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The fossil record of *Berberis* (Berberidaceae) from the Palaeocene of NE China and interpretations of the evolution and phytogeography of the genus

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ABSTRACT

Extant *Berberis* is a member of the basal eudicots with a South America (group *Australes*)-Old World (group *Septentrionales*) disjunctive distribution pattern. Different hypotheses have been proposed to explain the formation of this pattern. Recent molecular studies suggest that this pattern was caused by a vicariance event in the Cretaceous. More fossil evidence is required to evaluate these hypotheses. Here a new species of *Berberis* from the Palaeocene Wuyun flora is established based on a detailed comparison with all other fossil and related living *Berberis*. The occurrence of a Palaeocene *Berberis* in NE China and other fossil data suggest that 1) the genus originated in eastern Asia, 2) the leaf venation of the genus probably evolved from pinnate to acrodromous, leaf margins from densely spinose teeth to only occasionally toothed or even entire, 3) the genus would appear to have migrated from eastern Asia to North America in the Oligocene, via Beringia. *Berberis* probably arrived in Europe from Asia during the late Oligocene when Eurasia was reunited after the retreat of the Turgai Straits. *Berberis* could have migrated to India from eastern Asia, arriving before the last major upheaval of the Himalayas in the Pleistocene.

1. Introduction

Berberis s. str. (true *Berberis*, Berberidaceae), a member of the basal eudicots (A.P.G. II, 2003), has ca. 500 living species that are shrubs, with single or 3–5 branched spines on the stems and branches; simple leaves (Ahrendt, 1961; Cronquist, 1981; Whetstone et al., 1997; Ying and Chen, 2001); short petioles, elliptic, ovate, obovate or oblong blades, pinnate (Yu and Chen, 1991; Landrum, 1999), acrodromous (Ramirez and Cevallos-Ferriz, 2000) and actinodromous (Landrum, 1999) venation; racemes, umbels or solitary flowers; flowers 3-merous with 6 petals, and 6 stamens; berries with 1–10 seeds, which are tan to red-brown or black (Ahrendt, 1961; Cronquist, 1981; Whetstone et al., 1997; Ying and Chen, 2001).

The genus with a South American-Old World disjunctive distribution is divided into two groups: *Septentrionales* Schneider and *Australes* Schneider (Schneider, 1905). The group *Septentrionales* (Old World, mainly Asia) consists of ca. 300 living species that have red berries, 1–3 (–5)-fold spines, yellow flowers and edentate stamens (Ahrendt, 1961; Landrum, 1999). Most species of *Septentrionales* occur in Eurasia, except for two in North America and four in North Africa (Ahrendt, 1961; Landrum, 1999). The group *Australes* (South America) contains about 200 living species that have black berries, foliaceous spines, deep orange flowers and dentate stamens (Ahrendt, 1961; Landrum, 1999). Most species of the *Australes* occur in South America with a few in Middle America (Ahrendt, 1961; Good, 1974; Landrum, 1999).

A recent molecular study supports the treatment of two groups within *Berberis* based on the internal transcribed spacer (ITS) sequences (Kim et al., 2004). The ITS phylogeny suggests this pattern was formed by a vicariance event in the Cretaceous.

Berberis-like fossil remains are usually preserved as leaves in the Oligocene to Pleistocene sediments of Northern Hemisphere, i.e. the Oligocene sediments of western USA and Mexico in North America, the Upper Oligocene sediments of France and Hungary, Miocene sediments of Germany, Czech Republic, Russia, Serbia, Bulgaria, Romania, Hungary, Greece, Austria, and Pliocene sediments of France in Europe; and the Miocene sediments of Hokkaido, Japan and Pleistocene sediments of Kashmir of India in Asia (see Appendix A).

Ramirez and Cevallos-Ferriz (2000) proposed the hypothesis of a North American origin of *Berberis* based on their fossil finds, and

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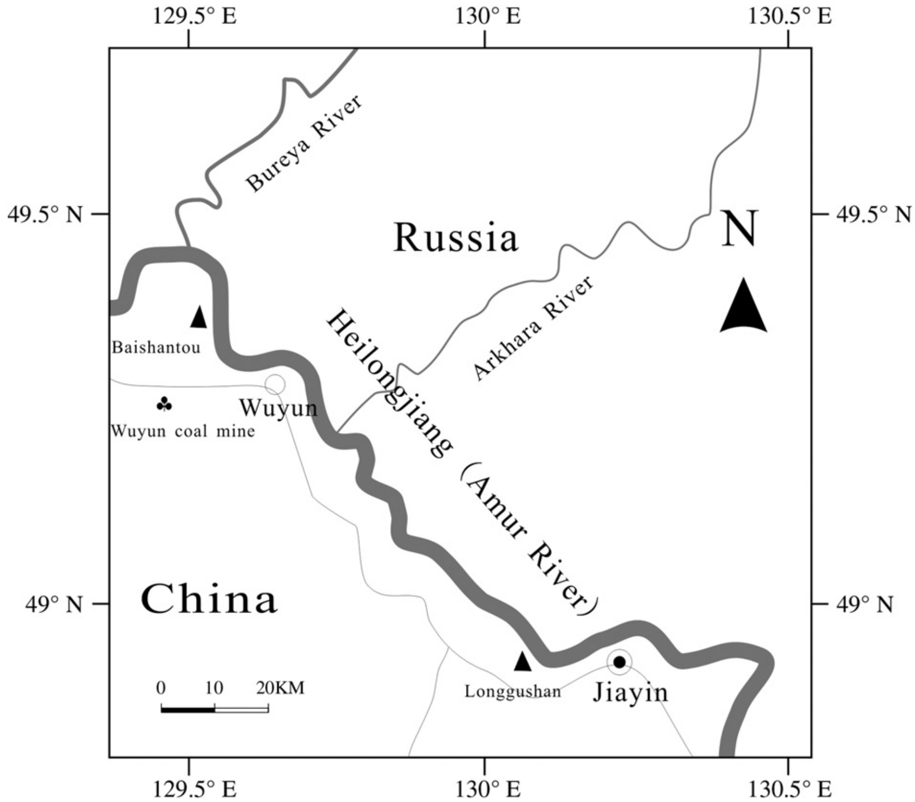

