late Pliocene (3.5–2 Ma). *Squares +O. lacosti* and *O.* sp, Late Pliocene–Early Pleistocene (2.5–0.8 Ma). *Stars +O. lacosti*, *O. cuniculus* and *+O. burgi*, Middle Pleistocene (0.8–0.1 Ma). *Dots O. cuniculus*, Upper Pleistocene (0.1–0.01 Ma)

tanaiticus, etc. In some cases, fossil attributions to modern species are well supported by morphological data (*Lepus* cf. *californicus* and *Sylvilagus* cf. *audubonii* in late Pleistocene of North America, *Lepus cf. granatensis* in middle Pleistocene of Spain, *Lepus timidus* in late Pleistocene of Switzerland, France and Euskadi in Spain). Other cases have not yet been justified enough (*O. cuniculus* in Pleistocene of Anatolia and Africa, Fig. 10; *Lepus europaeus* in France; *L. timidus* in the central Iberian Peninsula).

The Fossil Record of the European Rabbit

The European rabbit genus *Oryctolagus*, now spread worldwide, appeared in the fossil record before any other modern Leporinae genus. The first recorded *Oryctolagus* species is *+O. laynensis* from Middle Pliocene (about 3.5 Ma) from northeastern, central and southern Spain and probably southeast France, associated to an arid, warm (sub)tropical savannah-type fauna. Earlier indices from a late Miocene site in southern Spain may be distrusted. This site with equatorial African mammals dated to 6 Ma has delivered an isolated P2 tooth tentatively attributed to *Oryctolagus*, yet its morphology may agree with advanced *+Trischizolagus* species recorded from Spanish

Pliocene sites. Albeit previous conjectures of an African origin, the European rabbit has not been confidently signaled in Africa during late Miocene to Pleistocene times (8–0.1 Ma ago), when species attributed to the leporid genus +*Serengetilagus* dominates most assemblages from northern, central and eastern Africa (Fig. 7). Thus the fossil data indicates the Iberian Peninsula as the probable ancestral area of the European rabbit.

If the biogeographical origin of *Oryctolagus* seems to be somewhat constrained, its phylogenetic origin is less clear. The widespread Leporinae +*Alilepus* and after +*Trischizolagus* were precursors of *Oryctolagus* in its ancestral area and its surroundings. +*Trischizolagus* has been proposed as a probable *Oryctolagus* ancestor, as well as for *Lepus* and other leporines, although no transitional populations have yet been found. Instead, cladistic phylogeny links *Oryctolagus* more closely to *Lepus* than to *Trischizolagus* (Averianov 1999). Molecular phylogenies give also contradictory results, connecting *Oryctolagus* either to *Lepus*, to *Bunolagus* or to *Caprolagus* (Halanych and Robinson 1999; Mathee et al. 2004).

During the Mio-Pliocene transition (6–3 Ma), the leporids +*Alilepus,* +*Hypolagus,* +*Trischizolagus*, +*Pliopentalagus* and +?*Serengetilagus* were present in Europe; but none of them was associated with the oldest *Oryctolagus* species, +*O. laynensis*. Up to now, this ancient rabbit has only been recorded from 3.5–2.5 Ma in Spain (sites in Castilla-Leon, Castilla-La Mancha, Catalonia and Western Andalousie) and probably in southeast France. The Iberian +*Trischizolagus* (sites in Aragon, Valencia, Murcia and eastern Andalousie from 6–3 Ma) preceded and clearly overlapped its chronological distribution with *Oryctolagus*, but they did not occur in the same localities. Iberian +*Trischizolagus* record the most primitive species of the genus (+*Trischizolagus crusafonti* from Late Miocene and +*Trischizolagus maritsae* from early Pliocene), both different and small-sized that the type species +*Trischizolagus dumitrescuae* from the Late Pliocene of Eastern Europe. *Lepus* appears as a late immigrant, first recorded around 2 Ma ago in Eastern Europe, and about at the same date in North America (not much older than 2.5 Ma). It could be older in Africa. Thus, the fossil record suggests that *Oryctolagus* and *Lepus* do not share a common ancestral area, although both may be related to their predecessors +*Alilepus* and +*Trischizolagus*.

