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REVIEW

The origin and evolutionary history of Lagomorpha (Mammalia) in China

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Abstract

Fossil lagomorphs from China play a pivotal role in understanding the origin and evolutionary history of this group. In this paper, we summarized the fossil lagomorphs discovered in China to date and their updated chronological distributions. A cladistic analysis was applied to selected, well-represented taxa. The phylogenetic results support the ordinal-level divergence of the Mirorder Duplicidentata in the Early Paleocene. The Mimolagidae taxa (*Mina*, *Gomphos*, and *Mimolagus*) form a side branch of Duplicidentata. The genus *Mimotona* is placed at the most basal position of Lagomorpha, suggesting that the origin of the order Lagomorpha dates back to at least the late Early Paleocene. *Ordolagus*, basally positioned in the Leporidae, first appeared in the lowermost horizon of the Oligocene. *Desmatolagus*, as the earliest Ochotonidae taxon, first appeared in the Late Eocene, implying the splitting of Leporidae and Ochotonidae deep in the Eocene. The chronological distribution of Chinese lagomorph fossil record exhibits a major gap in leporids, between the Late Oligocene and the Leporidae datum of the late Late Miocene, approximately 19 million years long. Given the overall conservative tooth morphology of lagomorphs, we anticipate further discoveries of skull specimens will improve the current phylogeny and taxonomy of Lagomorpha.

Keywords Biochronology · Lagomorpha · Morphology · Phylogeny · Taxonomy

Introduction

Lagomorpha (rabbits, hares, and pikas) is one of the least diversified mammalian orders, with only two extant families: Leporidae and Ochotonidae (Wilson and Reeder 2005). Having a global distribution, a long evolutionary history, and unique characteristics, Lagomorpha is a strong exemplar for biological research and for studying macro- and micro-scale patterns of morphological change (Kraatz et al. 2021). However, systematic studies on lagomorph fossils are still lacking, leaving debate over the phylogeny and taxonomy. Their early diversifications remain ambiguous.

Since hares were grouped with mice and rats in Glires by Linnaeus in 1735, the close phylogenetic relationship of lagomorphs and rodents had long been followed until 1912, when Gidley published his paper "The lagomorphs an independent order", listing ten major differences between lagomorphs and rodents. Further differences in the masseteric muscle segmentation and microstructure of incisor enamel (Korvenkontio 1934) as well as other morphological differences (Wood 1957) convinced many researchers that lagomorphs might have a different origin from that of rodents (Simpson 1945; McKenna 1975). In 1977, the story was flipped back when fossil materials of *Mimotona* and *Heomys* were discovered from the Early and Middle Paleocene strata in Qianshan, Anhui Province, China, exhibiting mixed characters of lagomorphs and rodents that suggest their close phylogenetic relationship (Li 1977). The monophyly of Glires was confirmed later by a series of systematic studies by Meng and Wyss (1994, 2001, 2005), Meng et al. (2003), Asher et al. (2005, 2019). However, definitions of the order Lagomorpha remain controversial. Asher et al. (2005) and Wible (2007) listed *Gomphos* and *Mimotona* as stem Lagomorpha, while López-Martínez (2008) listed these two taxa in Mixodonts. Following the question by Wood (1957), Ruedas et al. (2018) raised a similar

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question: What, if anything, is a lagomorph? They further expected that Wood might rather ask: What is Glires, and where in Glires do we draw the line between Lagomorpha and non-Lagomorpha?

Following the classification of Rose (2006), Li and Zhang (2019) listed Glires as a Grandorder, which includes the mirorders Duplicidentata and Simplicidentata, with the Duplicidentata including Lagomorpha (with two pairs of upper and one pair of lower incisors) and Mimotonida (with two pairs of upper and two pairs of lower incisors). Based on available data, Mimotonida may be a paraphyletic group (Meng and Wyss 2005; Wible 2007) because *Gomphos* and *Mimotona* do not form a monophyletic clade. According to Li et al. (2007), *Dawsonolagus* is by far the earliest and most primitive taxon in the order Lagomorpha. Lopatin and Averianov (2021) named a new clade, Eulagomorpha, with *Arnebolagus* being the oldest taxon. Li and Zhang (2019) synonymized the type and only species *Arnebolagus leporinus* with *Dawsonolagus antiquus*.

