

# How and when did Old World ratsnakes disperse into the New World?

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## Abstract

To examine Holarctic snake dispersal, we inferred a phylogenetic tree from four mtDNA genes and one scnDNA gene for most species of the Old World (OW) and New World (NW) colubrid group known as ratsnakes. Ancestral area distributions are estimated for various clades using divergence–vicariance analysis and maximum likelihood on trees produced using Bayesian inference. Dates of divergence for the same clades are estimated using penalized likelihood with statistically crosschecked calibration references obtained from the Miocene fossil record. With ancestral areas and associated dates estimated, various hypotheses concerning the age and environment associated with the origin of ratsnakes and the dispersal of NW taxa from OW ancestors were tested. Results suggest that the ratsnakes originated in tropical Asia in the late Eocene and subsequently dispersed to the Western and Eastern Palearctic by the early Oligocene. These analyses also suggest that the monophyletic NW ratsnakes (the Lampropeltini) diverged from OW ratsnakes and dispersed through Beringia in the late Oligocene/early Miocene when this land bridge was mostly composed of deciduous and coniferous forests.

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## 1. Introduction

Investigating faunal exchange between the New (NW) and Old World (OW) continents of the Holarctic Region in the Tertiary relies upon explicit tests of dispersal hypotheses as continental positions were roughly in the same orientation as they are today. During the mid-to-late Tertiary, two major routes for this exchange existed, either trans-Atlantic or trans-Beringian (Pacific). Examination of the frequency of route use by 57 extant nonmarine animal species suggests that trans-Atlantic routes were most common during the early–mid Tertiary (70–20 mya) and trans-Pacific paths of faunal exchange were more common during the late Tertiary (20–3 mya; [Sanmartin et al., 2001](#)). Assessing the direction of these exchanges suggests that

movements either from the OW to the NW or from the NW to the OW were equally common across many animal groups. These trends were summarized mainly for the following groups of animals: crustaceans, insects, arachnids, teleost fishes, birds, and mammals ([Sanmartin et al., 2001](#)).

Although snakes of individual families and subfamilies (Colubrinae, Elapidae, Natricinae, and Viperidae) are found across the Holarctic Region, literature explicitly examining areas of origin of these groups and the dates and routes of dispersal from areas of origin does not exist ([Lawson et al., 2005](#)). This is surprising given that these families and subfamilies dominate the snake fauna of the Holarctic Region ([Pough et al., 2004](#)). In this paper, we examine the area of origin, dates of origin, area of dispersal, and dates of dispersal for one of the most well-known and conspicuous groups of the holarctic snake fauna, the ratsnakes. For this group, we infer the phylogeny, assess ancestral areas of origin, and use key internal-node divergence dates to investigate the areas and date of origin of the holarctic ratsnakes.

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The ratsnakes are currently represented by 19 genera that have a holarctic and oriental distribution. Once considered members of a single genus, *Elaphe*, the ratsnakes have recently been divided into a number of OW and NW genera. In the OW are the genera *Elaphe*, *Zamenis*, *Rhinechis*, *Oocatochus*, *Orthriophis*, *Euprepiophis*, *Oreocryptophis*, *Coelognathus*, and *Gonyosoma*. The Western Palearctic smooth snakes, *Coronella*, are considered closely related to OW ratsnakes (Dowling and Duellman, 1978; Nagy et al., 2004; Utiger et al., 2002). Alternatively, NW ratsnakes are considered part of a monophyletic tribe, the Lampropeltini, which includes the genera *Arizona*, *Bogertophis*, *Cemophora*, *Lampropeltis*, *Pantherophis*, *Pituophis*, *Pseudelaphe*, *Rhinocheilus*, *Senticolis*, and *Stilosoma* (Dessauer et al., 1987; Dowling, 1952; Dowling et al., 1983; Dunn, 1928; George and Dessauer, 1970; Keogh, 1996; Lawson and Dessauer, 1981; Minton, 1976; Pearson, 1966; Rodríguez-Robles and de Jesús-Escobar, 1999; Schwaner and Dessauer, 1982; Utiger et al., 2002) and, as a group, appears to be related to OW ratsnakes. Therefore, in this paper we refer to the group that collectively includes the OW ratsnakes and the Lampropeltini simply as ratsnakes.

