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Fagaceous foliage from the latest Cretaceous of the Koryak Upland (northeastern Russia) and its implications for the evolutionary history of Fagaceae

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ABSTRACT

The first record of the genus *Fagopsiphyllum* (Fagaceae) from the Maastrichtian Kakanaut Formation of the Koryak Upland, northeastern Russia, is described and compared to other recorded of Fagaceae and fagaceous-like leaves from the Cretaceous and Paleogene of the Northern Pacific Region. The distribution and morphological variability of *Fagopsiphyllum groenlandicum* are investigated. *Fagopsiphyllum groenlandicum* leaves resemble mainly the foliage of the extinct genera *Fagopsis* and *Barykovia*. New finding of *Fagopsiphyllum groenlandicum* extends the stratigraphic range of this taxon and contributes to the Cretaceous morphological diversity of extinct leaf forms assigned to Fagaceae. Taxonomic position of *Fagopsiphyllum* is discussed.

1. Introduction

The family Fagaceae currently includes ten recognized genera (*Fagus* L., *Castanea* Miller, *Castanopsis* Spach, *Chrysolepis* Hjelmquist, *Colombobalanus* Nixon et Crepet, *Formanodendron* Nixon et Crepet, *Lithocarpus* Blume, *Quercus* L., *Trigonobalanus* Forman, *Notholithocarpus* Manos, Cannon et Oh) and about 600–1100 species (Nixon, 1997; Govaerts and Frodin, 1998; Huang et al., 1999; Manos et al., 2001, 2008; Oh and Manos, 2008). This group is known mainly from the Northern Hemisphere, except for some genera that extend into the Southern Hemisphere (Heywood, 1993).

In spite of extensive molecular data, some questions regarding the phylogenetic relationships of recent Fagaceae are still unresolved (Manos et al., 2001, 2008). Possibly this is due to the existence of many extinct lineages, which cannot be analyzed. Therefore, the knowledge on fossil members of Fagaceae is necessary for a reconstruction of real history of this family.

The representatives of Fagaceae started playing an important role in the vegetation from the beginning of the Paleogene. The earliest unequivocal fossils of modern genera, confirmed by findings of cupules and nuts, are known from the lower Eocene (*Quercus*, Kvaček and Walther, 1989; *Fagus*, Manchester and Dillhoff, 2005). Besides, several extinct genera, based on leaf and fruit remains, have been described from the Paleocene and the lower Eocene: *Dryophyllum* Debey ex Saporta, *Eotrigonobalanus* Walther et Kvaček, *Trigonobalanopsis* Kvaček et Walther, *Fagopsis* Hollick, *Fagopsiphyllum* Manchester, *Contracuparius* Nixon et Crepet, *Pseudofagus* Smiley et Huggins (Denk and Grimm, 2010).

The Cretaceous records of Fagaceae remain sparse. Flowers and pollen are known from the Santonian of North America (Herendeen et al., 1995; Sims et al., 1998; Denk and Tekleva, 2014) and from the Coniacian of Japan (Takahashi et al., 2008).

Fossil leaves similar to foliage of extant Fagaceae appeared also in the Late Cretaceous. However, they have not been well documented and investigated. Therefore, our understanding of the origin and early evolutionary history of this group is still incomplete.

In this paper we describe leaves of *Fagopsiphyllum groenlandicum* (Heer) Manchester from the Cretaceous of the Koryak Upland (northeastern Russia) and compare them with fagaceous-like leaves from Cretaceous and Paleogene deposits of the Northern Pacific region. Furthermore, their affinities to other genera of Fagaceae are discussed.

Fagopsiphyllum groenlandicum was originally described as *Quercus groenlandica* Heer from Paleocene Atanekerdluk Formation of West Greenland (Heer, 1868). Later it was reported from the Paleocene deposits of the USA (Hollick, 1936; Brown, 1962), Isle of Mull, Scotland (Boulter and Kvaček, 1989), the Koryak Upland, northeastern Russia (Golovneva, 1994a), and Spitsbergen (Budantsev and Golovneva, 2009). Subsequently, Manchester (1999) formally established a genus for this species, because the confirmed remains assigned to the extant genus *Quercus* are known only from the Eocene.

