

A review of the phylogeny of the European rabbit (*Oryctolagus cuniculus*)

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Abstract. The present work aims to synthesize the origin and phylogeny of the European rabbit (*Oryctolagus cuniculus*), of the Family Leporidae, Order Lagomorpha. Lagomorpha is an order of mammals which splits into two living families: Family Leporidae and Family Ochotonidae. Lagomorpha may have descended from the group of mimotonids (Anagaloidea). The diversity of Lagomorphs was certainly higher in the past than in the present, with around 75 genera and more than 230 species represented in the fossil record. These statistics of fossil record are evidences supporting that lagomorph lineages are declining in the present times. The living genera of the Family Leporidae emerged in the early Miocene, with the two most diverse genera, Genus *Lepus* (hare species) and Genus *Sylvilagus* (cottontail rabbits), first recorded in the fossil deposits dating back about 8.6 and 7.2 million years ago, respectively. The literature is scarce regarding the phylogeny of Genus *Oryctolagus*. The genus *Oryctolagus* comprises a single species (*O. cuniculus*) and six subspecies, and is the ancestor of all domesticated breeds. The paradox of this species is that, although the group to whom it belongs is in decline, the European rabbit is a species with an extraordinary plasticity, giving birth to a multitude of breeds and varieties of shape and color.

Key Words: Lagomorpha, Leporidae, modern breeds, *Oryctolagus*, phylogenetic data.

Introduction. The present work aims to synthesize the origin and phylogeny of the European rabbit (*O. cuniculus*), of the Family Leporidae and of the Order Lagomorpha. The work is realized based on experience as rabbit breeders of some authors from the collective, as well as based on a broad analysis of the scientific literature.

Mammals. Today's mammals consist of Monotremes, Marsupials, and Placentals. Together, they form Class Mammalia. The subclass Prototheria (nowadays, represented by Order Monotremata) comprises the five species of egg-laying mammals: four echidna and one platypus species. The infraclasses Metatheria (Marsupialia) and Eutheria (Placentalia - placental mammals) together compose the subclass Theria (Murphy et al 2001).

Phylogenetics in the Genomic Era. In the 3rd millennium, molecular biology studies have been developing, so that many taxonomic and phylogenetic approaches that relied strictly on comparative anatomy, external morphology, and inter-fecundity, have begun to use the results of molecular biology research (Gissi et al 1998; Shimodaira & Hasegawa 1999; Robinson & Matthee 2005). Then, new disciplines related to molecular biology have emerged, such as genomics, proteomics, phylogenomics, metabolomics, etc. Phylogenomic research, new fossil records and innovative morphological interpretations now classify more than 4600 living species of eutherians into four large super-ordinal clades: Euarchontoglires (which includes Lagomorpha, Rodentia, Scadentia, Dermoptera and Primates), Laurasiatheria (which consists of Eulipotyphla, Pholidota,

Chiroptera, Carnivora, Perissodactyla and Cetartiodactyla), Xenarthra, and Afrotheria (which includes Macroscelidea, Tubulidentata, Afrosoricida, Hyracoidea, Sirenia, and Proboscidea) (Murphy et al 2001). A phylogenetic tree based on more precise data was drawn. This tree of mammals is very helpful in unifying the parts of a puzzle in comparative mammalian cytogenetics and related scientific disciplines (Figure 1; Figure 2).

Order Lagomorpha. Lagomorpha is an order of mammals which splits into two living families: the hares, rabbits (both included in Family Leporidae), and pikas (Family Ochotonidae) (Awadi et al 2016; Lissovsky et al 2016, 2019; Álvarez-Castañeda & Lorenzo 2017; Silva et al 2019).

Over time, several names have been assigned to this group: Duplicidentata - Illiger, 1811; Leporida - Averianov, 1999; Ochotonida - Averianov, 1999; Neolagomorpha - Averianov, 1999; and Palarodentia - Haeckel, 1895 (Hoffmann & Smith 2005a). All these names are synonymous with Order Lagomorpha, but it is preferable not to use them.

Initially, the species of this group were included in the group Rodentia (a clade related to Lagomorpha), and are characterized by the possession of double incisor teeth. There are 91 living species of lagomorph, including about 30 species of pika, 29 species of rabbit and cottontail, and 32 species of hare (Wikipedia.org 2019c).

