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MID-CRETACEOUS GREBENKA FLORA OF THE NORTH-EASTERN RUSSIA: TWO STRATEGIES OF OVERWINTERING

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ABSTRACT. Most of the plants from the Grebenka flora (latest Albian-early Cenomanian, North-eastern Russia) were deciduous. Deciduous taxa are found within the caytonealeans, ginkgoaleans, czekanowskialeans, some conifers, angiosperms, and even some cycadophytes shed their leaves synchronously. Ferns probably died back to rhizome systems during the winters. However, there is no evidence that such plants as *Araucarites anadyrensis*, *Pagiophyllum triangulare*, *Sequoia* ex gr. *reichenbachii*, *Cupressinocladus cretaceus* were capable of leaf or shoot shedding. These conifers also possess some xeromorphic features, which are not consistent with the humid climate reconstructed for the flora. Because there is little reason to assume that there were cold winters and/or a pronounced relatively dry season in Arctic during the Middle Cretaceous, the deciduousness of the Grebenka plants (palaeolatitude 72–74°N) most probably reflects their adaptation to the continuous winter darkness for five or six weeks. However the frost-free Arctic climate, combined with high-latitude light regime and evergreenness, could have led to a respiratory drain of the energy resources of evergreen plants during the winter. The xeromorphic characters of evergreen Grebenka plants can be attributed to their adaptation to reduce their demand for water and metabolic load during the winter. In this case the cost of foliar respiration during dark and warm winters probably must have been less than the alternative cost of canopy replacement in spring. Therefore, two different strategies of overwintering were favourable for mid-Cretaceous Arctic plants: shedding foliage and evergreenness.

KEY WORDS: Cretaceus, flora, adaption, climat

INTRODUCTION

The latest Albian – earliest Cenomanian (96 Ma) Grebenka flora (Krivorechenskaya Formation, Upper Subformation) has been regarded as "the most important Late Cretaceous palaeofloristic record" (Terekhova 1988, p. 100) in North-eastern Asia, and during the last 40 years every publication discussing North-eastern Russian regional phytostratigraphy and palaeobotany has referred to it. Moreover, the Grebenka flora seems to be one of the most diverse middle Cretaceous floras of Eurasia, and possibly of the world, despite its position within the Cretaceous Arctic Circle. The Grebenka flora represents a range of plant communities in several stages of development growing very close to the mid Cretaceous North Pole. The age of the flora is constrained by Ar^{39}/Ar^{40} analyses of biotites in air-fall tephras and minimally water transported volcaniclastics. The age is further determined by–biostratigraphic correlation of the plant-bearing non-marine and marine beds of the Krivorechenskaya Formation and overlying deposits of the Dugovskaya Formation (Devyatilova *et al*. 1980, Herman & Shczepetov 1992, Herman 1999, Shczepetov *et al*. 1992).

RESULTS

Our detailed sedimentological studies have shown that rapidly aggrading alluvial volcaniclastics 'captured' the various communities. From palaeosol development and sedimentary characteristics we estimate that a thickness of 100m of sediments was deposited in no more than a few thousand years. This high rate of deposition led to excellent preservation and also accounts for the diversity of this flora (at least 85 angiosperm megafossil foliage taxa, plus non-angiosperms and woods), because both pioneer species and mature forest communities are represented.

The geologically short time span involved means that palaeoclimatic analyses derived from the flora represent a 'snapshot' of mid Cretaceous climate. The flora represents vegetational communities that grew under climatic conditions associated with one small part of a precession cycle, i.e., the shortest Milankovitch cycle of orbital climate forcing. No longer – term averaging of climatic change caused by tectonic factors is involved.

In the modern Earth, there are no analogues of the Grebenka flora. Based on its systematic composition and physiognomy, the Grebenka flora could be characterized as mixed coniferous and broad-leaved deciduous (or predominantly deciduous) forest. However, the existence of this floral type in high latitudes of Arctic (approximately 70–75°N: Smith *et al*. 1981) could not be explained based on modern climate and vegetation distributions, because nowadays the analogous forests occur no farther northwards than 55°N in Asia and North America. In Northern Scandinavia boreal forests occur up to 70°N but these forests possess much lower plant diversity than that of the Grebenka flora. Any climatic analogy is misplaced because modern high latitudes experience considerably colder winters than in the Cretaceous.