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Recently *Fagopsiphyllum groenlandicum* (Heer) Manchester was found in the Maastrichtian of the Kakanaut Formation (Koryak Upland, northeastern Russia). The discovery of a common Paleocene species in the Cretaceous is of particular interest. The dominance of members of recent families such as Fagaceae, Betulaceae, Junglandaceae in fossil floras begins in the Paleocene (Manchester, 1999). However, the systematic relationships of Cretaceous taxa with fagaceous morphological affinities are still far from resolved. Detailed descriptions and comparative morphological studies of early, extinct members of Fagaceae are of particular importance for the analysis of diversity patterns.

2. Locality, stratigraphy and material

The specimens of *Fagopsiphyllum groenlandicum* were collected from nonmarine volcanogenic-terrigenous sediments of the Kakanaut Formation, exposed in the lower part of the Kakanaut River basin, in the southeastern Koryak Upland (Fig. 1).

The Kakanaut Formation is about 1000 m thick and consists of tuffaceous sandstones and siltstones, tuff, tuffites and andesibasaltic rocks (Volobueva and Terekhova, 1974), that are interpreted as lacustrine and fluviodeltaic sediments of near-shore lowlands (Volobueva and Krasniy, 1979; Godefroit et al., 2009; Shczepetov et al., 2008; Golovneva et al., 2011). The lava flows and tuff material in the sediments indicate the proximity to an active volcano. This formation overlies marine deposits containing the late Maastrichtian ammonite *Pachydiscus subcompressus* and the bivalve *Schachmaticeramus kusiroensis* (Zonova and Yazykova, 1994; Yazykova, 2004), which is in turn overlain by marine sediments of the Kokuy unit, containing a latest Maastrichtian invertebrate fauna (\Golovneva and Shczepetov, 2010). The Maastrichtian strata are covered by lower Paleogene effusive-pyroclastic deposits. A palynological assemblage from the plant-bearing layers has been attributed to the late Maastrichtian *Wodehouseia spinata* — *Aquilapollenites subtilis* Palynozone (Markevich and Bugdaeva, 1997). Thus, the age of the Kakanaut Formation can be constrained as early late Maastrichtian. This formation contains the richest Maastrichtian fossil plant assemblage of the Arctic Region (Golovneva, 1994a, 1994b, 1995) as well as dinosaur remains (Nessov and Golovneva, 1990; Godefroit et al., 2009). The fossil plant and vertebrate localities occur along the banks of several creeks flowing into the Kakanaut River (Fig. 2).

The Kakanaut floristic assemblage contains more than 50 species (Golovneva, 1994a, 1994b), including bryophytes, horsetails, ferns, cycadophytes, ginkgos, conifers and angiosperms. The prevailing groups are conifers and angiosperms. The cycadophytes (*Nilssonia*, *Encephalartopsis*) and *Ginkgo* are abundant in some layers, usually forming monodominant associations.

The conifers are represented by the families Taxodiaceae, Cupressaceae and Pinaceae as well as several genera of unknown systematic position. *Sequoia* is the most common element at the fossil sites. Angiosperms include about 30 species and the following extant families can be confidently recognized: Platanaceae (*Platanus*), Cercidiphyllaceae (*Trochodendroides*), Hamamelidaceae (*Platimelis*), Betulaceae (*Corylus*), and Rosaceae (*Peculnea*, *Arctoterum*). The other genera, such as *Celastrinites*, *Cissites*, *Liriophyllum* and *Kakanautia*, appear to belong to ancient groups, exhibiting no clear phylogenetic links to modern taxa.