+*O. laynensis* was a robust rabbit with relatively wide choanae, long bony palate, small auditory bullae, large posterior molars, shallow hypoflexus, relatively short, asymmetric anteroconids and a frequent enamel lake in the p3 (Fig. 9). No transitional forms are known between this species and the modern *O. cuniculus*. However, they appear closer to each other than +*O. lacosti*, a larger-sized rabbit species recorded between 2.5 and 0.6 Ma in southwest Europe (Spain, France, Italy and isolated findings from Hungary and Greece). The distinctive features of this peculiar rabbit (deep crenulated hypoflexus, short palatine portion of bony palate, choanae width larger than palatal length, large, robust skeleton) mislead some authors to describe it as a hare (‘*Lepus valdarnensis*’, ‘*Lepus etruscus*’, ‘*Lepus issiodorensis*’. . .). Its limb ratio and p3 morphology (large lingual anteroconid, longitudinally oriented anterior fold) are however clearly rabbit-like. Another large rabbit species (+*O. burgi*) possibly related to +*O. lacosti* has been described in Middle Pleistocene of Italy.

The living species *O. cuniculus* is first recorded in southern Spain in Middle Pleistocene (about 0.6 Ma) associated to a relict, warm-type fauna. An Early Pleistocene reference to this species in Turkey needs to be confirmed. Relatively robust races of this species are recorded in Middle Pleistocene of France and the central Iberian Peninsula (+'*O. c. lunelensis*', +'*O. c. grenalensis*'), contemporaneous of the large-sized lineage +*O. lacosti* -+*O. burgi*. In the Late Pleistocene, only the modern rabbit survived, spreading to peri-Mediterranean area and northern Europe where it coexisted with *L. timidus* (Fig. 10). During the maximum glacial period and Early Holocene, the European rabbit seems again confined to the Iberian Peninsula and southern France, where it constituted an important trophic resource for the survival of large predators. The European rabbit suffered a remarkable genetic differentiation in Iberia during the glacial period (Branco et al. 2002; Callou 2003). Its size was then larger than the recent Iberian rabbits, and increased again, reaching 15% more length during the Neolithic period, until its worldwide anthropic expansion.

Remarks and Discussion

The fossil record is a unique way of documenting the past history of an organism and testing our hypotheses about their evolution. Initiatives such as 'The Palaeobiology Database' implemented by J. Alroy greatly contribute to this goal. Concerning lagomorphs, important advances in phylogenetic studies in exploration of Asiatic fossil localities and a two-fold increase in the number of fossil lagomorph taxa can be noted in the later years. Even so, through the numerous studies and materials collected by different approaches, techniques and authors, the timing and diversity pattern of the lagomorph succession shown by the fossil record have a remarkable stability, which allows us to assess its reliability. Through the joint efforts of palaeontologists, the fossil record of lagomorphs, continuously refined and improved, shows confidently a solid pattern, in spite of minor discrepancies in systematic distinction and in the nomenclatural translation of phylogenies.

The pattern of the lagomorph fossil record can be compared with phylogenetic and phylogeographic trees of extant lagomorph evolution proposed with molecular data. Apart from discrepancies between morphological- and molecular-based phylogenies, which are common to many other cases, disagreements appear when comparing the ages of divergence for lagomorph sister taxa inferred by the molecular clock and by the fossil record.

The origin of Lagomorpha according to the fossil record is between 60 Ma (ghost lineage -'long fuse' model), and 45 Ma (stem lagomorph 'explosive' model) (Fig. 3), while for molecular clock is 71 Ma (estimates ranging between 81 and 28 Ma). The fossil constraint for dating the divergence between ochotonids and leporids (20–40 Ma) is at odds with molecular studies indicating 50 Ma age. According to the molecular clock, all modern Leporidae genera are Miocene in age (14–8 Ma), against a Pliocene age (4–2 Ma) according to the fossil record. Another important disagreement is the *Lepus* origin, dated by molecular phylogeny between 4 and 11.8 Ma (much earlier than rabbits according to Matthee et al. 2004), while the opposite is verified in the fossil record (*Lepus* appearing 2.5 Ma ago, later than rabbits, around 4 Ma).

In front of the numerous disagreements in this and many other cases, some authors discard the morphological data because of convergences, and the fossil data classically qualified as 'incomplete' (which ironically supposes that other data sets are more 'complete'). In fact, many cases show a high level of coincidence between morphological, paleontological, and molecular studies. Poor resolution and disagreement problems are often attributed to rapid evolutionary radiations. The fossil record is rich in examples of explosive evolution, like lagomorphs showing a nearly complete renewal of genera and species in a very short time. The 'explosive' model of evolution is now admitted as data, not noise, and is even observed in fossils of very recent age, when maximum chronological resolution can be obtained.