Fig. 1. Map showing the fossil locality of *B. wuyunensis* sp. nov.

inferred that it subsequently migrated to South America and Asia during the Tertiary.

In this article, we establish a new species of *Berberis* from the Palaeocene of NE China, compare it to fossil and living *Berberis*, and describe the leaf morphological evolution and potential migration routes of *Berberis* during the Cenozoic.

2. Materials and methods

The fossil leaf specimen described here was collected from the sediments of the Wuyun Formation at the Wuyun coal mine, Jiayin County, Heilongjiang Province, NE China (Fig. 1, 129°28′ E; 49°14′ N). It is preserved as an impression in a matrix of gray-yellow sandy mudrock. The age of the Wuyun Formation is regarded as Danian, Palaeocene (Luo et al., 1983; Xiong, 1986; Liu, 1990; Liu et al., 1999; Feng et al., 2000a, 2000b; Wang et al., 2001; Feng et al., 2002; Feng et al., 2003; Sun et al., 2005; Wang et al., 2006) although it has been referred to the Maastrichtian, latest Cretaceous (Hsü, 1983) or Maastrichtian–Danian (Zhang, 1983; Tao and Xiong, 1986a,b), based on lithostratigraphic and biostratigraphic grounds. Unfortunately, a more precise radiometric dating for the Formation has not yet been published (G. Sun personal communication, 2008).

The fossil leaf architecture characters were exposed by dégagement and examined under a stereomicroscope and an environmental scanning electron microscope. The herbarium sheets of *Berberis* from PE used for comparison were cleared in 10% aqueous solution of NaOH. The line-drawings were drawn using CorelDRAW 12 software. The terminology of leaf architecture follows that of the Leaf Architecture Working Group (LAWG, 1999).

The data of palaeolatitude and palaeolongitude were converted from those of latitude and longitude of fossil sites using “PointTracker for Windows” software, and plotted on 5 individual palaeogeographical maps on Projections of Lambert Equal-Area Azimuthal (North Pole) by using ArcView GIS 3.2 software. The maps cover 5 time intervals, i.e. Palaeocene (ca. 60 Ma), Oligocene (ca. 30 Ma), Miocene (ca. 14 Ma) from Scotese (1997), Pliocene (ca. 3 Ma) and Pleistocene (ca. 1 Ma) from PointTracker software.

3. Results

3.1. Systematics

Order	Ranunculales
Family	Berberidaceae
Genus	*Berberis* Linné 1753
Species	*Berberis wuyunensis* Y. L. Li, Z. Kvaček, D. K. Ferguson, Y. F. Wang, C. S. Li, J. Yang, T. S. Ying, A. G. Ablaev et H. M. Liu. sp. nov.

3.1.1. Description of fossil material from the Wuyun Formation

Leaf simple, symmetrical, blade oblong, more than 3.5 cm, about 4 cm in length, 1.3 cm in width; laminar L:W ratio ca. 3:1 (Plate I, 1). Leaf margin serrate, with simple spinose teeth (Plate I, 1; Plate II, 1–2; Plate III, 1; Plate IV, 1, 5; arrows a–b); each tooth 0.25 mm in length, apical side concave, basal side straight, sinuses rounded (Plate II, 1–2; Plate III, 1; Plate IV, 5); The central principal veins of tooth straight, accessory veins connivent with principal veins (Plate II, 2; Plate III, 1; Plate IV, 5), tooth apex spinose (Plate II, 1–2; Plate III, 1). Leaf apex rounded (Plate I, 1). Leaf base cuneate inferred from the basal trace of venation (Plate I, 1; Plate IV, 1). Venation pinnate (Plate I, 1; Plate IV, 1). Primary vein thick, straight or slightly curved (Plate I, 1; Plate IV, 1). Secondary veins with festooned brochidodromous venation, 4 pairs diverging at an angle of 10°, 18°, 18° and 25° from base to apex, looping with upper secondary veins (Plate I, 1; Plate IV, 1). Secondary vein spacing increasing toward base (Plate I, 1; Plate IV, 1). Inter-secondary veins simple, fusing with secondary veins (Plate I, 1; Plate IV, 1). Tertiary veins forming a randomly reticulate pattern, tertiary vein angle