The Leporid Datum: a late Miocene biotic marker

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ABSTRACT

1. Although Lagomorpha (rabbits, hares and pikas) have a long evolutionary history in Eurasia and Africa, including primitive genera of Eurasia historically considered assignable at the family level to Leporidae, the predecessors of modern rabbits were absent throughout this vast region for most of the Miocene until late in that epoch. During the early and middle Miocene, crown group Leporidae differentiated in North America, then dispersed to northern Asia in the late Miocene around 8 Ma (million years before present) and afterward. They then spread widely and apparently rapidly throughout Eurasia, reaching South Asia by 7.4 Ma and penetrating Africa about 7 Ma.

2. The apparently abrupt introduction of Leporidae is a striking late Miocene event that we call the Leporid Datum. Perceived in terms of biochrons, the Leporid Datum includes localities in Europe and western Asia of late MN11 (Mammifères Néogènes system) age and younger, and precedes by less than one million years the Bahean-Baodean land mammal age boundary in China.

3. The late Miocene spread of Leporidae throughout Eurasia was a successful invasion in terms of the numerous occurrences and abundant fossils preserved. Where dating is sufficiently robust, the Leporid Datum is late Miocene, nowhere certainly more than ~8 Ma.

4. In contrast to this sudden and widespread invasion, rare older finds suggest two possible refinements to this scenario: stem lagomorphs close to modern Leporidae may have lingered into the middle Miocene of Eurasia, or an independent, unsuccessful leporid invasion from North America may have preceded the 8 Ma datum.

5. The Leporid Datum marks an important palaeoecological event for the Old World and complements the significance of molecular dates for origins of modern genera.

INTRODUCTION

Imagine a world without rabbits and hares. You are picturing most of the world until late in the Miocene Epoch. The abundant extant Leporidae of Eurasia and Africa were absent from these continents until the late Miocene. Primitive lagomorph groups were widespread, but had become extinct throughout Eurasia by the earliest Miocene. Modern Leporidae appeared in the Old World as a late Miocene invasion from North America (López-Martínez 2008), an event that we call the Leporid Datum and place at about 8 Ma (million years before present).

Today, the 11 extant leporid genera are distributed globally such that neither their distribution nor molecular patterns indicate a center of origin. Molecular work (Matthee et al. 2004, Robinson & Matthee 2005) demonstrates the cohesive nature of the group that is evident from their morphology, and establishes their monophyly. However, while this research suggests that the deepest splits in leporid phylogeny date to the early Miocene Epoch, it cannot distinguish where the early evolution of the group occurred. Herein we discuss the Old World record, which clearly shows that modern Leporidae were late invaders to Asia.

Robinson and Matthee (2005) reviewed analyses of leporid phylogeny, including classic palaeontological studies that place the fossil genus *Alilepus* on a phylogenetic tree as a close outgroup to the extant radiation. *Alilepus* and other extinct genera are stem Leporidae, although some fossil lineages may be found ultimately to fall within the crown group. The fossil record shows a long North American history for stem leporids, and because *Alilepus* has an older record in North America (at least 12 Ma) than in Asia

(Voorhies & Timperley 1997), it is clear that modern Leporidae dispersed westward across Beringia.

Taxonomy, including of genera outside crown Leporidae, has significantly changed over the last decades, and conflicting classifications and phylogenies have been proposed (e.g. Dawson 1958, 1967, McKenna & Bell 1997, Averianov 1999, López-Martínez 2008). According to Dice (1929), Wood (1940), and Dawson (1958, 1967), the Leporidae comprise the subfamilies Palaeolaginae, Archaeolaginae and Leporinae, which are diagnosed primarily on dental characters of the third lower premolar (p3) and second upper premolar (P2). However, recent phylogenies based on cranial and dental features place fossil members of Palaeolaginae as a distinct family outside the Leporidae and even outside Lagomorpha (Asher et al. 2005, Wible 2007). The distinction is confirmed by other dental characters (von Koenigswald et al. 2010). The groups recognized classically by leporid systematists tend to be structural clusters rather than monophyletic groups. Some fossil genera such as *Hypolagus* thrived during the late Miocene but show relatively primitive morphology and are considered Archaeolaginae by some experts. We believe that ongoing research could lead to defining a monophyletic taxon more inclusive than living Leporinae, one at the family level and containing genera such as *Hypolagus* and *Alilepus*, which are close to the modern radiation. As yet there is no consensus on the content of such a group. López-Martínez (2008; her fig. 3) illustrates the relationships of Cenozoic Asian lagomorphs and the late Miocene appearance of leporids, but no formal cladogram based on parsimonious distributions of skeletodental structures has yet been developed to embrace all fossil taxa.