The Kakanaut flora belongs to the Gornorechenian floral stage of the Anadyr palaeofloristic province (Golovneva, 1994a, 1994b, 1998, 2014). The flora of this stage has a peculiar species composition and differs considerably from the Maastrichtian floras of Sakhalin and Canada, at both the generic and specific levels. In the Late Cretaceous, the Kakanaut area was located at palaeolatitudes estimated between 70° and 75° N within the palaeo-Arctic Circle. Mean annual temperature at this area according to a CLAMP analysis was about 10 °C, and mean temperature during cold months between 0 °C and 6 °C. Mean annual precipitation ranged between 1500 and 1700 mm (Golovneva, 2000b).

The mixture of the typical Late Cretaceous and younger Paleocene elements is a characteristic feature of the Kakanaut flora. The former are represented by cycadophytes and ancient conifers (*Elatocladus*,

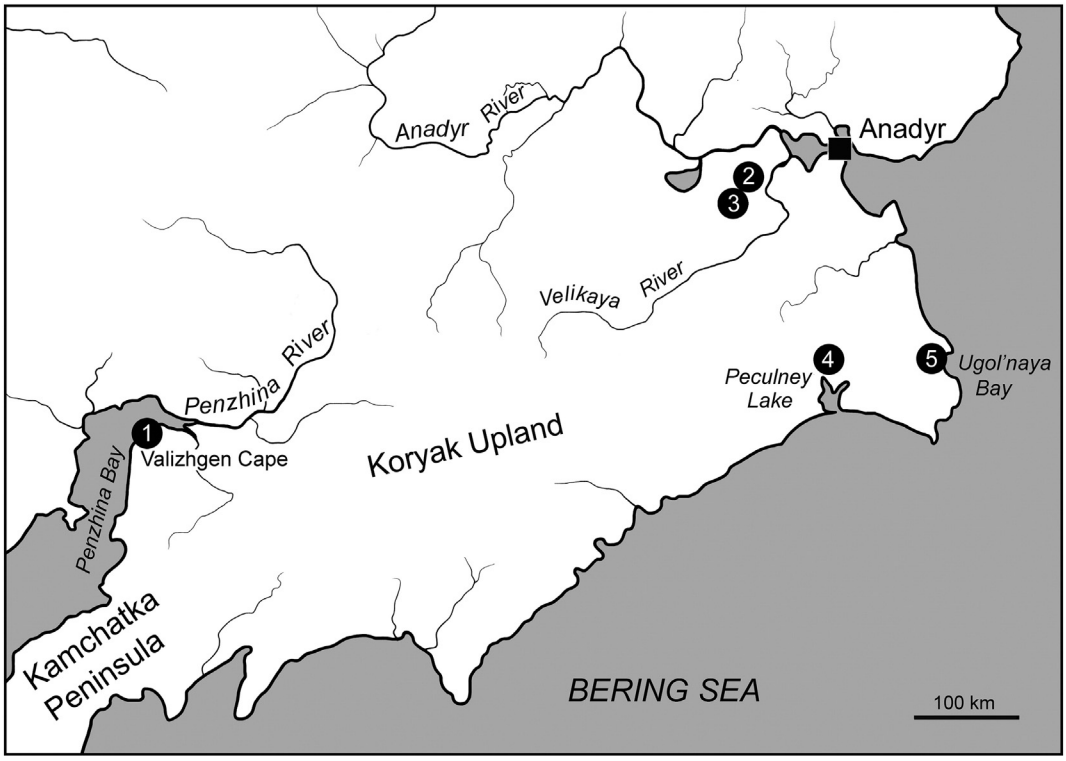

Fig. 1. Map of the Koryak Upland, Russia, showing the geographical position of the fagaceous foliage localities: 1 — Valizhgen Cape, upper part of Bystrinskaya Formation, late Santonian?–early Campanian; 2 — Rarytkin Ridge, Rarytkin Formation, late-Maastrichtian-Paleocene; 3 — Talyain River, Right Talyain Formation, late Eocene; 4 — Kakanaut River, Kakanaut Formation, early late Maastrichtian; 5 — Ugolnaya Bay; Barykov Formation, early Campanian.