The extinct family Prolagidae is represented by a single known species, the Sardinian pika, *Prolagus sardus*, fossils of which are known from Corsica, Sardinia, and the neighboring islands from the Tyrrhenian Sea. It is believed that the species survived until 1774 (Hoffmann & Smith 2005b).

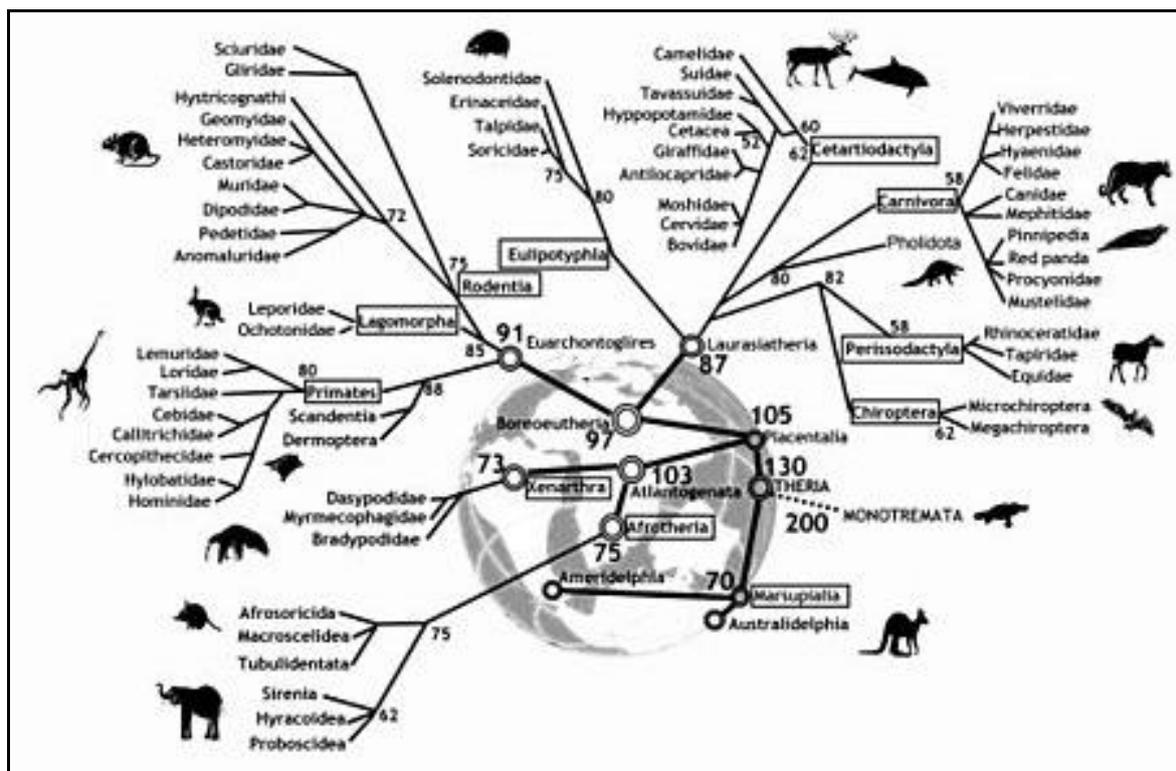


Figure 1. A phylogenetic tree of Mammalia which presents historical divergent relationships between the living orders of mammals according to a consensus view of several decades of molecular genetic, morphological and fossil inference. Double rings in the picture indicate mammalian super-taxa, while numbers indicate the probable time of divergences (Wikipedia.org 2019a from Graphodatsky et al 2011).

