Reconstructing Origin, Speciation and Migration of *Berberis* Species across Karakoram Mountain Ranges, Pakistan: A Novel Phytogeographic Hypothesis

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Abstract: Genus Berberis (Berberidaceae), a worthwhile plant taxon used for treating different forms of cancer, hepatic disorders, cardiovascular anomalies and bone healing. Its phylogeny, taxonomy, speciation and migration across continents and intra-continent are uncertain. Many scientists believe in a North hemispheric origin followed by a Southward migration. Present study deals with migration and speciation of Berberis within Asia and revealed a Northward migration and speciation within Karakorum Mountain Ranges, Pakistan. This phenomenon has occurred during late Oligocene period. Endemism and morpho-molecular affinity of *B. pseudumbellata* ssp. *gilgitica* to other closely related Berberis species found in Himalaya provide a strong justification infavour of the hypothesis.
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Introduction

Origin of simple-leaved Berberis has not got an end and still there are certain confusions. Most of the researchers are with the consensus that it (Ranunculeae) has a Northern Hemisphere origination during Eocene (56 to 33.9 million years) period (**Emadzade and Hörandl, 2010**). Similarly, in view of Ahrendt (1961) it has Eurasian origin contrast to the compound-leaved Berberis, which exhibit a North American origin followed by a subsequent migration towards Eurasia i.e. China and Himalaya. Adhikari (**2010**) also seems infavour of Ahrendt (**1961**) for his ideas of its origin from compound-leaved Berberis (Mahonia).

Based on the fossil record (Table 1) and its occurrence of Palaeocene (66 to 56 million years ago) in North-Eastern China, Li et al. (**2010**) believe that Berberis is originated in Eastern Asia and migrated to North America during Oligocene (33.9 million to 23 million years) (**Li et al., 2010**). Simple-leaved Berberis fossils have been recorded from Oligocene sediments (table) from Upper Hyanes Creek (Idaho) (**Axelrod, 1998**) and from Puebla, Mexico (**Ramirez and Cevallos-Ferriz, 2000**). It is also believed that besides migration of several plant and animals, such a migration of Berberis happened between continents through land bridge, birds, fish, marine mammals and wind. There would have been more such land bridges but Beringia (now Bering Straits) is latest in geological history (Figure 1).

Some 21,000 years ago, the bridge (Beringia) once formed a flat, grassy treeless plain stretching one thousand miles wide area (see figure) from north to south across two continents (**NPS, 2015**). The modern distribution of plant species between Eastern Asia and North America reflects migration, speciation, and extinction since the last glacial period (**Milne, 2004**).

Berberis fossils documented from Hokkaido, Japan belong to Miocene (23.03 to 5.332 million years) (**Tanai, 1961**). Fossils reported from Kashmir (India) are Pleistocene (2.6 million to 11,700 years ago) sediments (**Puri, 1947**). Berberis probably reached India from eastern Asia before the last major upheaval of the Himalayas in the Pleistocene (**Li et al., 2010**).

Berberis arrived in Europe from Asia during the late Oligocene (**Li et al., 2010**). Berberis leaf fossils from late Oligocene and Miocene have been documented in Europe (**Kvacek and Erdei, 2001; Kovar-Eder et al., 2004**). Which are similar to the present day Berberis growing in the Himalayas and Eastern Asia (**Kvacek and Erdei, 2001; Kovar-Eder et al., 2004**).

Origin of the simple-leaved Berberis species might have happened in Eurasia or in North America which will be comprehendible with further geological explorations and documentation of fossils along with more precise dating are necessary to confirm their place of origin (**Adhikari, 2010**). Moreover, the South American simple-leaved Berberis diversification took place before the union of North and South America (**Ahrendt, 1961**). According to Adhikari (**2010**), the South American Berberis species may have been dispersed from Eurasia. However, the possibility of its dispersal from North America to South America, with subsequent extinction in North America cannot be completely

ruled out (**Adhikari, 2010**). In 2000, Ramíreza and Cevallos-Ferriz supported hypothesis of North American origin of Berberis and its migration towards South America (**Ramíreza and Cevallos-Ferriz, 2000**).