In the Middle Cretaceous the high-latitude areas of Asia and Alaska belonged to a temperate humid phytoclimatic zone (Spicer & Parrish 1986; Spicer & Corfield 1992, Vakhrameev 1991). Moreover the high temporal resolution and floristic diversity of the Grebenka flora site provides an extremely reliable quantitative climatic signal of conditions near the mid Cretaceous North Pole. Using leaf physiognomic multivariate analysis (CLAMP) on the whole composite flora (Wolfe 1993, Spicer & Herman 1998), we determine that the mean annual temperature experienced by the Grebenka vegetation was 13.0°C with a cold month mean temperature of 5.5°C. However analyses of individual florules yield slightly different results and help constrain the uncertainties inherent in such an approach. At high latitudes in the Southern Hemisphere there is some evidence of seasonally frozen ground indicating cold winter temperatures in mid-Cretaceous (Aptian) (Constantine *et al*. 1999). However there is little reason to assume cold winters with substantial (weeks or months) periods of subfreezing conditions existed in North-eastern Asia and Alaska this time (Brouwers *et al*. 1987, Spicer & Corfield 1992, Herman & Spicer 1996, 1997, Spicer & Herman 1998).

High humidity in the arctic areas of Asia and Alaska in mid Cretaceous times is confirmed by wide-spread Cretaceous coals (Spicer *et al*. 1992; Chumakov *et al*. 1995) and by lack of xeromorphic features in most of fossil plants from these areas. According to our CLAMP estimates (Spicer & Herman 1998), the mean annual precipitation experienced by the Grebenka flora was about 1250 mm, and a pronounced dry season was lacking.

Near-polar insolation critically depends on latitude. Providing temperatures are high enough winter photosynthesis at high latitudes can occur, but only during a small portion of each twenty-four-hour period. However in summer, daylight duration at high latitudes exceeds by far that at low latitudes. High latitudes receive annually about half the solar energy of near-equatorial areas, but in summer the amount of photosynthetically useful solar radiation is greater that that at low latitudes due to considerably longer day. High latitude solar energy is however different to that at lower latitudes in that it consists of more diffuse light. Diffuse light is utilized by plants more efficiently than direct light, and is absorbed more effectively. Prevalent diffuse light at high latitudes is caused by the relatively low sun position above the horizon (low angle of light incidence), high vapour content in the atmosphere of polar areas, and frequent cloudiness and mists. Modelling of Cretaceous climate, and the observed geological evidence for polar humidity at that time suggests that cloudiness and mists would have been more frequent than now (Valdes *et al*. 1999). Therefore, the existence of the Grebenka flora in high latitude of Arctic was unlikely to have been restricted by temperature, moisture or scarcity of daylight during the growing season.

Most of the plants from the Grebenka flora were deciduous, i.e. they were able to drop individual leaves, or shoots with leaves attached, during unfavourable episodes (usually winter). Examples include caytonealeans, ginkgoaleans, czekanowskialeans, some conifers (*Cephalotaxopsis, Taxites, Elatocladus*, some *Sequoia, Parataxodium*) and angiosperms. At least some cycadophytes were deciduous as well: plants with *Nilssoniocladus* shoots were capable not only of shedding individual leaves but discarding it's the "unwanted" leaf load extremely rapidly in the short autumn by abscising short shoots and attached leaves as single units (Spicer & Herman 1996). Shedding complete short shoots is well known in palaeobotanical record among Czekanowskiales, conifers etc. and can not be regarded as an only an adaptation to the polar light regime. However the pronounced deciduousness of the *Nilssoniocladus* plants from the Grebenka flora probably reflects a strong adaptation to polar light seasonality.