The family-level taxonomy of Lagomorpha is also controversial. Gureev (1964) adopted four families in the order Lagomorpha: Eurymylidae, Palaeolagidae, Leporidae, and Lagomyidae. Erbajeva (1988) listed five families: Mimolagidae, Palaeolagidae, Leporidae, Ochotonidae, and Prolagidae. López-Martínez (2008) listed Leporidae and Ochotonidae and considered other taxa as stem groups. Dawson (2008) and Li and Zhang (2019) listed only two families, Leporidae and Ochotonidae, in Lagomorpha.

While extant lagomorphs are widely distributed across Eurasia, America, and Africa, an Asian Origin of Lagomorpha was hypothesized and supported by McKenna (1982), Li and Ting (1993), and Beard (1998). Thus, lagomorph fossils from Asia, especially from China, are essential to the study of the early diversification, phylogeny, and taxonomy of this group. Research on fossil lagomorphs in China dates back to 1924 when Schlosser described abundant dental materials of *Ochotona lagreli* from Ertemte, Nei Mongol. Since then, 27 genera and 88 species from China have been described, with an evolutionary history of over 55 million years from the Early Eocene to the Late Pleistocene (see references in Li and Zhang 2019) (Table 1).

Table 1 Taxonomy of fossil lagomorph genera from China (Li and Zhang 2019)

incertae sedis	*Dituberolagus Tsaganolagus*
incertae familiae	*Dawsonolagus Erenolagus*
Family Leporidae	*Lushilagus*, *Strenulagus*, *Shamolagus*, *Gobiolagus*, *Hypsimylus*, *Ordolagus*, *Alilepus*, *Hypolagus*, *Sericolagus*, *Pliopentalagus*, *Trischizolagus*, *Nekrolagus*, *Nesolagus*, *Lepus*
Family Ochotonidae	*Desmatolagus*, *Sinolagomys*, *Plicalagus*, *Alloptox*, *Bellatona*, *Bellatonoides*, *Ochotonoma*, *Ochotonoides*, *Ochotona*

Here, we aim to focus on the lagomorph phylogeny and taxonomy based on the updated fossil records from China, clarify significant morphological transitions, and further indicate their potential biochronological significance.

Fossil data and methods

In 2013, the late Prof. Li Chuankui and the first author of the present paper started to edit the Duplicidentata and Mixodontia volume of Paleovertebrata Sinica, which was published in 2019 (Li and Zhang 2019). In this volume, most of the taxa were revised based on reexamination of fossils and their updated geological age. With the raw data from the volume, we compiled a data matrix based primarily on the 59 craniomandibular characters listed by Wible (2007). Twenty tooth characters (characters 60–79) were added to the dataset. The new dataset includes 79 characters (Online Resource 1) and 91 taxa, including taxa included by Wible (2007). The masseteric spine (Ch. 18 in Wible 2007) is present on all analyzed taxa, here rescored as vertical (0) and laterally expanded (1). A few character states of *Palaeolagus haydeni* were updated according to the detailed morphological study by Wolniewicz and Fostowicz-Frelik (2021) (Ch. 16: 0>1; Ch. 37: 0>1; Ch. 56: 0>1; Ch. 57: 1>0; Ch. 58: 0>1; Ch. 59: 0>1). Some character states of *Gomphos elkema* were revised based on the skull specimen MAE-BU-14,425 (Asher et al. 2005) (Ch. 4: 1>0; Ch. 16: 1>0; Ch. 18: 1>0; Ch. 23: 1>0). Some character states of *Mimotona wana* were rescored with reference to specimen IVPP V 7500 (Ch. 1: 1>2; Ch. 5: 0>?; Ch. 9: ? >0; Ch. 10: 0>1; Ch. 18: 1>0; Ch. 33: 1>2; Ch. 35: ? >0). Re-examination of the type specimen IVPP RV 51,001 of *Mimolagus rodens* resulted in some modified character states (Ch. 2: 1>0; Ch. 3: ? >1; Ch. 18: 1>0; Ch. 32: 1>?). Character states A and B in the matrix (Wible 2007) were replaced by undetermined. All revised states are marked in red in Online Resource 3.