Table: Various fossil records and its documentation according to their age, oldest first.				
Series	Geological Time Period	Period in years	Continent	Area
1	Palaeocene	66 to 56 million years ago	Asia	NE China
2	Oligocene	33.9 to 23 million years	North America	North America
3	late Oligocene	33.9 to 23 million years	Europe	Europe
4	Miocene	23.03 to 5.332 million years	Asia	Hokkaido, Japan
5	Pleistocene	2.6 million to 11,700 years ago	Asia	Kashmir, India

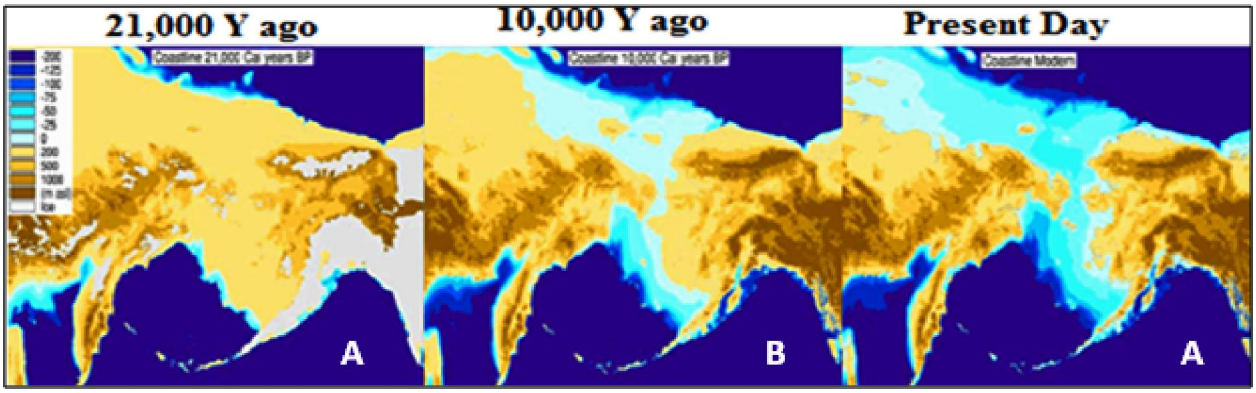

Figure 1: Land connectivity between two continents through Beringia and potential migration of flora and fauna. **A**). During 21,000 years ago Beringia showing connected continents at least 200 m above sea level. **B**). Beringia around 10,000 years ago shows disconnect and submerge at least 50 m deep. **C**). Beringia with Bering Straits and two continents totally disconnected.

Material and method

Geography: Present study deals with the migration and speciation of Berberis across Karakoram Mountain Ranges of Pakistan.

Literature: Composition of this review mostly relies on the print and online available publication and databases of the world.

Results

Hypotheses regarding Origin of Berberis: Since Ahrendt (**1961**), many researchers have attempted to resolve the question of origin of Berberis, its timeframe and location. Various supporting tools and techniques have been used including fossil records, cpDNA, ITS, palynolgical studies, morphological indices and different statistical tools to trace out phylogenetic roots, linkages and lineage. All these hypotheses can be grouped into four major proposed centres of origin (Figure 2). These are as following;

1. Eurasia: Ahrendt (**1961**) and Adhikari (2010) are more infavour of Berberis origin in Eurasia.

2. South America: In view of Kim et al. (**2004**), Berberis species might have originated in South America.

3. North America: Several researchers including Axelrod (**1987**), Axelrod (**1998**), Adhikari (**2010**), Kvacek and Erdei (**2001**), Kovar-Eder et al. (**2004**) and Ramíreza and Cevallos-Ferriz (**2000**) suppose its origin in North America.

4. East Asia: In 2010, Li et al. suggested its origin in North-East China. Their supposition is based on the fossils documented from Palaeocene (66 to 56 million years ago). (See figure with its proposed dispersal route).