Here we reserve the formal term Leporinae for the crown group (living hares and rabbits); close fossil genera are stem Leporidae. For geologically older genera distantly related to the modern radiation, we use 'leporid' informally, or simply 'lagomorph'.

METHODS

The small mammal fossil record has improved greatly over the last half-century and shows a rich Palaeogene history of stem ochotonids and leporids. It has revealed the reality of the Old World extinction of basal leporid-like genera by the early Miocene (*Ordolagus* being one of the last of these; Erbajeva 2007) and sudden repopulation by modern stem Leporidae (Dawson 1967, López-Martínez 2008). Our central hypothesis is that Oligocene Old World leporid-like lagomorph genera became extinct without survivors, and that living species of Eurasia and Africa originated from a late Miocene influx of stem Leporidae from North America. To understand the timing of the Leporid Datum, the rapid spread throughout the Old World of stem leporids, we review the late Miocene record of leporid occurrences and comment on the precision of their dates. This review of published data is coupled with our own ongoing investigations.

The appearance of Leporidae in Eurasia and somewhat later in Africa is due to dispersal into Eurasia from North America via the northern land connection of Beringia (see, e.g. White 1991, Voorhies & Timperley 1997, Matthee et al. 2004), an event with widespread results occurring over a relatively short temporal interval. This event is a datum with temporal significance, constrained in geological time. Toward the goal of defining the Leporid Datum in time, we present the Miocene record of early leporid occurrences in Eurasia and Africa (Fig. 1).

Concerted efforts by many researchers now begin to document precisely the invasion of Leporidae, and we compile representative records of their first occurrences. This survey is not exhaustive and emphasizes late Miocene Leporidae, excluding fossils that are clearly Pliocene in age (MN14 and later). The MN system of reference localities has become highly refined for relative dating of fossil sites in Europe and western Asia. While the MN system orders spatially distant localities, there remain dating issues, which must be evaluated. Also, not all localities have equal informational value. For some, correlations (and therefore dating) are poorly constrained. For others, association of leporid remains with the rest of the fauna may be an issue. Furthermore, identifications are not uniformly validated. We discuss some of these issues, but recommend review of all records as a broader objective so that they may be incorporated into historical scenarios.

Late Miocene Eurasian fossil rabbits are commonly assigned as species of *Alilepus*, *Hypolagus* or *Trischizolagus*,

based largely on complexity of the third lower premolar (Fladerer & Reiner 1996, López-Martínez et al. 2007). There are other features that distinguish taxa, but this tooth (p3) is the most commonly preserved complex element (White 1991). We note identifications of taxa from some localities if these are informative, but because the systematic status of many fossil samples has not been reviewed, we hesitate to endorse all identifications. In fact, Miocene identifications are particularly problematic, in contrast to better differentiated Pliocene lineages. We find many assignments of Miocene samples to be questionable at the generic level. A thorough systematic revision is overdue to characterize species of these and other taxa such as *Serengetilagus*.
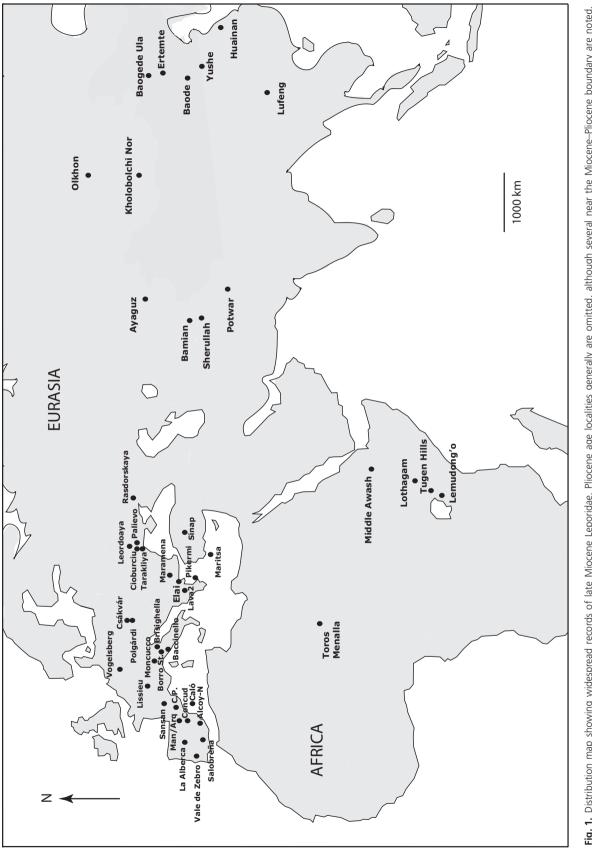
LATE MIOCENE LEPORID LOCALITIES IN THE OLD WORLD