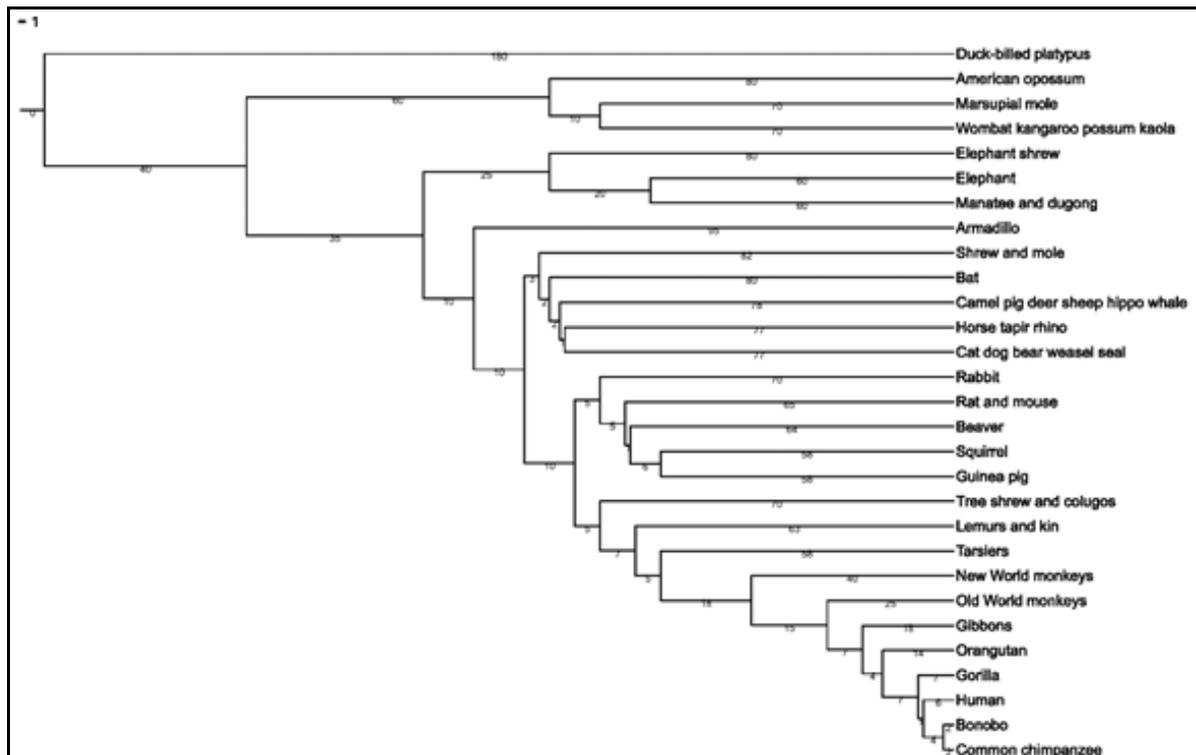


Figure 2. Another type of mammalian phylogenetic tree, based on dichotomous split (Picture by Fred Hsu, Wikipedia.org 2019b from Dawkins & Wong 2016).

The Origins of Lagomorpha. Lagomorphs first appear in the late Paleocene to early Eocene of Eurasia and North America, between about 55 and 57 million years ago (Lacher et al 2016). The fluctuation in number of genera over time was estimated on a basis of fossil records as shown in Figure 3.

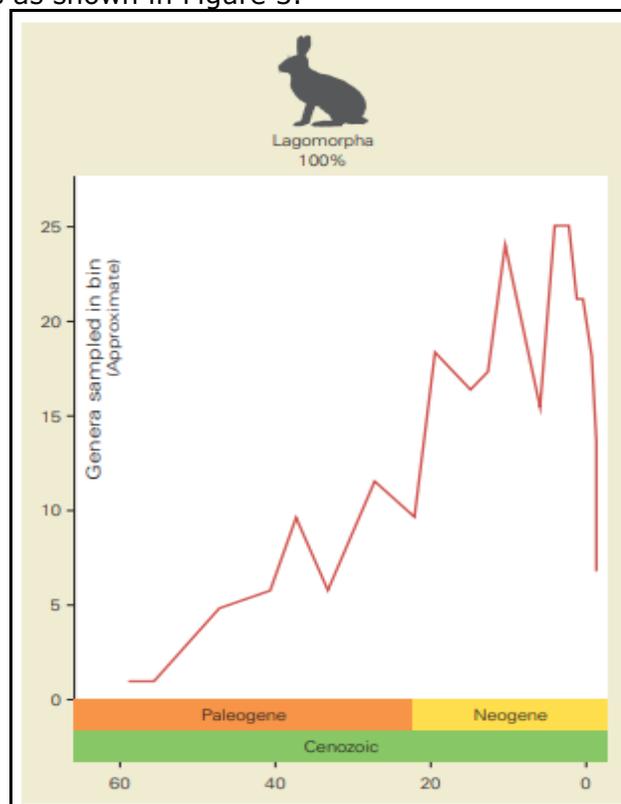


Figure 3. Number of genera of fossil lagomorphs recorded over time, grouped on geological periods. Peak generic richness appeared during the Miocene. Data were taken from the Paleobiology Database website (<https://paleobiodb.org/navigator/>) (see also Lacher et al 2016).

