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Diversity and richness of the Devonian terrestrial plants in the Southeastern Mountainous Altay (Southern Siberia): Regional versus global patterns

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ABSTRACT

Devonian deposits of the Southeastern Mountainous Altay, a large region in Southern Siberia, contain abundant remains of terrestrial plants. A semi-quantitative analysis of this regional palaeobotanical record reveals how both the diversity (number of taxa) and richness (number of taxa with an account of their abundances) of floristic assemblages changed during the Emsian–early Famennian time interval. A total of 60 species, representing 42 genera, are known from 8 regional assemblages. Changes in diversity of species and genera occurred simultaneously. The number of taxa was high in the early Emsian, declined in the late Emsian, rose again in the Eifelian–middle Givetian, dropped in the late Givetian, reached the highest values in the early Frasnian, and experienced the greatest decline taking place in the late Frasnian–early Famennian. The standing diversity (number of taxa crossing the time boundaries) was maximal in the Middle Devonian. The dynamics of terrestrial plant richness was similar to that of diversity with an exception of middle Givetian decline in richness despite growth of diversity. The floras were dominated by pteridophytes. Propteridophytes were less abundant, and pinophytes were very rare. Propteridophyte extinctions were high in the middle Givetian, concurrent with a brief decline in pteridophytes. Some regional and global patterns of floral dynamics were similar. However, propteridophyte decline was not abrupt globally. The main abiotic driving factor influencing species richness and diversity appears to have been regional shoreline shifts. It does not appear that climate changes was important for regional changes in phytodiversity, although both regional and global phytodiversity was at its high during the Middle Devonian cooling phase. A comparison of palaeobotanical data from the Southeastern Mountainous Altay and Kazakhstan suggests palaeogeographic proximity and proves an idea of Altay-Mongolian terrane wandered between Gondwana, Kazakhstan, and Siberia. The early Emsian and the early Frasnian, when floras of the study region were diverse and rich, are characterized by the very high degree of similarity. Thus, interregional floral exchanges would facilitate plant radiations.

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1. Introduction

Terrestrial floras had evolved prior to the Devonian (Gensel, 2008; Heckman et al., 2001; Masuda and Ezaki, 2009; Russell, 2009; Steemans et al., 2009; Strother, 2000; Wellman et al., 2003), but radiated globally during this period (Bateman et al., 1998; Burgoyne et al., 2005; Edwards and Richardson, 2004; Gensel and Edwards, 2001; Gray, 1993; Kenrick and Crane, 1997; Meyen, 1987; Philippe et al., 1999; Stewart and Rothwell, 1993; Taylor and Taylor, 1993). This radiation is depicted clearly in phytodiversity curves (Anderson et al., 1999; Boulter, 1997; Boulter et al., 1988; Knoll, 1986; Knoll et al., 1984; Niklas et al., 1983, 1995; Raymond and Metz, 1995), which, however, lack sufficient detail to reveal precise timing of events (e.g., Ruban and van Loon, 2008). Only some large-scale environmental perturbations are evident (Raymond and Metz, 1995; Streel et al., 2000). The rise of terrestrial floras might have itself contributed to these major events (Algeo et al., 1995).

In the present article, an analysis of floristic data gathered from the southeastern part of the Mountainous Altay (also transliterated as Gorny Altay) region in Central Eurasia is presented. These data reflect an exceptional record of Devonian floristic dynamics in the Proto-Angaran Realm (Antonova, 2008).

2. Geological setting

The Southeastern Mountainous Altay is a large region in Southern Siberia (Fig. 1). It belongs to the Central Asian Orogenic Belt (Jahn et al., 2004). Devonian deposits occur widely in this region (Antonova,

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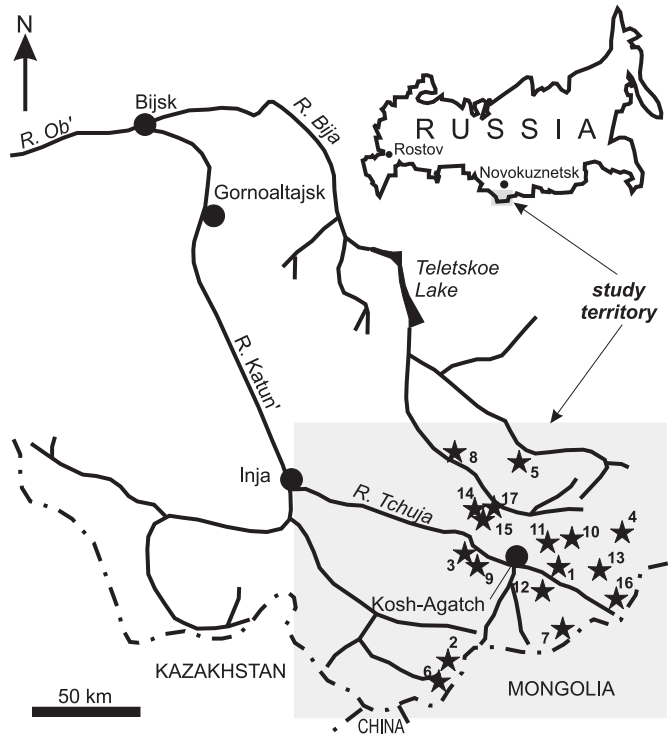

Fig. 1. Fossil plant localities in the study area: 1—Koksair, 2—Kalguty, 3—Akkaja, 4—Buguzun, 5—Kumurlu, 6—Argamdzhi, 7—Kyzylkyptchal, 8—Baltyrgandu, 9—Tchagan-Uzun, 10—Korsak-Tytugem, 11—Taboshak, 12—Buraty, 13—Dzhilkidal, 14—Kujtash, 15—Bertozek, 16—Boguty, 17—Jantchaktushken.