Europe and western Asia

The European record of later Cenozoic localities is relatively rich, and has long supported the absence of crown Leporidae in Europe until the late Miocene (Boon-Kristkoiz & Kristkoiz 1999). The widespread late Miocene leporid records of Europe and western Asia (Fig. 1) show that the introduction of modern Leporidae was a Turolian age event. The European MN biochron system subdivides the Miocene and may be related to the geological time scale to estimate the time of introduction of leporids into Europe to millions of years. Whereas the latest Miocene MN13 localities record Leporidae throughout Europe, and many finds date to MN12, few date definitively to MN11 (early Turolian). The approximate maximum age of MN12 in Europe is 8 Ma (Steininger 1999) or somewhat less (Şen 1997), but the undefined age limits of MN zones appear to be diachronous (see Gómez Cano et al. 2011), so assignment of local assemblages to MN zones is often problematic. That few European records discussed here are demonstrably MN11 in age suggests that the immigration of leporids was probably at the end of that unit, and that the Leporid Datum does not greatly predate 8 Ma.

The large stem leporid *Alilepus turolensis* was recognized at several localities in the late Miocene of Spain and named for material from El Arquillo by López-Martínez (1977). López-Martínez (1989) noted the oldest indication of this species at Los Mansuetos, attributed to MN12, and later wider distribution in the Iberian Peninsula in deposits considered MN13 (for example, El Arquillo). Montoya et al. (2006) add MN13 leporid fossils of Alcoy-Barranco.

Also widespread, but sparsely represented, is the genus *Trischizolagus*, a form distinguished from *Alilepus* by its p3 trigonid, which is set off by three reentrant folds (see Averianov & Tesakov 1997). López-Martínez et al. (2007) noted other distinctions and morphological change through

Fig. 1. Distribution map showing widespread records of late Miocene Leporidae. Pliocene age localities generally are omitted, although several near the Miocene–Pliocene boundary are noted. Some points on the map represent multiple localities at a smaller scale: Potwar, for example, represents a number of sites in the Dhok Pathan Formation of northern Pakistan (Winkler et al. 2011); Tugen Hills, Kenya, includes sites in the Lukeino Formation and the Mpesida Beds. A few localities north of the Black Sea could be added, but these have not been published or we have not yet evaluated their lagomorph records; they include Chimishliya, Gura Galbene, Egorovka 2, Tretya Krucha. Locality abbreviations: Man/Arq, Los Mansuetos and El Arquillo, Teruel Basin (Spain); C.P., Can Ponsic (Spain); Caló, Caló den Rafelino, Mallorca (Spain); Borro St, Borro Strolla (Italy); Elai, Elaiochoria 2 (Greece).

time in the *Trischizolagus* lineage. Some localities previously assumed to contain *Alilepus* may, in fact, record *Trischizolagus*. *Trischizolagus* occurs on the Iberian Peninsula (e.g. at Alcoy-N, Salobreña and La Alberca; López-Martínez 1989; and at Vale de Zebro, Portugal; Antunes et al. 1986). López-Martínez (1989) also noted a derived species at Salobreña that may not be assignable to *Trischizolagus*. *Trischizolagus* is documented in Tuscany at the late Miocene Borro Strolla site (Angelone & Rook 2012), and it occurs in Greece at Maritsa (near the Miocene–Pliocene boundary, possibly MN13 according to Doukas 2005). Koufos (2006) notes an advanced leporid at Lava-2, Greece. Again these identifications are in need of review in light of the small samples and scant differences apparent among *Alilepus*, *Trischizolagus* and *Serengetilagus*.

Yet another leporid occurs in the Balearic Islands. Quintana et al. (2010) described *Hypolagus balearicus* from Caló den Rafelino, Mallorca, and they considered the remains as earliest Pliocene (MN 14). The species shows some similarities to older *Hypolagus igromovi*, and the arrival of a leporid on the Balearic Islands by mainland connection would have to have occurred during the striking drop in sea level of the late Miocene (MN 13) Messinian Salinity Crisis. Therefore, *Hypolagus* would have been present on the late Miocene mainland of the Iberian Peninsula at the same time as *Alilepus* and *Trischizolagus*.