Conclusions

Fossil lagomorph taxa, which doubled in the last 40 years, show a general stability in chronology and diversity pattern. The main results of this survey are summarized as follows:

(1) The lagomorph fossil record contains about 78 genera and 236 species in Old World and North America. The number of living taxa is much lesser, indicating a decline in the evolution of this mammalian order. The number of coexisting species has also decreased. Nowadays, more than three sympatric lagomorph species is extremely rare, while up to eight sympatric lagomorph species are recorded in Asia in Paleogene times and up to seven in North America in Neogene.
(2) Around 60 Ma is a maximum age for the divergence between lagomorph and mixodont Glires, implying a ≈15-Ma gap (ghost lineage) between the first true stem lagomorphs and their mixodont sister group *Mimotona*. Alternatively, lagomorphs could appear later on (around 45 Ma) by explosive radiation.
(3) Asia is probably the ancestral area for Lagomorpha, as well as for Ochotonidae, first recorded there about 33 Ma ago.

(4) North America is the ancestral area of Leporidae (family definition restricted to advanced lagomorphs, excluding stem lagomorphs). The first Leporidae appeared there about 37 Ma ago. Leporidae and Ochotonidae thus evolved independently from different stem lagomorphs in different areas.

(5) Modern Leporinae are related to +*Pronotolagus* and +*Alilepus*, first recorded in North America between 16 and 13 Ma ago.

(6) Important time lags between first arrival and definite settlement are observed: e.g., in Europe a 8-Ma lag time occurred between lagomorph entry (33 Ma ago) and final settlement (25 Ma ago). Also, 6 Ma elapsed for Leporidae settlement in Europe (recorded 13 Ma ago but extremely rare until around 7 Ma ago), and for *Ochotona* in North America (documented around 6 Ma ago, then absent until a new arrival 2 Ma ago).

(7) Explosive radiation occurred in Pliocene times, when more than 16 new lagomorph genera appeared in the four continents. Most of them became extinct at the end of this period or during the Quaternary.

(8) Many living lagomorph genera lack a fossil record. The others are mainly recorded by extinct species, indicating a recent renewal of the lagomorph fauna.

(9) The most widespread lagomorph, *Lepus*, is poorly represented in the fossil record. It is confidently recorded around 2.5 Ma ago, later than several rabbit genera.

(10) The European rabbit has one of the longest leporid fossil records, dating back to 3.5 Ma years ago in the Iberian Peninsula. One of its precursors, +*Alilepus* or +*Trischizolagus*, could be its ancestor. Four parapatric species from two lineages spread in Western Europe. The living rabbit, recorded around 0.6 Ma ago in southern Spain, is the only survivor.

References

Many students of fossil lagomorphs are not referenced because limitations of space. For additional information, the reader is referred among others to works by C. Angelone, R. Angermann, B. Bohlin, H. deBruijn, J.J. Burke, B.Q. Cai, C. Callou, O. Carranza-Castaneda, S. Cermak, G. Daxner, R.J. Emry, M. Erbajeva, O. Fejfar, F. Fladerer, L.J. Flynn, C.J. Forsyth Major, L. Fostowicz-Frelik, D. Geraads, M. Green, A.A. Gureev, K. Heißig, C.W. Hibbard, F.E. Koby, Y. Lei, D.G. MacInness, C. deMuizon, G. Nocchi, M.V. Pages, R. Patniak, Z.D. Qiu, J. Quintana, C. Radulesco, B. Sala, P. Sampson, S. Sen, N.S. Shevyreva, J.E. Storer, E. Unay, Y. Tang, H. Tobien, J. Viret, A. Winkler and the authors of The Palaeobiology Database (http://paleodb.org)

Asher RJ, Meng J, Wible JR, McKenna MC, Rougier GW, Dashzeveg D, Novacek MJ (2005) Stem Lagomorpha and the antiquity of Glires. Science 307:1091–1094

Averianov AO (1994) Early Eocene mimotonids of Kyrgyzstan and the problem of Mixodontia. Acta Palaeont Pol 4:393–411

Averianov AO (1999) Phylogeny and classification of Leporidae (Mammalia, Lagomorpha). Vestnik zoologii 33:41–48

Branco M, Ferrand N, Monnerot M (2000) Phylogeography of the European rabbit (*Oryctolagus cuniculus*) on the Iberian Peninsula inferred from RFLP analysis of the cytochrome *b* gene. Heredity 85:307–317