2008; Gutak, 1989, 2000, 2001, 2002; Turkin and Fedak, 2008), particularly in the Kalguty Depression, the Justyd Depression, and grabens of the Teletskoe–Tchulyschman Zone (Fig. 2). These Devonian deposits are dominated by siliciclastics with carbonate interbeds and uncommon volcaniclastics, with a total thickness of 1300 to 7500 m. An abundance of faunal remains (conodonts, brachiopods, bryozoans, corals, crinoids, bivalves, nautiloids, fish) permits a precise biostratigraphic framework (Fig. 2). Particularly, many standard conodont zones (Ogg et al., 2008) are recognized. An analysis of palaeobotanical data allowed Antonova (2008) to identify characteristic assemblages of fossil plants in the Emsian to lower Famennian interval (Fig. 2).

According to global plate tectonic reconstructions of Stampfli and Borel (2002), Scotese (2004), and Torsvik and Cocks (2004), the Southeastern Mountainous Altay was located on or near the margin of an isolated Siberian landmass. Buslov et al. (2004) suggested the study region as a part of the Altay-Mongolian terrane, which was not joined with Siberia until the Late Devonian.The closest neighbouring landmass was Kazakhstan, where chains of islands and small terranes were grouped. The distance between Siberia and Kazakhstan narrowed during the Silurian–Devonian, which led to their final amalgamation in the Carboniferous (see a discussion below). The study region remained tectonically stable until the end of the Early Devonian. Emergence of a volcano-plutonic belt, initiated with strike-slip displacements followed by an interval of extension, resulted in the deformation of the continental margin in the Middle Devonian through to the Famennian. A compressional regime was established at the beginning of the Carboniferous. Sea level fluctuations in the entire Southern Siberia region (Gutak and Ruban, 2007; Gutak et al., 2008) and local tectonic activity were important controls of palaeoenvironmental changes in the study region. Whereas continental facies occur in the early Emsian, the Eifelian–early Givetian, and the early Frasnian, marine depositional environments were established in the late Emsian, part of the Givetian, and in the late Frasnian–Famennian intervals. Lateral differences in facies are also conspicuous; e.g., the lower Frasnian siliciclastics with carbonate interbeds of the Boguty Fm. in the Justyd Depression are marine, whereas coeval siliciclastics of variegated colour (defined as the Kujtash Fm. and the Bertozek Fm. in the Teletskoe–Thulyshman Zone) were deposited in subaerial environments.

3. Materials and methods

3.1. Material

This study is based on field data collected by Antonova (2008), who carefully investigated 17 Devonian plant localities in the Southeastern Mountainous Altay (Fig. 1). Only localities with good-to-exceptional preservation of plant remains are considered. Terrestrial plant taxa have been found both in continental and marine strata, with as many as 60 species, representing 42 genera, identified. Their suprageneric taxonomy was established according to Meyen (1987), who recognized Proteridophyta, Pteridophyta, and Pinophyta as major plant divisions. This classification is based, particularly, on general plant organization (e.g., separation of root and stem). This classification deals also with satellite taxa.

A succession of assemblages was recognized by Antonova (2008) and includes the early Emsian, late Emsian, Eifelian–early Givetian, middle Givetian, late Givetian, early Frasnian, late Frasnian, and early Famennian assemblages. The age of assemblages is based on the chronostratigraphy of Menning et al. (2006) and Ogg et al. (2008). Although different in their durations, these assemblages characterize the principal stages in the Devonian evolution of the regional flora. The distribution of each species within these assemblages was established based on extensive field collection, and the relative abundance was evaluated using a 1 to 5 ranking system, where 1 is minimal abundance and 5 is maximal one (Table 1).

3.2. Methods

The number of species and genera in each assemblage was used to measure changes in *diversity*, while the relative abundance of each species was used to evaluate floristic *richness*. Another measure, namely *standing diversity*, was also employed. It was proposed by Raymond and Metz (1995), who evaluated the number of taxa shared by neighbour time intervals including those taxa with a stratigraphic range interruption. Additionally, a comparison of richness dynamics of the major terrestrial plant groups, as designated by Meyen (1987) (Propteridophyta, Pteridophyta, and Pinophyta), allows interpretation of changes in the structure of the regional vegetation. Seven species were excluded from this analysis because of their uncertain suprageneric affinity and rare occurrence.

In order to evaluate the possible influences of fossil record biases (sampling, facies, taphonomic, etc.), which is inevitable in quantitative analysis of palaeobotanical data (e.g., Raymond and Metz, 1995), a number of fossil plant localities for each time interval was measured and then compared with the curves of diversity and richness. A coincidence of maxima and minima is considered as an evidence of more or less significant bias.

4. Diversity dynamics

4.1. Regional patterns

Species phytodiversity in the Southeastern Mountainous Altay region was high during the Devonian, but diversity within individual genera was low. The most diverse genera were the Late Devonian *Archaeopteris* (8 species) and Early–Middle Devonian *Drepanophycus* (6 species). All other genera were represented by only one or two species.

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