Alilepus occurrences are scattered across European localities assigned as late Miocene, for example the MN13 locality at Lissieu, France (Mein 1999). *Alilepus hungaricus* occurs at the important MN13 locality Polgárdi, Hungary, and *Alilepus* sp. is cited a few kilometers to the north at Csákvár (Kretzoi 1954, Rabeder 1989). In Greece, *Alilepus turolensis* is recognized from Maramena (de Bruijn 1995), and *Alilepus* sp. occurs at Pikermi (MN12; López-Martínez 1976). In Tuscany, *Alilepus meini* is documented from Ribardella (Angelone & Rook 2011) and other localities of the Bacinello V3 Basin.
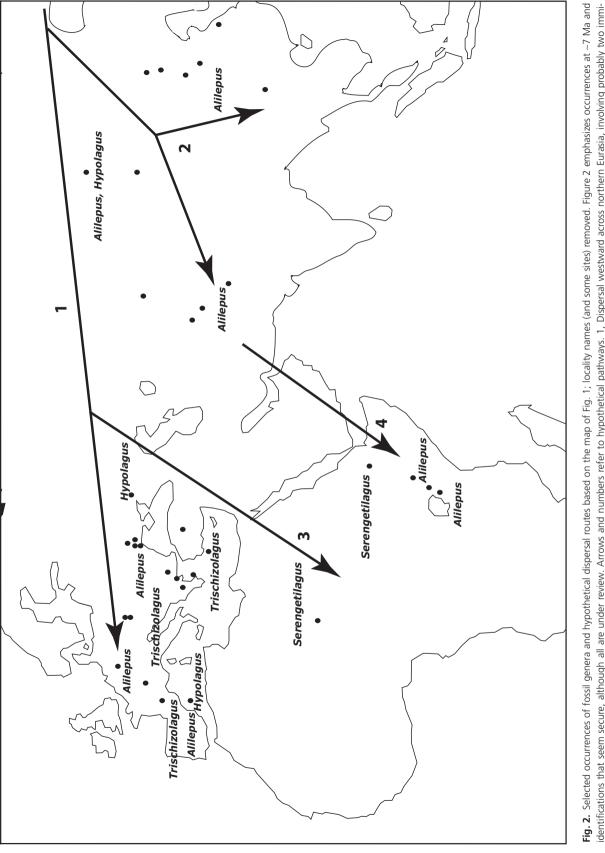
A century ago, Khomenko (1914) defined *Alilepus laskarewi* for material from the Moldovan locality Tarakliya (MN 12). Elsewhere in Moldova and the Ukraine, late Miocene leporids are documented from many localities, e.g. Chimishliya, Cioburciu, Gura-Galbene, Leordoaya, Palievo, Egorovka 2, and Tretya Krucha (Sinitsa 2005, 2008, 2009, Delinschi 2008, Lungu & Rzebik-Kowalska 2011, unpubl. data). These have close morphodimensional affinities with *Alilepus laskarewi*, and some are given an age of MN11 with varying degrees of confidence. These early occurrences of Eurasian leporids are close to *Alilepus laskarewi* and judged as indicating early Turolian (MN11) presence of *Alilepus*.

To the east at Rasdorskaya in the Don River region near the Black Sea, fossils document the late Miocene occurrence of *Hypolagus*, which differs significantly from *Alilepus*. This good sample of cranial and postcranial material (Averianov

1996) documents the MN13 presence of *Hypolagus igromovi*. The genus *Hypolagus* is characterized by a simple p3, which usually has only an anteroexternal and a posteroexternal reentrant. Patnaik's (2002) spline analysis of leporid p3 evolution places *Hypolagus* on a different trajectory of morphological change than that of *Alilepus*. The distinction of Eurasian *Hypolagus* from other leporids and the similarity to some older North American species of *Hypolagus* suggest that more than one advanced leporid crossed Beringia from North America (Čermák 2009). Because currently known *Hypolagus* fossils postdate the earliest remains of *Alilepus*, we suggest that *Hypolagus* may have been a later immigrant (Fig. 2). How many lineages immigrated, and whether immigration was simultaneous, remain to be tested in the fossil record.

Africa

While the end of the Miocene saw widespread appearance of diverse leporids north and east of the Mediterranean Sea, López-Martínez et al. (2007) were struck by the apparently later influx of Leporidae into the late Miocene African record (Fig. 1; see also the summary of African lagomorph history by Winkler & Avery 2010). López-Martínez et al. (2007) named the putatively most primitive species of the mainly Pliocene genus *Serengetilagus* (*Serengetilagus tchadensis*) for fossils from the Toros Menalla deposits of Djurab Erg, Chad, which date to approximately 7 Ma (Brunet et al. 2002, 2005, Vignaud et al. 2002, Brunet & MPFT 2004). *Serengetilagus* has also been reported from the late Miocene of the Middle Awash, Ethiopia (Adu-Asa Formation, 5.8–5.2 Ma; Wesselman et al. 2009), and from the Tugen Hills, Kenya (Lukeino Formation, 6.1–5.8 Ma in Mein & Pickford 2006; but see further discussion). We consider a single isolated p3 from the late Miocene of Lemudong'o, Kenya (c. 6 Ma; Darwent 2007) to pertain to *Serengetilagus*. Analyzing *Serengetilagus tchadensis*, López-Martínez et al. (2007) suggested that *Serengetilagus* and *Hypolagus* were related, and distinct from other genera.