Hypotheses of Berberis Migration: Various researchers have proposed origin and migration hypotheses which can be grouped into seven major migration routes or phytogeographic locations (Figure 2). These are described here below;

1. Eurasia to South America
2. Eurasia to North America
3. South America to Eurasia
4. North America to Eurasia
5. North America to Eurasia and South America
6. North America to South America
7. East Asia to North America

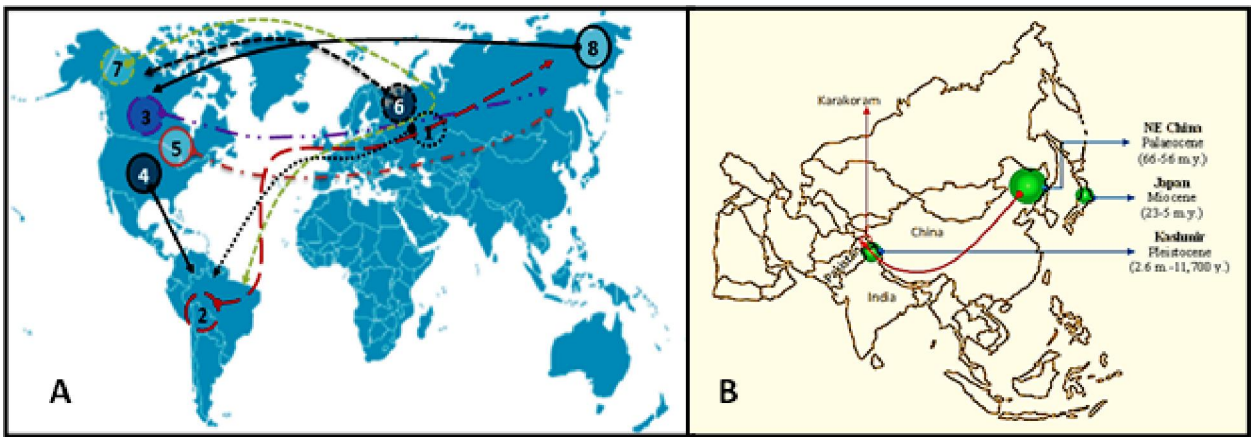

Figure 2: **A):** Various hypotheses and subsequent migration across the globe. Numbers express various hypotheses on biogeographic spread of Berberis s.s. across the globe from its origin. Arrow start and ending and passage do not reflect the exact place of origin, arrival and route but continents. 1) Ahrendt (1961), Adhikari (2010), origin Eurasia; 2) Kim et al. (2004b), origin South America; 3) Axelrod (1987) and Axelrod (1998b), origin North America; 4) Adhikari (2010), Ramíreza and Cevallos-Ferriz, 2000; 5) Kvacek & Erdei (2001) and Kovar-Eder et al. (2004); 6) Ahrendt (1961), Adhikari (2010), Origin: Eurasia; 7) Adhikari (2010) origin North America, Route: North America-Eurasia-South America; 8) Li et al. 2010. **B)**: Fossil record and potential migration in Asia

Origin of Karakoram and Diversification of Berberis: The Karakorum is one of the greater Mountain Ranges in Asia (**BBC, 2015; WikiK2, 2015**) stretching over an area of 700 km long and more than 100 km width (**UNESCO, 2015**). It lies to the southeast of the Pamir and to the northwest of the Tibetan Plateau, along the international boundary of China and Pakistan, India and Kashmir (**WikiK2, 2015; UNESCO, 2015**). They are the highest mountains in the world except for the Himalayas. They have a length of more than 700 km and a width of more than 100 km. it covers regions of Gilgit-Baltistan (Pakistan) in the West, Xinjiang region (China) in the North-East and Ladakh (India) in the East (**WikiK2, 2015**). It is home to the highest concentration of highest peaks over 8000 m to be found anywhere on earth (**BBC, 2015**) including K2, the second highest peak in the world with a height of 8,611 m (28,251 ft). It is the most heavily glaciated region of the world outside poles (**Richardson and Reynolds, 2000**).