The phylogenetic analysis was applied using the TNT 1.6 software (Goloboff and Morales 2023). Following Wible (2007), *Rhombomylus* sp. was set as the outgroup. A traditional search was applied. Not surprisingly, the strict consensus tree shows poor resolution due to the lack of skull characters in many taxa. For this reason, we excluded some poorly documented taxa, keeping the genotypic species and the species that have better preserved fossils (37 taxa included). Online Resource 2 provides the data source with references and specimens for the coding. Online Resource 3 listed the data matrix. A reanalysis using the simplified data matrix was then applied using TNT 1.6 with 1000 replicates, collapsing branches with no possible support (rule three), and saving 100 trees per replicate. All characters are coded as unordered. Bremer support values (Bremer 1994)

were subsequently calculated with all the most parsimonious trees retained.

Lagomorph fossils are rich in terrestrial strata and have major significance for biostratigraphy. Stratigraphically well-constrained fossil records can also serve as biomarkers to help calibrate magnetostratigraphy and chronostratigraphy of the Cenozoic terrestrial sequences. Thanks to the continuous efforts of several generations of researchers, the Chinese Cenozoic land mammal ages have been well established (Tong et al. 1995; Qiu et al. 2013). With more magnetostratigraphic data becoming available, many sedimentary sequences have now been well dated or better constrained (e.g., Deng et al. 2019; Wang et al. 2019; Wang et al. 2021; Wasiljeff et al. 2020). Within the refined time frame, the chronological distribution of the fossil records of lagomorph genera from China was calibrated. The phylogenetic relationships of the genera were referred from the topology of Fig. 1 (Fig. 2).

The figures were prepared with Adobe Illustrator 2025. The time scale in Fig. 2 was built with Time Scale Creator GPTS2020.

Abbreviations: IVPP: Institute of Vertebrate Paleontology and Paleoanthropology; **RV**: revised catalogue numbering.

Results

Phylogeny of Lagomorpha

A traditional search with the simplified data matrix resulted in 8,100 most parsimonious trees (MPTs) retained of 150 steps each with a consistency index of 0.75 and retention index of 0.88. A strict consensus tree was produced from MPTs, and the Bremer support values are shown under the nodes (Fig. 1). The resolution is better than the consensus