It is now clear that the *Alilepus* leporid group was also present in East Africa. Winkler (2003) signaled *Alilepus* at Lothagam, Kenya; the specimens are dated at 6.57–6.54 Ma. Darwent (2007) tentatively recognized *Alilepus* at Lemudong'o, Kenya, based on an incomplete maxilla (this record may be in addition to a p3 that we refer to *Serengetilagus*, or all remains may pertain to a single genus). *Alilepus* is also present in the Tugen Hills, Kenya (Lukeino Formation, 6.2–5.6 Ma; Winkler et al. 2011). Mein and Pickford (2006) assign other leporids from the Lukeino Formation to *Serengetilagus*, but Winkler et al. (2011) do not consider this identification definitive for all specimens, based on given descriptions and illustrations. An isolated leporid incisor that cannot be assigned to any genus was

Fig. 2. Selected occurrences of fossil genera and hypothetical dispersal routes based on the map of Fig. 1; locality names (and some sites) removed. Figure 2 emphasizes occurrences at ~7 Ma and identifications that seem secure, although all are under review. Arrows and numbers refer to hypothetical pathways. 1, Dispersal westward across northern Eurasia, involving probably two immigrants, *Alilepus* and (possibly somewhat later) *Hypolagus*. 2, Southward dispersal into South China and the Indian Subcontinent of the *Alilepus* group (no *Hypolagus* in evidence; *Alilepus* could have entered Afghanistan and the Indian Subcontinent by another route). 3 and 4, Two possible routes for dispersal into Africa. For Africa two lineages are apparent, *Alilepus* and *Trischizolagus*, which López-Martínez et al. (2007) consider derived from *Hypolagus*; these could have entered Africa by another route, including southward from the Iberian Peninsula.

recovered from the Mpesida Beds, Tugen Hills, Kenya (7–6.2 Ma; Winkler 2002). All of these records date to 7 Ma or are more recent, but show that two kinds of leporids, at least, had dispersed into Africa.

Eastern and southern Asia

Small mammal localities in northeastern Asia demonstrate late Miocene occurrences of Leporidae, in contrast to their earlier absence (Erbajeva & Alexeeva 2013). The middle Miocene of Asia shows, instead, a diversity of ochotonid lagomorphs. Because the fossil record in this region is being developed, it is not yet densely sampled, so the age for introduction of rabbits into the Old World is imprecise. In Siberia, Erbajeva and Alexeeva (2013) record both *Hypolagus* and *Alilepus* from the late Miocene of Olkhon Island in Saray Bay of Lake Baikal, specifically the Odonimskii Fauna. Thus, at 52° N latitude, at least two Leporidae were present in the late Miocene of eastern Asia. As noted above, *Hypolagus* may represent a leporid stock separate from *Alilepus*, with independent crossing of Beringia from North America (Fostowicz-Frelik 2003).

Kholobolchi Nor, Mongolia, yielded a specimen of *Trischizolagus* sp. (Flynn & Bernor 1987); this site is younger, near the Miocene–Pliocene boundary. Apparently, another invader accompanied leporid immigrants: marmots spread from North America into Asia at this time (Erbajeva & Alexeeva 2009).

Alilepus annectens occurs in late Miocene Baodean age localities of the Yushe Basin (Flynn 1997) and at Baode, both Shanxi Province, North China. The maximum age for the Baodean biochron is 7.2 Ma (Zhu et al. 2008). Ertemte and Baogede Ula of Inner Mongolia, late and early Baodean, respectively, also produce remains of *Alilepus* (Z. D. Qiu et al. 2013). Southward in Yunnan, China, *Alilepus longisinuosus* is encountered at Lufeng (Qiu & Han 1986). This site is estimated at less than 7 Ma (Qi et al. 2006). Jin (2004) described *Alilepus lii* and *Pliopentalagus huainanensis* from the 'latest Miocene' of Huainan, Anhui.