The historical processes that have shaped the distribution of these snakes may include extinction, dispersal, and vicariance (Futuyma, 2005). Using a phylogeny of the extant taxa with geographic distributions mapped onto the tree permits the inference of ancestral distributions found within internal nodes of this phylogeny. These ancestral distributions along with an estimation of time, in turn, may help to identify possible dispersal routes or vicariant events that have produced the current distribution of extant species. For taxa with a poorly known fossil record, such as snakes, using phylogenies of extant species may provide the only means to estimate the date and ancestral area of origin and subsequent trans-Holarctic dispersal events.

The study of snake evolution, where the availability and identification of fossils of modern groups prior to the Miocene is limited (Holman, 2000; Rage, 1987), underscores the need for a combined technique of estimating ancestral area and divergence time using extant taxa. Fossil representatives of the largest extant snake family, the Colubridae, prior to the Miocene are poorly known with respect to affinities with modern taxa (Holman, 2000; Rage, 1984, 1987), although fossils do indicate that this family dates back to the late Eocene in Thailand and from the early Oligocene in North America and Europe (Holman, 2000; Rage et al., 1992; Szyndlar, 1994). Evidence from the fossil record suggests that an explosive radiation in snake diversity with clear modern affinities, particularly with respect to Colubridae, occurred in the early Miocene of Europe and North America (Holman, 2000; Rage, 1987). It is presumed that relatives of modern colubrid groups must have lived throughout the Oligocene, but did not fossilize, remain undiscovered, or are improperly identified. Therefore, the fossil record alone cannot be used to determine the area and date of origin of extant colubrid groups, including the holarctic ratsnakes, with probable occur-

rence prior to the Miocene. Thus, combining ancestral area and divergence date estimation using a phylogeny of extant taxa provides the only means of identifying the area and date of origin for modern species of snakes. As stated by Near and Sanderson (2004), the taxa that necessitate molecular divergence date estimation are usually those with a poor fossil record.

Using DNA sequences of four mitochondrial and one single-copy nuclear gene from NW and OW ratsnakes, along with the European and North American Miocene colubrid fossil record (Holman, 2000; Ivanov, 2001, 2002; Rage, 1987) to calibrate rates of molecular evolution, we: (i) infer a phylogeny for the ratsnakes, (ii) assess putative ancestral areas, and (iii) estimate times of divergences at key nodes. Although generally accepted, but poorly demonstrated, we examine the assumption that the Lampropeltini are a monophyletic NW group derived from OW ratsnakes (Dessauer et al., 1987; Dowling, 1952; Dowling et al., 1983; Dunn, 1928; George and Dessauer, 1970; Keogh, 1996; Lawson and Dessauer, 1981; Minton and Salanitro, 1972; Pearson, 1966; Rodríguez-Robles and de Jesús-Escobar, 1999; Schwaner and Dessauer, 1982; Utiger et al., 2002). Provided that the Lampropeltini are monophyletic and derived from OW ratsnakes (Utiger et al., 2002), we infer the ancestral area for these groups and estimate dates of divergence from their most recent common ancestor (MRCA). With this ancestral area and divergence date information, we test two possible dispersal routes connecting the Nearctic and Palearctic: the older pre-Oligocene trans-Atlantic land bridges connecting Europe with Eastern North America (Liebherr, 1991; McKenna, 1983; Tiffney, 1985) and the more recent trans-Beringian land bridge connecting Eastern Asia with Western North America (Lafontaine and Wood, 1988; Mathews, 1979; McKenna, 1983; Nordlander et al., 1996; Tangledler, 1988). Both of these land bridges might have provided suitable habitat for snakes to cross from the OW to the NW throughout the earlier part of the Tertiary (65–45 mya; Fig. 1; Table 1). If dispersal occurred after 45 mya but prior to 14 mya, then movement across the warmer Beringia with associated suitable habitat (Pielou, 1979) appears more probable, given that the trans-Atlantic routes either no longer existed or did not provide appropriately warm habitats after this date (Fig. 1; Table 1; Sanmartin et al., 2001). This approach assumes that ancestral ratsnakes dispersing across either of these northern routes were adapted to the same environmental conditions as extant taxa that live in OW and NW northern extremes (*Pantherophis obsoletus*, *Pituophis melanoleucus*, *Lampropeltis triangulum*, *Coronella austriaca*, *Elaphe dione*, *E. longissima*, and *Oocatochis rufodorsatus*) (Arnold et al., 1978; Conant and Collins, 1991; Schulz, 1996; Staszko and Walls, 1994). Our tests also assume that divergences between OW and NW taxa did not occur prior to the Tertiary, because hypotheses of dispersal between these areas assume that the continents are roughly in the same positions as they were from the Eocene to modern times.

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