Branco M, Monnerot M, Ferrand N, Templeton AR (2002) Postglacial dispersal of the European rabbit (*Oryctolagus cuniculus*) on the Iberian Peninsula reconstructed from nested clade and mismatch analyses of mitochondrial DNA genetic variation. Evolution 56:792–803

Callou C (2003) De la garenne au clapier: étude archéozoologique du lapin en Europe occidentale. Publ Sci Mus Nat Hist Nat Paris, pp 1–358

Dashzeveg D, Russell DE (1988) Palaeocene and Eocene Mixodontia (Mammalia, Glires) of Mongolia and China. Palaeontology 31:129–164

Dawson MR (1958) Later Tertiary Leporidae of North America. University of Kansas Paleontological Contributions, Vertebrata 6:1–75

Dawson MR (1967) Lagomorph history and the stratigraphic record. Essays in paleontology and stratigraphy. Raymond C. Moore commemorative volume. Univ Kansas Dept Geol Spec Publ 2:287–316

Dice LR (1929) The phylogeny of the Leporidae, with description of a new genus. J Mammal 10:340–344

Donard E (1982) Recherches sur les léporinés Quaternaires (Pleistocène moyen et superieur, Holocène). These doct. Université de Bordeaux I, 2 vols

Gawne C (1978) Leporids (Lagomorpha, Mammalia) from the Chadronian (Oligocene) deposits of Flagstaff Rim, Wyoming. J Paleont 52:1103–1118

Gibb JA (1990) The European rabbit. In: Chapman JA, Flux JEC (eds) Rabbits, hares and pikas: status survey and conservation action plan. IUCN, Gland, Switzerland, pp 116–120

Halanych KM, Robinson TJ (1999) Multiple substitutions affect the phylogenetic utility of Citochrome b and 12S rDNA data: examining a rapid radiation in Leporid (Lagomorpha) evolution. J Mol Evol 48:369–379

Li CK, Ting SY (1985) Possible phylogenetic relationship of Asiatic eurymylids and rodents, with comments on mimotonids. In: Luckett P, Hartenberger JL (eds) Evolutionary relationships among rodents. NATO ASI Ser A. Plenum Press, New York, pp 35–58

Li CK, Ting SY (1993) New cranial and postcranial evidence for the affinities of the Eurymylids (Rodentia) and Mimotonids (Lagomorpha). In: Szalay FS, Novacek MJ, McKenna MC (eds) Mammal phylogeny. Springer, Berlin Heidelberg New York, pp 151–158

López-Martínez N (1989) Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario inferior de España. PhD Univ. Madrid 1977 publ Mem Museo Paleont, Univ Zaragoza, Madrid

López-Martínez N (1985) Reconstruction of the ancestral cranioskeletal features in the order Lagomorpha. In: Luckett P, Hartenberger JL (eds) Evolutionary relationships among Rodents. NATO ASI Ser A. Plenum Press, New York, pp 151–189

Massini F (1989) Prolagus sorbinii n. sp., a new Ochotonid (Mammalia, Lagomorpha) from the Messinian of Italy. Bol Soc Paleont Ital 28:295–306

Matthee CA, Van Vuuren BJ, Bell D, Robinson TJ (2004) A Molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. Syst Biol 53:433–447

McKenna M (1982) Lagomorph interrelationships. Geobios, Mem Spec 6:213–223

Mein P, Méon H, Romaggi JP, Samuel E (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 Nat Lyon 21:37–44

Meng J, Hu YM, Li CK (2003) The osteology of Rhombomylus (Mammalia, Glires): implications for phylogeny and evolution of glires. Bull Am Mus Nat Hist 275:1–247

Sych L (1971) Mixodontia, a new order of mammals from the Paleocene of Mongolia. Paleont Pol 25:147–158

Voorhies MR, Timperley CL (1997) A new Pronotolagus (Lagomorpha, Leporidae) and other Leporids from the Valentine Railway Quarries (Barstovian, Nebraska), and the Archaeolaginae-Leporine transition. J Vert Paleont 17:725–737

White JA (1991) North American Leporinae (Mammalia, Lagomorpha) from Late Miocene (Clarendonian) to Latest Pliocene (Blancan). J Vert Paleont 11:67–89

Wood AE (1940) Part III. Lagomorpha. In: Scott WB, Jepsen GL (eds) The mammalian fauna of the White River Oligocene. Trans Am Phil Soc Phil 28:271–362