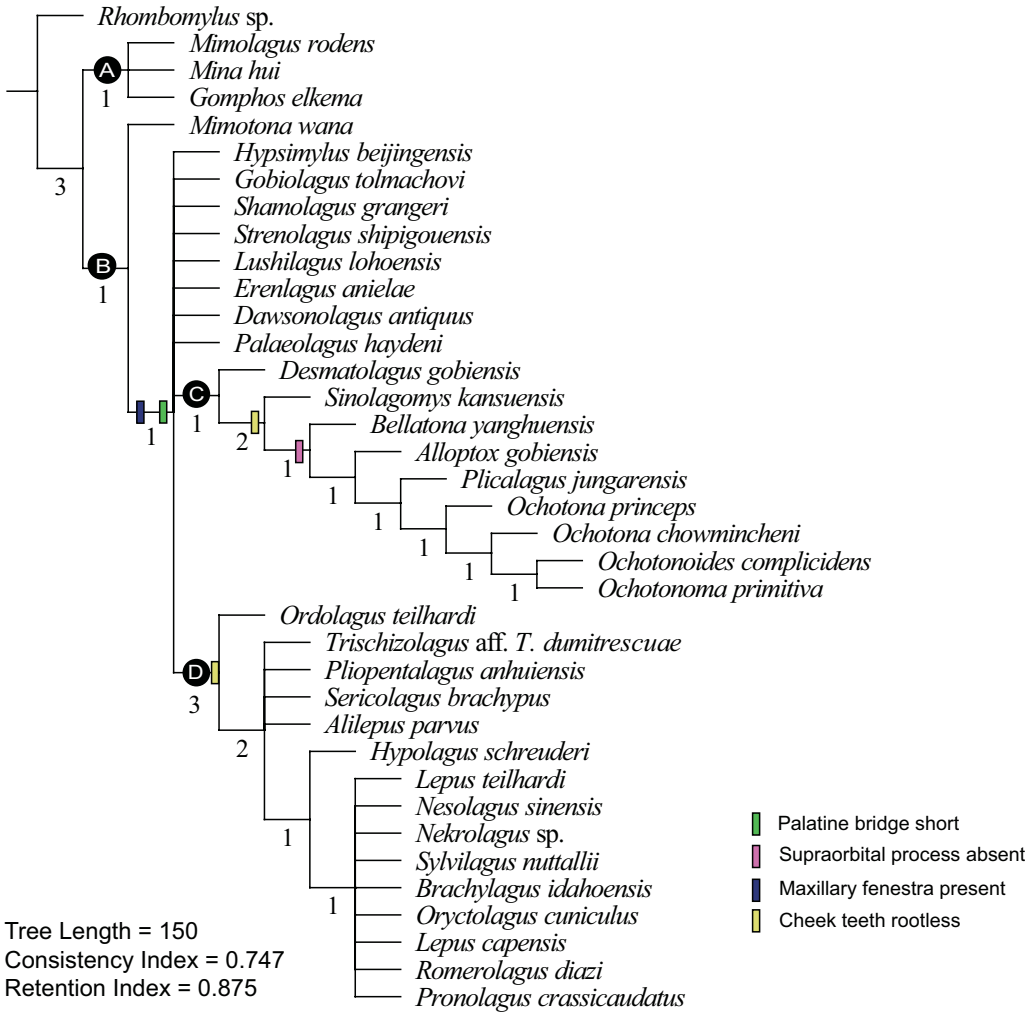

Fig. 1 Strict consensus tree of 37 taxa. Bremer support values are shown under the nodes. Lettered clades A-D are discussed in the Results section. Synapomorphies of labeled clades: **A**, Ch. 19 (1→0); **B**, Ch. 2 (0→1), 51 (0→1), 61 (0→1); **C**, Ch. 34 (0→1), 69 (1→0); **D**, Ch. 6 (0→1), 10 (0→1), 13 (0→1), 25 (0→2), 62 (1→2), 63 (1→2), 65 (0→1), 68 (1→2), 69 (1→2), 72 (0→2), 76 (1→2), 79 (0→1)