Taphonomic evidence in the form of leaf mats on single bedding planes and the general lack of post mortem degradation has been used to argue for synchronous and rapid leaf shedding by many high latitude Cretaceous taxa, including those of the Grebenka flora (Spicer & Parrish 1986, Shczepetov *et al*. 1992). Ferns probably died back to rhizome systems during the winters. However, some conifers were apparently evergreen: there is no evidence that such plants as *Araucarites anadyrensis*, *Pagiophyllum triangulare*, *Sequoia* ex gr. *reichenbachii*, *Cupressinocladus cretaceus* were capable of leaf and/or shoot shedding. It should be emphasized that these conifers possess xeromorphic features: small scale-like or rigid hook-like leaves. This xeromorphy is not, at first sight, consistent with the moist climate reconstructed for the Grebenka flora (see above).

The absence of a sufficiently long cold winter period implies that the deciduousness of most of the Grebenka plants can be attributed to the prolonged winter darkness. However, the assumption that the Grebenka flora included some evergreen conifers raise doubts on their ability to survive during the winter period. If the obliquity of the Earth was the same as present (there is strong evidence in favour of this supposition: Parrish & Spicer 1988, Spicer & Herman 1996), the Grebenka flora plants must have experienced continuous winter darkness of at least five or six weeks bounded by a continuous twilight period of three weeks in the spring and autumn (Anonymous 1978). A warm temperate frost-free climate, combined with near-polar light regime and evergreenness, would inevitably have led to a respiratory drain on the plant's resources during the winter. Modern high-latitude plants (e.g. in Northern Scandinavia) do not experience the same combination of warm air temperature and darkness during winter periods, low temperature depress their metabolic rates thus obviating respiratory drain.

With winter warmth, however, the cost of foliar respiration during dark winter is not necessarily higher than the alternative cost of canopy replacement in spring (Read & Francis 1992). Moreover, winter temperature about 5.5°C estimated for the Grebenka flora (see above) was probably low enough to reduce considerably metabolic rates (and the cost of foliar dark respiration) in leaves of evergreen plants. Experimental "overwintering" of modern plants under conditions of 10 weeks of darkness and 4°C or 15°C temperature shows that most of the plants investigated were able to tolerate this treatment quite well, and plant tissue death was significantly less in the 4°C dark treatment than in the 15°C dark treatment (Read & Francis 1992).

Therefore, theoretically two different strategies of overwintering could be possible for mid-Cretaceous polar plants: shedding foliage (and reducing respiratory costs during the dark winter) and evergreenness (and economy of plant resources in spring). Both strategies can be observed in plants of the Grebenka flora. Xeromorphic features of evergreen Grebenka plants probably reflect their adaptation to reduce water loss and foliage drought during winter periods.

Read and Francis (1992, p. 287) also emphasized that the advantages of deciduousness depend on resource availability and temperature of the growing season "... since high assimilation rates may be necessary to supply the energy cost of canopy replacement". It means that a proportion of deciduous plants to evergreen ones in floras that did not experience a significant stress during an adverse period (e.g., winter frost that could kill all foliage) could reflect the "quality" of the growing period. A higher proportion of deciduous plants in the Grebenka flora indicates that they did not experience any scarcity of resources, including light and warmth, in the spring.

REFERENCES

ANONYMOUS. 1978. C.I.A. handbook, polar regions atlas. National Foreign Assessment Center, C.I.A. USA. 66 pp.

BROUWERS E.M., CLEMENS W.A., SPICER R.A., AGER T.A., CARTER L.D. & SLITER W.V. 1987. Dinosaurs on the North Slope, Alaska: high latitude, latest Cretaceous environments. Science, 237(4822): 1608–1610.

CHUMAKOV N.M., ZHARKOV M.A., HERMAN A.B., DOLUDENKO M.P., KALANDADZE N.N., LEBEDEV E.L., PONOMARENKO A.G. & RAUTIAN A.S. 1995. Climatic belts of the mid-Cretaceous time. Stratigraphy and Geological Correlation, 3(3): 241–260.

CONSTANTINE A., CHINSAMY A. VICKERS-RICH P. & RICH T.H. 1999. Periglacial environments and polar dinosaurs. Paleontologicheskii Zhurnal, 2: 59–65 (in Russian).

DEVYATILOVA A.D., NEVRETDINOV ED.B. & FILIPPOVA G.G. 1980. Upper Cretaceous stratigraphy in the basin of the Anadyr River middle reaches. Geologiya i Geofizika, 12: 62–70 (in Russian).