The phylogeny of the lagomorphs is not yet fully elucidated, but rather the older and less probably presumptions are replaced by others, better scientifically substantiated and which seem more probable. This situation is the same in terms of origins of Lagomorpha, but also in terms of phylogeny of the sub-ordinal clades (Figure 4). Until several decades ago, it was generally accepted that *Eurymylus* spp. (e.g. *Eurymylus laticeps*), which lived in eastern Asia and date back to the late Paleocene or early Eocene, were ancestors of the lagomorphs (Palmer 1999). Further studies and careful analysis of available fossils suggest that Lagomorpha may have instead descended from the group of mimotonids (Anagaloidea), while *Eurymylus* spp. were more closely related to Rodentia (Palmer 1999).

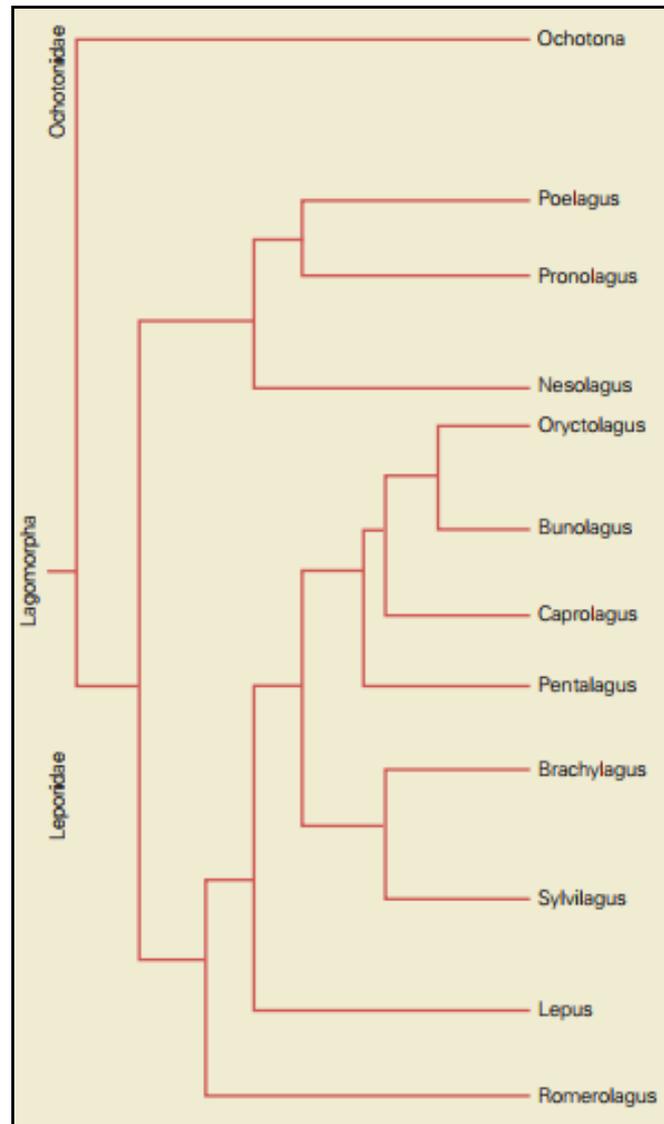


Figure 4. A likely hypothesis upon the phylogeny of genera included in Order Lagomorpha (Lacher et al 2016). Important to note that we can find in literature for this group different variants of hypothetical phylogeny and none of them is unanimously accepted.

The diversity of Lagomorphs was certainly higher in the past than in the present, with around 75 genera and more than 230 species represented in the fossil record and many more species in a single biome. These statistics of fossil record are evidences supporting that lagomorph lineages are declining in the present times (Lacher et al 2016).

A recent research of Rose et al (2008) suggests an Indian origin for the clade. They assume that the group of lagomorphs evolved in isolation on Indian continent in the Paleocene, when India was a separate island. The joining of the island (India) to the

Asian continent, as a result of translation, released the lagomorphs, which spread to the neighboring continents.