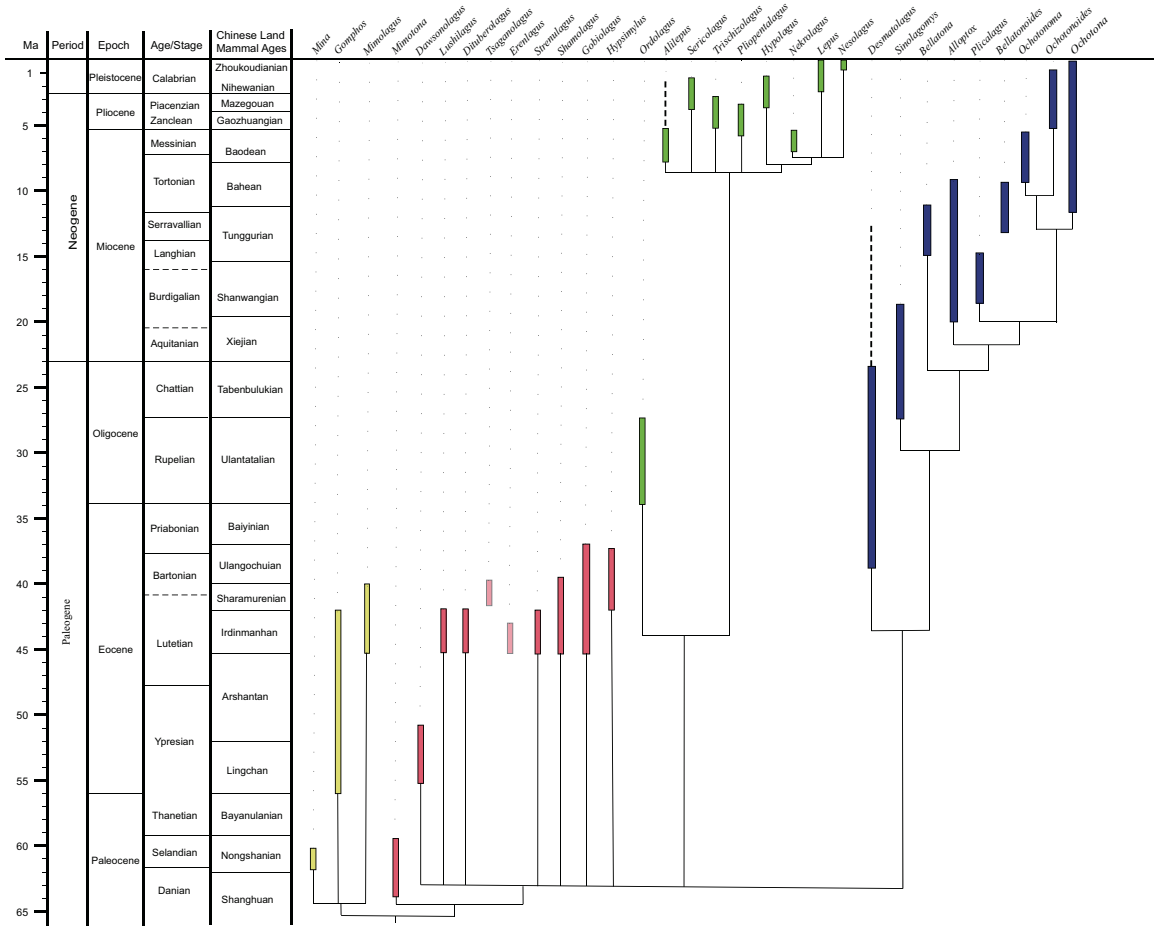

Fig. 2 Chronological distribution of fossil lagomorphs from China. Chinese Land Mammal Ages follow Tong et al. (1995), Qiu et al. (2013), Deng et al. (2019), Wang et al. (2019, 2021). Phylogenetic relationships of the genera are based on the topology of Fig. 1

tree with all taxa included. While polytomies still remain, some important nodes can be recognized by the topology.

The Duplicidentata taxa included in the analysis are separated into clades, which may indicate the splitting of two order-level lineages (clades A and B in Fig. 1).

Clade A includes the Paleocene genus *Mina* and the Eocene taxa *Gomphos* and *Mimolagus*. The monophyly of the Mimolagidae is weakly supported herein by the shared absence of the zygomatic fossa.

The second clade (B) includes *Mimotona* at the basal position, and also the taxa attributed to the Order Lagomorpha by Li and Zhang (2019) and the extant taxa listed by Wible (2007). Clade B is supported by three synapomorphies: narrow posterodorsal process of premaxilla contact with frontal, anteriormost mental foramen positioned back of diastema, and presence of anterior groove on DI2.

In the Lagomorpha clade, there are two monophyletic groups (clades C and D in Fig. 1).

Clade C includes the taxa: *Desmatolagus*, *Sinolagomys*, *Bellatona*, *Alloptox*, *Plicalagus*, *Ochotonoma*, *Ochotonoides*, and *Ochotona*. *Desmatolagus* is grouped with the other genera which are defined in the family Ochotonidae by Erbajeva et al. (2011). Taking all these genera into the Ochotonidae, the clade is supported by the presence of premolar foramen and no lingual enamel connections on p4-m3.

Clade D includes the Oligocene taxon *Ordolagus* at the basal position, and taxa (*Alilepus*, *Lepus*, *Oryctolagus*, *Sylvilagus*, etc.) in the Leporidae as suggested by López-Martínez (2008). The Leporidae clade is well supported by several synapomorphies: presence of braincase pitting, reduced but prominent pointed lacrimal tubercle, sphenopalatine foramen within palatine, presence of root exposure in orbit floor, narrow posterior squamosal, M3 reduced to a single lobe, rootless upper and lower cheek teeth, molarized P3, and lingual enamel connection of trigonid and talonid on p4-m2, etc.

Lushilagus, *Strenolagus*, *Shamolagus*, *Hypsimylus*, *Erenlagus*, *Gobiolagus*, together with *Palaeolagus* from North America, are placed at basal position on the tree with polytomy branching. The supposed most primitive Lagomorpha

taxon *Dawsonolagus* (Li et al. 2007) is nested in the Lagomorpha clade.

Chronological distribution of Chinese fossil lagomorphs

Figure 2 illustrates the present chronological distribution of all the genera of Chinese lagomorphs and Mimolagidae. The three genera of Mimolagidae range from late Early Paleocene to Middle Eocene. The lagomorph taxa cover most of the ages of Cenozoic.