To the west, indeterminate leporids close to *Alilepus* occur in the late Miocene of Afghanistan. Neither the Bamian (or Bamyan) Basin nor the Sherullah, Khordkabul Basin locality (Lang & Lavocat 1968; Şen, personal communication; see Fig. 1) is well dated, but both are regarded as late Miocene. Late Miocene specimens of another leporid, possibly *Hypolagus* sp., were discovered at Ayaguz in southeast Kazakhstan (Erbajeva 1982).

Leporidae appear abruptly in the late Miocene Siwaliks of the Indian Subcontinent, where scattered remains form the basis for the species *Alilepus elongatus* (Winkler et al. 2011). Palaeomagnetic age control allows dating of several Potwar Plateau localities in Pakistan, the oldest of which is 7.4 Ma. Barry et al. (2002) considered the spotty quality of the fossil record to assess whether the actual introduction of lagomorphs into the Siwaliks could have been earlier. Their conclusion was that an inferred first appearance of Leporidae would not exceed 7.8 Ma; before that date, leporids were unlikely to have been present south of Tibet. Introduction of leporids into northeastern Asia at a time earlier than observed in southern Asia is testable by new fossil finds from early late Miocene localities.

MIOCENE RECORDS BEFORE MN11

In contrast to the abundance of the Turolian leporid records are the few fossil occurrences suggesting that lagomorphs were present in part of Eurasia prior to 8 Ma. We stress that these finds need further evaluation of both age and taxonomy. López-Martínez (1989) and Sesé (2006) signaled two early late Miocene indeterminate leporid occurrences in Spain. The early Vallesian (MN9) locality Can Ponsic produced an upper premolar of apparently derived morphology that may represent a modern leporid. The younger San Miguel de Taudell, considered MN10, also yields a few specimens indicating early appearance of advanced forms (López-Martínez 1989). Hulva et al. (2007) mentioned leporid remains from the Vallesian/Turolian locality Elaiochoria 2, Greece (MN10–11). The Moldovan localities Keinar and Pitushka record leporids and have been correlated to MN10 by Lungu and Rzebik-Kowalska (2011); we have not reviewed these fossils or their age assessments.

A leporid-like lower molar at Sinap, Turkey (Şen 2003), not diagnostic at the genus level, occurs at the top of a section and was therefore not clearly associated with other fauna. If truly a part of the Locality 12 fauna of Sinap, its age would be about 9.6 Ma (Fortelius et al. 2003). A significantly older find is represented by a few teeth from the rich fauna of Sansan, Gers, France. López-Martínez (2012) was surprised by the discovery of this endemic, large leporid in this middle Miocene locality of France, dated to about 15 Ma. This strange occurrence presenting a mix of derived and primitive features cries out for more palaeontological field work and cautions us in simplistic biogeographic scenarios.

DISCUSSION

The Miocene of Eurasia and Africa lacked hares and rabbits between *c.* 23 Ma and possibly as late as 8 Ma, a span of about 15 million years. The appearance of stem Leporidae in the fossil record is a 'datum' in the sense that fossil evidence shows a relatively sudden and widespread dispersal of leporids throughout Eurasia and Africa. The purpose of this overview is to survey the diversity and ages of fossils of early Old World stem Leporidae as a pathway to discerning the

timing of the Leporid Datum, the number of immigrant forms, and the significance of the datum for systematics and ecology.

There exists no phylogenetic tree that embraces living Leporinae along with the diverse North American fossil Lagomorpha, the archaic lagomorphs of Eurasia and the late Miocene immigrants to the Old World. Consensus view of cladistic relationships would plot *Alilepus* in a sister position to (if not within) Leporinae (Dawson 1981). *Hypolagus* may be more distant (a stem leporid) and not a member of crown Leporinae, but this is uncertain. We noted that modern analyses place *Palaeolagus* and relatives outside Leporidae, and possibly outside crown Lagomorpha. The Oligocene genus *Desmatolagus* is a basal stem lagomorph, and *Ordolagus*, one of the last of the archaic stem taxa in Eurasia, shows autapomorphic features such as strongly recurved molars (Huang 1986) that rule out close relationship to Leporidae. Both genera are distinct from the leporid radiation of the late Miocene (López-Martínez 2008). Leporid researchers welcome thorough cladistic analysis of the diverse Leporidae, including stem taxa, to understand their phylogeny. The review of the fossil record that we support here is fundamental to this analysis.