The leporid group emerged in the late Eocene and rapidly spread throughout the Northern Hemisphere, following an adaptive radiation; they showed a trend towards increasingly long hind limbs as the modern leaping gait developed (Savage & Long 1986). Elongation of the hind limbs is not a unique adaptation observed only in lagomorphs, but the way they use them in movement is an original one.

The other clade of lagomorphs, pikas, appeared later, somewhere in the Oligocene period, in eastern Asia (Savage & Long 1986), and followed a series of successive diversifications. The most notable adaptive radiation was the one from Pleistocene (Mohammadi et al 2018).

Origins of the Family Leporidae. According to the opinion of Lacher et al (2016), which is slightly different from that of Savage & Long (1986), the family Leporidae (hares and rabbits) likely originated in Asia during the Eocene and diversified into both North America and Asia during the time-span of two epochs, Oligocene and Miocene. Among the early Eurasian leporid genera we can mention: *Lushilagus*, *Shamolagus*, *Dituberolagus* and *Strenulagus*. The early known North American fossil genera of Leporidae are *Megalagus*, *Mytonolagus* and *Tachylagus*.

Leporid species remained restricted to the Northern Hemisphere until the Miocene-Pliocene transition, when they spread to Africa and South America. Their largest adaptive radiation in the late Miocene may have been associated with the expansion of lush meadows during the early Neogene (in Miocene) (Lacher et al 2016).

The largest known leporid (a fossil leporid), the giant *Nuralagus rex*, weighing about 12 kg (Figure 5), was present on the island of Minorca, in the Mediterranean Sea, until the late Pliocene (Lacher et al 2016). In the absence of predators on the island, it became massive; it probably walked and could not hop (Lacher et al 2016).

The living genera of the Family Leporidae emerged in the early Miocene, with the two most diverse genera, Genus *Lepus* (hare species) and Genus *Sylvilagus* (cottontail rabbits) (Ruedas 2017; Silva et al 2019; Kim et al 2019), first recorded in the fossil deposits dating back about 8.6 and 7.2 million years ago, respectively. Then a diversification of their morphology, anatomy, physiology and ecology followed (Lacher et al 2016).

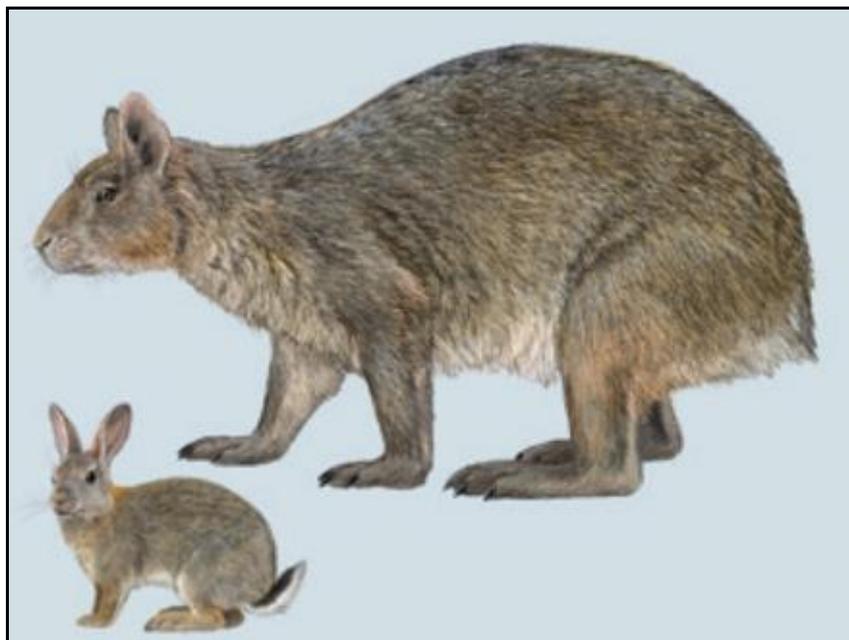


Figure 5. Reconstitution of the giant fossil leporid *Nuralagus rex* (above), alongside a modern European rabbit (*Oryctolagus cuniculus*) (Lacher et al 2016).

Phylogeny of the Genus *Oryctolagus*. The genus *Oryctolagus* comprises a single species (*O. cuniculus*) and six subspecies. However, subspecies are no longer considered valid taxa for Zoology.

The European rabbit is a species native to south-western Europe (Spain, Portugal, and France) and to north-west Africa (Morocco, Algeria) (Oroian et al 2014). However, it is present wide world due to multiple escape in the wild and successive introductions for hunting purposes (Oroian et al 2014; Petrescu-Mag 2018).