HERMAN A.B. 1999. On the composition and age of the Grebenka flora from the Anadyr river (middle Cretaceous, North-eastern Russia). Stratigraphy and Geological Correlations, 7(3): 265–278.

HERMAN A.B. & SPICER R.A. 1996. Palaeobotanical evidence for a warm Cretaceous Arctic ocean. Nature, 380(6572): 330–333.

HERMAN A.B. & SPICER R.A. 1997. New quantitative palaeoclimate data for the Late Cretaceous Arctic: evidence for a warm polar ocean. Palaeogeography, Palaeoclimatology, Palaeoecology, 128: 227–251.

HERMAN A.B. & SHCZEPETOV S.V. 1992. The Mid-Cretaceous flora of the Anadyr river basin (Tchukotka, NE Siberia). In: Palaeovegetational development in Europe and regions relevant to its palaeofloristic evolution. Proc. Pan-European Palaeobot. Conf. Vienna, 1991. Vienna, Mus. Nat. Hist.: 273–279.

PARRISH J.T. & SPICER R.A. 1988. Late Cretaceous terrestrial vegetation: a near-polar temperature curve. Geology, 16(1): 22–25.

READ J. & FRANCIS J. 1992. Responses of some Southern Hemisphere tree species to a prolonged dark perod and their implications for high-latitude Cretaceous and Tertiary floras. Palaeogeogr., Palaeoclimatol., Palaeoecol., 99(3/4): 271–290.

SHCZEPETOV S.V., HERMAN A.B. & BELAYA B.V. 1992. Middle-Cretaceous Flora of the Right Bank of the Anadyr River (Stratigraphic Setting, Systematic Composition, Atlas of Fossil Plants). Magadan, NEISRI FEB RAS, 165 pp. (in Russian).

SMITH A.G., HURLEY A.M. & BRIDEN J.C. 1981. Phanerozoic paleocontinental world maps. Cambridge, London, New York, New Rochelle, Melbourne, Sydney, Cambridge Univ. Press, 102 pp.

SPICER R.A. & CORFIELD R.M. 1992. A rewiev of terrestrial and marine climates in the Cretaceous with implications for modelling the "Greenhouse Earth". Geol. Mag., 129(2): 169–180.

SPICER R.A. & HERMAN A.B. 1996. *Nilssoniocladus* in the Cretaceous Arctic: new species and biological insights. Review of Palaeobotany and Palynology, 92: 229–243.

SPICER R.A. & HERMAN A.B. 1998. Cretaceous climate of Asia and Alaska: a comparison of paleobotanical evidence with a climate computer model. Paleontological Journal, 32(2): 105–118.

SPICER R.A. & PARRISH J.T. 1986. Paleobotanical evidence for cool north polar climates in middle Cretaceous (Albian-Cenomanian) time. Geology, 14(8): 703–706.

SPICER R.A., PARRISH J.T. & GRANT P.R. 1992. Evolution of vegetation and coal forming environments in the late Cretaceous of the North Slope of Alaska. In: McCabe P.J. & Parrish J.T. (eds.). Controls on the Distribution and Quality of Cretaceous Coals Geol. Soc. Amer. Spec. Pap., 267: 177–192.

TEREKHOVA G.P. 1988. On the age of the Krivorechenskaya Formation and the Grebenka floral assemblage. In: Stratigrafiya i Paleontologiya Fanerozoya Severo-Vostoka SSSR (Phanerozoic Stratigraphy and Palaeontology in the North-eastern USSR). North-

Eastern Integrated Research Inst., USSR Acad. Sci., Magadan: 100–117 (in Russian).

VAKHRAMEEV V.A. 1991. Jurassic and Cretaceous Floras and Climates of the Earth. Cambridge, Cambridge University Press, 318 pp.

VALDES P.J., SPICER R.A., SELLWOOD B.W. & PALMER D.C. 1999. Understanding Past Climates: Modelling Ancient Weather. CD ROM Gordon and Breach Publishers, Reading.

WOLFE J.A. 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geol. Surv. Bull., 2040: 1–73.