Discussion

Phylogeny and taxonomy of Lagomorpha

Gomphos and *Mimolagus* were considered as stem members of Lagomorpha by Asher et al. (2005) and Wible (2007). Li et al. (2016) and Li and Zhang (2019) grouped these two genera together with *Mina* in the family Mimolagidae of the Order Mimotonida characterized by the absence of anterior groove on DI2. Although Li et al. (2016) cautiously stated that it is premature to consider Mimolagidae as a natural group, they did not rule out the possibility. Our phylogenetic result groups them in one clade but with low Bremer support value, awaiting more fossil data to confirm an ordinal level classification.

Mimotona, previously referred in Mimotonidae of Mimotonida, was considered as the "morphotype" of the ancestor of lagomorphs (Li et al. 2016; Li and Zhang 2019). Based on the present phylogenetic analysis, *Mimotona* should then be listed as the earliest member of Lagomorpha. The Order Lagomorpha is characterized by the presence of anterior groove on DI2, narrow posterodorsal process of premaxilla contact with frontal, and the anteriormost mental foramen positioned back of diastema.

Although forming a monophyletic group on the strict consensus tree (Fig. 1), the Ochotonidae clade is not strongly supported with two questionable synapomorphies. The absence of lingual enamel connection of trigonid and taloned on p4-m3 occurs also on most stem members. The premolar foramen is present not only in ochotonids but also in some leporid and stem taxa as Fostowicz-Frelik and Meng (2013) indicated, suggesting that the premolar foramen may have evolved independently in several lineages of Lagomorpha.

The Leporidae is the best supported clade on the strict consensus tree, sharing both cranial and dental characters. *Ordolagus* was placed at the most basal position of the Leporidae, not a stem lagomorph member as suggested by López-Martínez (2008).

To obtain a better resolution of the phylogenetic relationships of the existing taxa, more craniomandibular materials are primarily necessary.

Some morphological transitions in the evolution of lagomorphs

As indicated by Gidley (1912) and many other researchers (e.g., Dawson 2008; López-Martínez 2008), lagomorphs exhibit some significant morphological transitions during their evolution. Here we discuss some skull and tooth characters with relatively well-preserved fossil records (marked with colored bars in Fig. 1).

Both the anterior and posterior supraorbital processes are absent in *Ochotona*, but they are well developed in Leporidae genera, though with shape variations among individuals of various ages as well as in populations of *Lepus* that inhabit different habitats (Ge et al. 2015). The Leporidae taxa from China, such as *Hypolagus* and *Sericolagus*, have both the anterior and posterior supraorbital processes, while the Ochotonidae genera *Alloptox*, *Bellatona*, and *Ochotonoides* have no supraorbital process. There is only the posterior supraorbital process in *Dawsonolagus* and *Palaeolagus*. The supraorbital process is unknown in other stem taxa. A plausible hypothesis is that leporids retained the posterior process and developed the anterior process, while ochotonids lost the posterior process from their ancestors.

The bony palatine bridges on the skulls of crown Lagomorpha are typically short, consisting of the palatine process of maxilla and horizontal portion of the palatine bone, bounded by the large incisive foramen (the incisive foramen plus the palatine vacuity, which are separated in some extant *Ochotona* species, such as *Ochotona pallasi*) anteriorly and the choanae (posterior nares) posteriorly. The posterior extension of the palatine vacuity is accompanied by shortening of the palatal process of the maxilla between the cheek tooth row, with the shortest length found in extant Ochotonidae. The horizontal portion of the palatine bone tends to be short with the extremity in extant Leporidae. Wible (2007) emphasized the elongated incisive foramen in *Gomphos*, *Mimotona*, *Mimolagus*, *Palaeolagus*, *Romerolagus*, and other leporids and the elongated palatal vacuity largely within the maxillae on skulls of *Ochotona* and *Prolagus*. The palatine processes of maxillae in *Mimotona* and *Gomphos* are well developed, however, with no sign of the palatine vacuity. The partial skull specimen of *Dawsonolagus antiquus*, unfortunately, preserves only part of the palatine process of the maxillae. The elongated incisive foramen on the skulls of *Palaeolagus* and other leporids suggests confluence of the incisive foramen and the palatine vacuity. The present fossil records display a general tendency of

decreasing relative length of the horizontal portion of the palatine bone.