Miocene immigrants

The majority of European and West Asian Leporid Datum sites are considered MN12 or MN13 in age, but a few appear to date to MN11, and are therefore somewhat older. At the transition zone between Western Europe and the Iberian Peninsula, where the Pyrenees have long contributed to a biogeographic barrier, the MN zones are not well constrained temporally, and time transgression is in the order of 10^5 years to one million years (Gómez Cano et al. 2011). Here and elsewhere, biochronological correlations can lead to inaccuracies in estimating chronological age, and we do not attempt to assign numerical ages to individual localities unless there is associated palaeomagnetic or radiometric dating. For general reference, however, MN13 dates from about 6.5 Ma to the Pliocene boundary, and the older MN12 is as old as 7.5 Ma (Krijgsman et al. 1996, Şen 1997) or 8 Ma (see Steininger 1999).

Eastern Asia, being adjacent to the North American source of modern Leporidae, should be important in dating the Leporid Datum. The terrestrial biochron system for this biogeographic province is characterized by two units: the older Bahean Age and the subsequent Baodean Age that terminates at the Pliocene boundary (Z. X. Qiu et al. 2013). The palaeomagnetically constrained boundary between the Bahean and Baodean is near 7.2 Ma (Zhu et al. 2008). The fossil record is biased, with relatively few Bahean localities in contrast to the many Baodean sites. To date, we have several Baodean records of Leporidae, but no eastern Asian

leporids are yet known from Bahean localities. In its totality, the Eurasian fossil record currently places the Leporid Datum at about 8 Ma.

Whereas the oldest known Leporidae in China are not much more than seven million years old, in Pakistan leporids are found at about 7.4 Ma and, given the low fossil richness of immediately preceding strata, it is conceivable that leporids entered the arena of South Asia somewhat earlier (Winkler et al. 2011). The African record suggests that invasion into that land mass did not occur before ~7 Ma. The fossil record suggests later entry of leporids into these areas than at higher latitudes.

There are several genera involved among late Miocene Eurasian Leporidae, but the oldest records appear to be species of *Alilepus*. This genus has a more advanced p3 structure than *Hypolagus*, which has a relatively simple p3 and is encountered in Asia somewhat later in the fossil record. Other taxa are *Trischizolagus*, *Serengetilagus*, and, at the end of the Miocene in China, *Pliopentalagus*. Some of these could be derived from a stem group represented by *Alilepus*, but interrelationships of the genera are unclear and ripe for study. López-Martínez et al. (2007) compared a number of scenarios of evolutionary relationships to set the stage for such an analysis, and found evidence for derivation of *Serengetilagus* from *Hypolagus*. Did the Leporid Datum represent a successful invasion by a single leporid group? Čermák and Wagner (2013) maintain that this may have occurred, but it has not yet been demonstrated. A reasonable alternative hypothesis is that two lineages arrived in Asia from North America in the late Miocene: an *Alilepus* group and – possibly later – a *Hypolagus* group (Fig. 2).

We have taken a parsimonious, simplistic approach to interpreting the fossil record. This entails envisioning a single immigration wave about 8 Ma, albeit one with possibly more than one immigrant. Yet we fully acknowledge that the actual pattern of intercontinental dispersal may have been one of multiple dispersals spaced over some length of time, and that the dynamic may have involved migration back into North America (see Robinson & Matthee 2005 concerning species of *Lepus*). Data are lacking for evaluating these fine-scale phenomena.

Fostowicz-Frelik (2003) examined late Neogene dispersal patterns, especially with reference to *Hypolagus*. In Fig. 2 we interpret late Miocene leporid biogeography in the Old World about 7 Ma based on tentative genus-level identifications. We consider two or more immigrants likely, both in the late Miocene, but not necessarily simultaneous. Multiple dispersal routes are hypothesized. *Hypolagus* is not observed in low-latitude Asia (see Fostowicz-Frelik 2003), but *Serengetilagus* may represent this lineage in Africa. Dispersal routes into the Indian subcontinent and into Africa are untested. Multiple hypotheses should be maintained as we develop scenarios for the history of Leporidae, including

scenarios that invoke models to explain observed molecular patterns. Over 20 years ago, White (1991) wisely called for broad comparison of Eurasian genera with North American Leporinae to assess vicariant relationships not otherwise apparent.

We note a few early fossils that seem anomalous in age; those from Can Ponsic, Spain, and Sansan, France, may attest to a complex leporid history. Such occurrences of indeterminate basal leporids in mid-Miocene localities must be evaluated by future researchers, but may require an additional hypothesis: (i) rare Palaeogene lagomorph derivatives could have continued into the mid-Miocene of southwestern Europe after extinction of most lineages, acquiring some advanced features in parallel with North American genera; or (ii) a limited dispersal of leporids into Eurasia may have occurred prior to the successful late Miocene influx. To support a scenario of parallel evolution or to recognize limited dispersal earlier than 8 Ma demands work: both the search for more fossils and the evaluation of the geological and systematic contexts of the existing ones.