Around 60-50 Myr ago Indian plate collided with Eurasian plate (**Searle et al., 2010; Upadhyay et al., 2004; Rowley 1996; Beck et al., 1995**). This resulted into subduction of Indian plate and buckling up of its upper crust around 45-35 Myr ago (Figure 3). During this phenomenon, migration of a variety of Eurasian fauna to the Indian landmass (**Adhikari, 2010; Valdiya, 2002**). Many plants including species of Caragana and Chenopodiaceae exhibiting Central Asiatic affinity exist in the arid region of the western Himalaya (**Gupta, 1994**). Himalaya being more or less parallel or nearly converging mountain chains, migrations would not have been in a straight line from north to south but would have followed the river systems (**Yoshida, 2006**). According to Qiao et al. (**2007**) Cedrus having Eurasian origin migrated southward to Himalaya during Tertiary climatic oscillations. Assam-Asia contact, which is also known as the Assam Gateway established during Eocene was most important pathway for the migration and interchanges of flora between plates (**Mani, 1974**). However, briskly up-rise of Himalaya in Miocene (9-7.5 Myr ago) caused disruption of wind circulation and culminating in the onset of monsoon leading to climatic changes (**Valdiya, 2002**). The Karakoram region is species-poor exhibiting arid Central-Asian and Tibetan elements (**Peer et al., 2007**).

Fossil records are an important source of phytogeographic origin and migrations. Berberis fossils documented from Indian Kashmir belong to Pleistocene sediments (**Puri, 1947**). However, relatively poor understanding of Karakoram geology does not allow us to construct linkage and lineages. Moreover, occurrence of fossilized coal and carbonaceous shale at Chipursan, Hunza (**Donnelly, 2004**) may provide some insights regarding geological information and subsequent migration of flora. In southwestern Asia desert xerophytes of Berberidaceae originated in response to the beginning of dry climate at different times (**Wang et al., 2007**).

Features of New Hypothesis: Fingerprinting using molecular marker techniques have proven valuable for tracing origin and population structure of invasive plants (**Mueller and Wolfenbarger, 1999**).

Based on the available phytogeographic, geological, nuclear DNA characterization, ITS (**Wang et al., 2007**), cpDNA sequencing information available does not support a migration of Berberis from Eurasian-Himalaya migration (particular in case of Karakoram). There are some major reasons for this hypothesis;