Lagomorphs are characterized by the presence of maxillary fenestra with a single, large opening in Ochotonidae and perforated by a lacework of small openings in Leporidae (Dawson 2008). According to Insom et al. (1990), there is no fenestra on the lateral wall of the maxillary corpus before birth; the bone was then absorbed after birth, forming a single large opening (maxillary fenestra, pars facialis and pars orbitalis; Wible 2007) on the skulls of *Ochotona*. Both *Mimotona* and *Gomphos* have no perforation on the lateral wall of the maxillary corpus. The fossil specimen of *Mimolagus rodens* described by Bohlin (1951) shows no sign of perforation on the preserved part of the maxilla. Well-preserved skull of *Palaeolagus* suggests the presence of numerous small openings on the pars facialis of maxillary fenestra which is present in Leporidae, and the pars orbitalis which is present in Ochotonidae but absent in Leporidae (Wolniewicz and Fostowicz-Frelik 2021). Further study on the early differentiation of these two fenestra patterns requires better-preserved specimens from Paleogene strata.

The attainment of ever-growing cheek teeth is an example of parallel evolution process, also occurring in many groups of extant and extinct mammals (Tapaltsyan et al. 2015). Both the extant Ochotonidae and Leporidae share the character of ever-growing cheek teeth (i.e., hypselodonty). The fully hypselodont or rootless cheek teeth first appeared in the leporid genus *Ordolagus*, which was recorded from lower Oligocene strata (Angelone and Zhang 2021). However, the first ochotonid taxa with rootless cheek teeth is *Sinolagomys* which occurred in the very beginning of the Late Oligocene, dated to 27.7 Ma (Wasiljeff and Zhang 2022). Thus, the transition from rooted to rootless cheek teeth is not synchronous in different lineages of Lagomorpha.

Chronological distribution of Chinese fossil lagomorphs

As the most basal member of lagomorphs, *Mimotona* was discovered from the upper part of Wanghudun Formation and Doumu Formation, considered to be late Early Paleocene to Middle Paleocene in age (Wang et al. 2021). This confirmed that the origin of Lagomorpha at least dates back to the late Early Paleocene, not in full agreement with the Cretaceous or close to K/Pg boundary origination hypothesis (Asher et al. 2005; Murphy et al. 2007). *Mina* from the upper part of the Wanghudun Formation is grouped in the side-branching lineage of Mimolagidae together with the Eocene taxa *Gomphos* and *Mimolagus* (Fig. 1), suggesting that their splitting with Lagomorpha dates back to the late Early Paleocene.

After a void of lagomorph fossil records of the Late Paleocene, *Dawsonolagus* appeared as the only Early Eocene taxon discovered from the Naomugen Formation (unpublished data cited in Li and Zhang 2019) and the bottom of the Arshanto Formation in Nei Mongol (Li et al. 2007).

The Middle Eocene Irdinmanhan Land Mammal Age witnessed the first radiation of lagomorphs. There are six genera recorded from China: *Lushilagus*, *Strenolagus*, *Dituberolagus*, *Erenlagus*, *Shamolagus*, and *Gobiolagus*. Of these, *Lushilagus*, *Strenolagus*, *Dituberolagus*, and *Erenlagus* are recorded from localities of Irdinmanhan strata. *Shamolagus* survived into the Sharamurunian age. *Gobiolagus* is the most diversified genus of the Eocene taxa recorded in China. The six species of *Gobiolagus* span the Irdinmanhan to the end of the Eocene. The enigmatic genus *Hypsimylus*, originally recorded in Beijing (Zhai 1977), was validated by new findings from Ulangochuian strata in Nei Mongol with more specimens (Meng and Hu 2004). The only documented lagomorph genus in China that survived the Eocene-Oligocene transition is *Desmatolagus*, which first appeared in the late Eocene Ulangochuian strata, represented by the most primitive species *D. vetustus.*

Possibly originated from the Eocene genus *Gobiolagus*, *Ordolagus* was previously documented from Wulantatal and Saint Jacques in Nei Mongol and the Valley of Lakes area in Mongolia (Burke 1941; Huang 1986; Daxner-Höck et al. 2010). Extensive survey by our team during the last decade of the long sequences in Saint Jacques and Wulantatal suggests that their occurrences are confined to the Early Oligocene, with no record in Late Oligocene strata (Wasiljeff and Zhang 2022; Wang et al. 2023 and unpublished data). From the Late Oligocene onward, there are no records of Leporidae from China until the Leporidae Datum in the late Late Miocene (~8 Ma; Flynn et al. 2014). The Leporidae may have been absent during this long interval on the Eurasian and African continents. The eco-space vacant left by the Leporidae may have then be occupied by the diversified Ochotonidae and also survivors of some stem taxa, such as *Desmatolagus.*