We see the ultimate successful invasion of crown Leporidae as originating in a sudden and definitive dispersal, the Leporid Datum. However, complementary scenarios allow that stem leporids could have crossed Beringia in advance of the late Miocene invasion (*c.* 8 Ma) and left a scant record of their arrival, or that an archaic lineage, as in the Iberian Peninsula, could have persisted from a basal leporid radiation that experienced near-complete extinction by the early Miocene.

Moving forward

There is great potential for constructive integration of palaeontological and molecular studies. Molecular data can indicate approximate antiquity of splitting events for extant taxa. Under a scenario of a single, late leporid invader giving rise to surviving Old World genera, a molecular tree should indicate Old World lineages as coalescing no less recently than about 8–9 Ma. If molecular data were to show some splits as late Miocene and some considerably older, then this would fit a hypothesis of multiple immigrants, perhaps at different times, and with some speciation events occurring in North America prior to the Leporid Datum. A date of 8 Ma may pose a useful maximum age calibration point for some nodes on a molecular tree.

Matthee (2009) saw coalescence of extant Ochotonidae and Leporidae nearly at 40 Ma based on molecular data; this is in accordance with fossil data supporting a separation of the surviving groups in the late Eocene (Dawson 1981). Within Leporinae, the phylogenetic tree of Matthee et al. (2004) postulated splitting relationships with dates estimated by assuming mostly constant rates of molecular change. Although some of these relationships are disputed

in morphological analyses, many age estimates are in line with a late Miocene radiation of extant genera of Leporidae. Some splits appear to be older, in the range of 14 to 9 Ma, and Halanych and Robinson (1999) see rapid diversification for certain extant leporid genera 12.2–16.3 Ma. This middle Miocene splitting is consistent with at least two independent immigration events of lineages that diverged in North America prior to traversing Beringia.

Matthee et al. (2004) proposed multiple dispersal events between North America and Asia, but could not distinguish direction of dispersal. On this point, the fossil record is clear; Leporidae arose in North America and were not in Eurasia until the late Miocene. Diversification of crown Leporinae probably began in North America before the late Miocene. Further cladogenesis would have been encouraged upon entry into the vast Eurasian land mass.

Fossil data argue strongly for a late Miocene entry of derived leporids into Africa, even later than seen in Eurasia. We see no evidence for derived leporids on that continent before 7 Ma, and there was low diversity at that time. These extinct forms split before 7 Ma, but we suggest that the diversification of extant African Leporidae postdates 7 Ma. We do not support Matthee et al. (2004), who propose an age of about 11 Ma for the first invasion of modern leporids into Africa (a range was given with 8.7 Ma at the young end of the distribution, which is also too old). We look to continued comparison of the fossil record with complementary molecular data to resolve the phylogenetic tree for Leporidae and date it.

As to the palaeobiology of fossil leporids, future comparative studies of faunal associations will be important in discerning possibly different ecological preferences for different lineages. Why did late Miocene crown leporids experience such success in their dispersal throughout the Old World? Ge et al. (2013) note that Old World leporids expanded at the time that ochotonids declined, and that living *Ochotona* clearly prefers C3 plants, while *Lepus* can exploit C4 plants. The late Miocene spread of C4 plants appears to be correlated with the success of crown Leporidae. Description of elements other than dentitions will also inform palaeobiology, although certain identification of postcrania is rare in the fossil record of leporids. Description of cranial material of any Miocene leporids is highly important in examining biomechanics and building lower-level systematics.

The impact of rabbits and hares on the ecosystem when they arrived in the Old World may well have been profound (e.g. Foran 1986), as it is today in formerly hare-free areas such as islands (Courchamp et al. 2003). From an Old World without them to an Old World with unoccupied habitat to invade, leporids may well have spread very successfully. The impact on the resident fauna, with leporids as added herbivores – and a new food source – suggests that

there must have been important readjustments among other herbivores and carnivores (e.g. Boutin et al. 1995, Vázquez 2002). In Holocene ecosystems leporids are significant herbivores (e.g. French 1985) and are a very important food source for carnivores (e.g. Zapata et al. 2007), raptors (e.g. Lloveras et al. 2009) and humans (e.g. Brugal & Desse 2004, Jones 2012). The breadth of habitats successfully conquered by leporids reminds us that simplistic assumptions about the ecology of fossil leporids are almost certainly erroneous. Study of the early invaders of the Leporid Datum will inform varied subdisciplines, from lagomorph systematics to terrestrial palaeobiology of the late Miocene to the origins of modern biotic interactions involving Leporidae.

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