As discussed above, the origins of the genus *Oryctolagus* have not been elucidated. We can only present a new set of three hypotheses of possible scenarios (Figure 6).

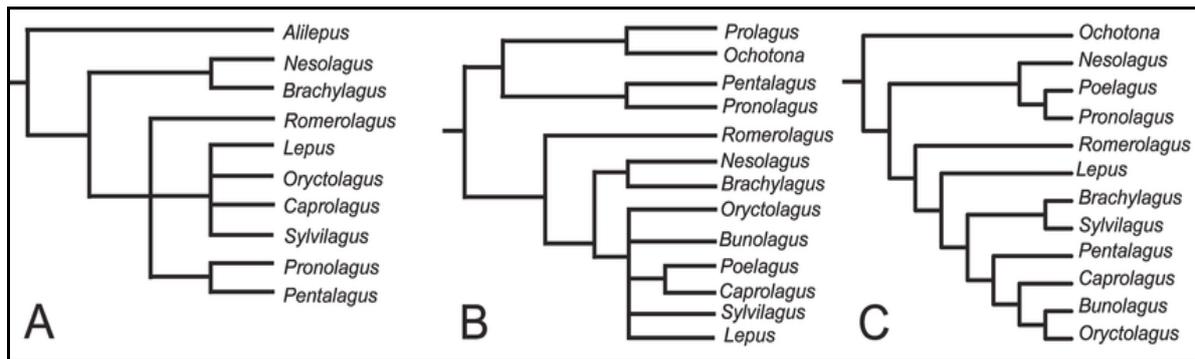


Figure 6. Generic phylogenetic hypotheses of living species of Lagomorpha. A - adapted from Dawson (1981); B - adapted from Stoner et al (2003); C - adapted from Matthee et al (2004) (source: Ge et al 2015).

Origins of the Domesticated Breeds. The history of rabbit domestication is quite unknown. Watson (2019) concluded in his recent study that rabbits were already being deliberately bred in the 4th century BC and probably in the 1st century AD as well. There are over 100 breeds domesticated rabbit breeds, with numerous fancy varieties for show and meat production lines, all descending from the European rabbit (*O. cuniculus*) (Naff & Craig 2012). Some rabbit breeds are ancient (Bud et al 2011), while others are newer (Petrescu-Mag et al 2009, 2011a, 2014; Botha et al 2013). Some breeds are genetically improved for excellent meat production and/or large litters and/or better lactation (Andreji & Fik 2018), while others are excellent for extensive or backyard farming (Petrescu-Mag et al 2011b,c, 2012). Some breeds are kept mainly for show purposes (Petrescu-Mag et al 2016), while some rabbit strains are bred mainly and continuously improved for meat production.

Let us not forget that the rabbit is one of the most important laboratory animals, hardy, with good adaptability for keeping under limited space conditions and with accessible food resources.

The paradox of this species is that, although the group it belongs to is in decline, the European rabbit is a species with an extraordinary plasticity, giving birth to a multitude of breeds and varieties of shape and color.

Conclusions. Order Lagomorpha is a group of mammals that splits into two living families: Leporidae and Ochotonidae. Lagomorpha may have descended from the group Anagaloidea. Diversity of Lagomorphs was certainly higher in the past than it is now, with around 75 genera and more than 230 species represented in the fossil record. These data are evidences supporting that lagomorph lineages are declining at present times. The living genera of the Family Leporidae emerged in the early Miocene, with the two most diverse genera *Lepus* and *Sylvilagus*, first recorded in the fossil deposits dating back to approximately 8.6 and 7.2 million years ago, respectively. The literature is scarce regarding the phylogeny of Genus *Oryctolagus*. The genus *Oryctolagus* comprises a single species (*O. cuniculus*) and six subspecies, and is the ancestor of all domesticated breeds. The paradox of this species is that, although the group it belongs to is in decline, the

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Received: 29 October 2019. Accepted: 23 November 2019. Published online: 27 December 2019.

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How to cite this article:

Petrescu-Mag I. V., Păpuc T., Oroian I., Botha M., 2019 A review of the phylogeny of the European rabbit (*Oryctolagus cuniculus*). *Rabbit Gen* 9(1):1-9.