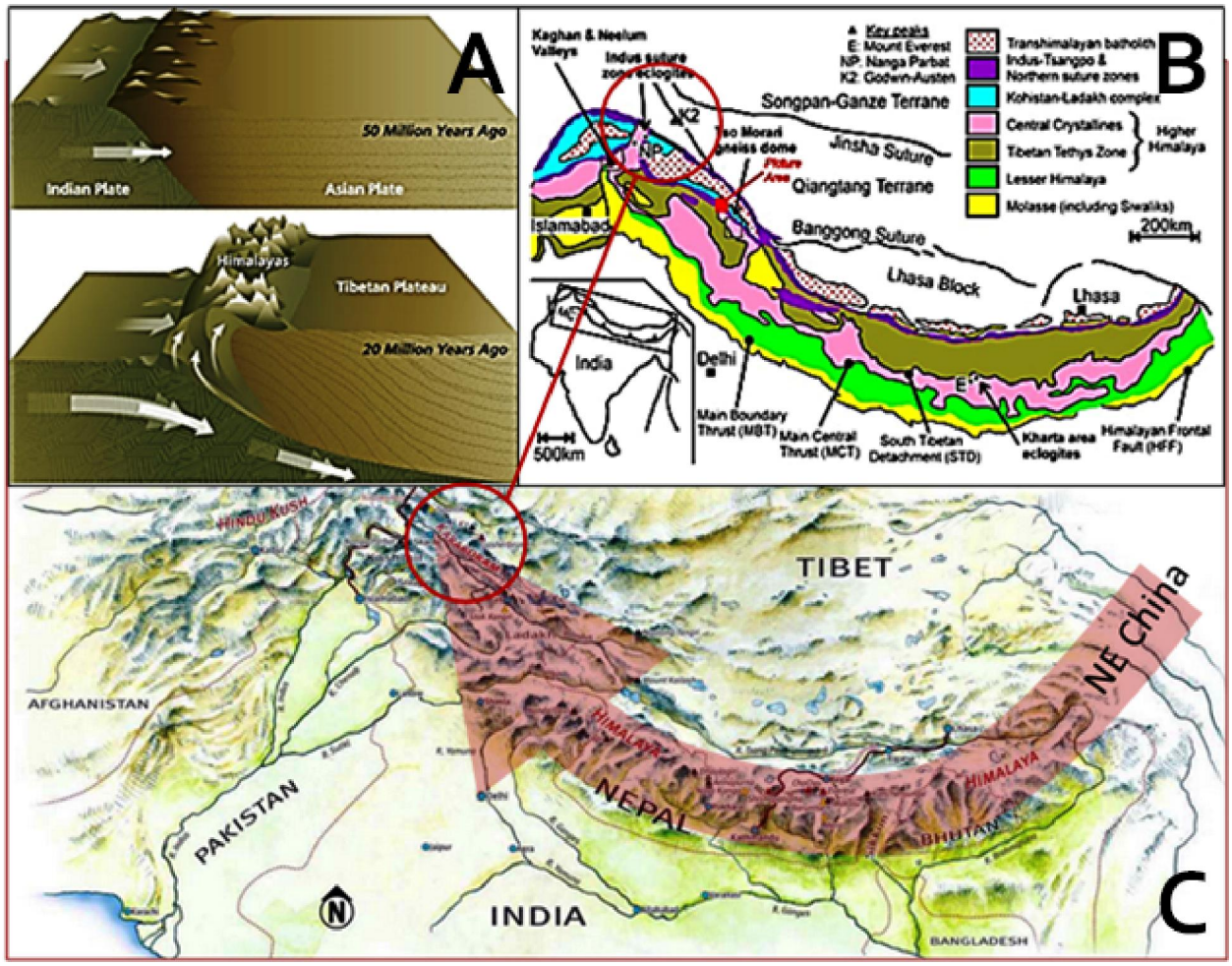

Figure 3: A) llustration by Jayne Doucette (Clif, 2004) | **B**) Karakoram-Himalayan geology [modified after O'Brien, 2011 | **C):** Map of the Mountain of Asia (Modified after Derrick, 2008)

1) Before Himalayan up rise, there might have been already few Berberis species in the area. Based on the present day area coverage of Berberis species, we assume that during late Oligocene (30-20 Myr ago) B. lycium and B. pseudumbellata were existing.

2) Twenty million years ago when Himalayan up rise was high enough blocking monsoon increased level of precipitation on the southern side leaving northern part dry and less precipitated (Figure 3). Moreover, few dispersed plants of B. pseudumbellata faced further disconnect due to elevation stratification and went under speciation. Those left at higher altitude transformed into subspecies B. pseudumbellata subsp. gilgitica and at lower altitude changed into B. pseudumbellata subsp. pseudumbellata. At present, their geographic locations are different and along altitude, they remain away from each other at least at a 500 m height. According to Bottini et al. (**2007**) ITS sequences of Berberis species, together with morphological, biochemical, AFLP (amplified fragment length polymorphism), and cytological characterizations data, support the existence of diploid and polyploid hybrid speciation in the genus. The diversification of some groups appears to have been triggered by the active uplift phase of the Himalaya during the Miocene (**Adhikari 2010**).

3) At present, subspecies *B.p. subsp. gilgitica* is endemic to Gilgit-Baltistan and B. pseudumbellata

subsp. pseudumbellata is the only link with rest of the Himalaya.

4) To trace any link with Central Asia, land accessibility was quite limited due to its glaciation and high elevation except possibility of its migration through migratory birds which is very poor to justify its dispersal. Seed dispersal via birds is less comprehendible because migratory birds fly during winters when neither Berberis berries nor seeds available at that time.

5) In its generic sense, Berberis might have entered into Indian subcontinent from NE of China but in particular case of Karakoram, Berberis migration from Himalaya upward Karakoram seems probable.

Discussion

There is scarcity of biogeographic information on Karakoram flora and this is first of its nature. In view of Adhikari (**2010**), no phylogenetic biogeographic study on Himalayas has been published so far and publications are mainly based on modern-day plant distribution patterns. Moreover, further documentation of fossils, which has never been carried out in Karakoram, will reveal more information to make any logical and reliable opinion. Furthermore, DNA based phylogenetic investigation of Berberis species will also be helpful to address questions related to its distribution and migration.

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