According to Wasiljeff and Zhang (2022), the lowest occurrence of the genus *Sinolagomys* was estimated to ~27.7 Ma by paleomagnetic dating, close to the lower boundary of the Late Oligocene Chattian Age. The Late Oligocene and Early Miocene are characterized by diversification of *Sinolagomys*, with six species described from China. The most recently described *Sinolagomys guchengensis* by Wang et al. (2025) may be the most derived species in the genus, possibly of the Shanwangian age. A detailed study on the biostratigraphy of *Sinolagomys* may improve the temporal resolution.

Although there is controversy about the species-level taxonomy, the genus *Alloptox* was widely discovered in China. The diminuitive species *A. xichuanensis* and *A. sihongensis* were mainly found from localities of the Shanwangian age. *A. minor* was known from the early Middle Miocene (Liu and Zheng 1997). The larger species *A. gobiensis* and *A. guangheensis* were discovered from the Tunggurian strata. The survival of *Alloptox* into the Late Miocene remains to be verified. The two species of *Bellatona* (*B. forsythmajori* and *B. yanghuensis*) have only been discovered in the Tunggurian localities (Qiu 1996). The earliest record of *Ochotona* is from Damiao, Nei Mongol, with an age estimate of ~ 12.1 Ma by paleomagnetic dating (Zhang et al. 2012; Kaakinen et al. 2015). At least 17 species of *Ochotona* have been described, covering the time interval from the Late Miocene to the Pleistocene (Li and Zhang 2019).

Alilepus fossils were discovered from Late Miocene Baodean localities in northern China (e.g., Baode and Yushe basins) and Yunnan in the South (Qiu and Han 1986; Wu and Flynn 2017). *Trischizolagus* and *Pliopentalagus* have been found from Pliocene strata, while *Hypolagus* and *Sericolagus* occurred from the Pliocene to the earliest Pleistocene. *Lepus ziboensis*, found in Shandong Province, is by far the earliest record of the extant genus *Lepus* in China, possibly of late Early Pleistocene age. The extant species of *Lepus*, *L. capensis* and *L. sinensis*, have been recorded in Middle Pleistocene Zhoukoudian localities (Zhang 2010).

Concluding remarks and future prospects

Our phylogenetic analysis on Chinese fossil lagomorphs – the first of its kind - implies the ordinal-level divergence of the Mirorder Duplicidentata in the Early Paleocene. The Mimolagidae taxa (*Mina*, *Gomphos*, and *Mimolagus*) form a side branch of Duplicidentata, which went extinct during the Middle Eocene. The genus *Mimotona*, previously assigned to Mimotonida, is placed at the basal-most position of Lagomorpha, suggesting that the origin of the order Lagomorpha dates back to at least the Late Early Paleocene. *Ordolagus*, basally positioned in Leporidae, first appeared in the lowermost horizon of the Oligocene. *Desmatolagus*, as the earliest member of Ochotonidae, first occurred in the Late Eocene strata which may imply the splitting of Leporidae and Ochotonidae deep into the Eocene. The chronological distribution of Chinese lagomorph fossils also reveals a significant gap in leporids, which spans the Late Oligocene to the Leporidae datum of the late Late Miocene, approximately 19 million years long.

The lagomorph fossil records from China are predominantly represented by teeth and jaw fragments, with only a few taxa represented by complete skulls. Given the conservative tooth morphology, improvement of the present phylogeny and taxonomy of Lagomorpha will rely on more skull specimens. Fossils from the Paleocene to the Early Eocene strata, in particular, will help clarify the origin and early evolutionary process of this widespread mammalian group.

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Author contributions ZZQ designed and prepared the data; WB performed the cladistic analysis; ZZQ and WB wrote and reviewed the manuscript.

Data availability All data generated and analyzed during this study are included in this published article and its supplementary files.

Declarations

Competing interests The authors declare no competing interests.

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