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THE MICROEVOLUTIONARY TRENDS IN THE QUATERNARY FLORAS OF THE EAST-EUROPEAN PLAIN

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ABSTRACT. The flora of the ancient glaciation province of the East-European plain was strongly affected by the Pleistocene glaciations and re-established itself during the interglacial epochs in a much changed and renewed form. The processes of emergence and extinction of taxa were very intensive in the Glaciopleistocene; despite this, the number of relics in the Pleistocene flora of Europe was much higher than might have been supposed. Changes in the taxonomic composition of the fossil floras were mostly evidenced in communities of aquatic and water mire plants studied at the microevolutionary level.

KEY WORDS: fossil flora, species, extinct taxa, evolutionary lines, Quaternary, *Potamogeton*, *Brasenia*

INTRODUCTION

The collections of fossil fruits, seeds and megaspores were assembled by the author over the last 30 years from more than 350 Pleistocene profiles of various age in Belarus, Lithuania, western areas of Russia and the northern part of the Ukraine. Floras of the interglacial, interstadial and periglacial types, which were formed at different stages of glacial activity, were discovered throughout a variety of fossil "seed floras" of the Glaciopleistocene. The specific composition of each main flora type and each age group was determined. In total, over 15 floristic complexes of different age were discovered and characterised, reflecting the complex pattern of the development of continental glaciations; these floras constitute a reliable biostratigraphic basis for the detailed subdivision of Quaternary deposits. Even at the early stages of some interglacial floras the researchers' attention was drawn to the dissimilarity in the morphology of some Pleistocene taxa and their modern analogues, and a few extinct species were described by P. Dorofeev (1963) and the present author (Dorofeev & Velichkevich 1971a, b). Further study of interglacial floras of the East-European plain, particularly of Early and Middle Pleistocene age, led to the discovery of some more species which were inherited from the previous Neogene flora or originated and disappeared at various stages of the Pleistocene. A large group of extinct Neogene-Quaternary or true Pleistocene species of the genera *Salvinia*, *Pilularia*, *Selaginella*, *Potamogeton*, *Caulinia*, *Aldrovanda*, *Brasenia*, *Nymphaea* and others were described (Velichkevich 1975, 1979, 1982). The practical application of SEM in palaeocarpological investigations, as well as the methods of anatomical sections and biometry of fossil fruits and seeds, made it possible to discover a large group of new morphological and anatomical features, whose evolutionary importance is not yet understood. It has recently become objectively necessary to carry out palaeocarpological investigations of the Quaternary floras at a new microevolutional level.

TWO EXAMPLES OF EVOLUTIONARY LINES

BRASENIA

Results of detailed morphological, anatomical and biometrical investigations of *Brasenia* fossil seeds from numerous interglacial profiles of Belarus and adjacent areas showed that the Quaternary history of this genus to be quite complex. The distribution of fossil *Brasenia* seeds in the interglacial floras of different age is highly variable. For instance, only one seed with an unclear taxonomy was found by Yakubovskaya (1978) in the deposits of the most ancient Interglacial of Belarus (exposure Korchevo, Western Belarus), while extremely abundant seeds of this interesting water plant are known from some interglacial sections of the Byelovezhian and especially of Muravian age. These belong to different polymorphic extinct species: *Brasenia borysthenica* Wieliczk. with a few separate varieties and *B. holsatica* (Web.) Weberb. These species, together with the ancient Neogene species *B. tanaitica* Dorof. and the contemporary *B. schreberi* J.F. Gmel. form the branched phylogenetic line of the genus *Brasenia*: *B. tanaitica* Dorof. – *B.*

borysthenica Wieliczk. s.s – *B. borysthenica* var. *dvinensis* Wieliczk. – *B. borysthenica* var. *nemenensis* Wieliczk. – *B. holsatica* (Web.) Weberb. – *B. schreberi* J.F. Gmel. (Velichkevich 1991).

In the type collection from the Middle Pleistocene flora of Nyzhninsky Rov on the Dnieper river, seeds of *B. borysthenica* Wieliczk. (Dorofeev & Velichkevich 1971 a) are quite variable in size: 2.5–3.8 × 1.7–2.5 mm, but large specimens outnumber small ones. Their main diagnostic feature is the prevalence of obovate seed form over the oval and ovate (Pl. 1, figs 13–15). This is evidently an ancient feature inherited from allied Pliocene species, such as *B. tanaitica* Dorof. (Pl. 1, figs 16–18) or *B. tuberculata* C. et E.M. Reid.

The seeds of the variety *B. borysthenica* var. *dvinensis* Wieliczk., described from Mogilevian interglacial flora of Smolenski Brod on the Western Dvina river (Velichkevich 1982; p. 186, Pl. 21, figs 4–16) are rather similar in size (2,4–3,8 × 1,9–2,8 mm) and shape to those of *B. borysthenica* Wieliczk. s.s., but not so clearly obovate in seed form, which is usually oval or cylindrical, with a higher apex and conspicuous cap. (Pl. 1, figs 10–12).

The seeds of variety *B. borysthenica* var. *nemenensis* Wieliczk., described from the Alexandrian interglacial flora of site Prinemanskaya (former Zhidovshchizna) on the river Nemen (Velichkevich, 1982; p. 187, Pl. 22, figs 1–4) are medium in size (2.5–3.0 × 1.9–2.1 mm), oval or slightly obovate, usually asymmetrical. The top of the seed is convex with a small, frequently deeply depressed cap (Pl. 1, figs 4–6). In more important morphological features, this variety is a transitional form between typical *B. borysthenica* and the extinct Neopleistocene species *B. holsatica*. The seeds of a particular Middle Pleistocene species, *B. interglacialis*, described by Dorofeev from the Pleistocene of Lipetskaya area in Russia (Dorofeev 1984) are very similar to some specimens of the latter variety and most likely can be considered as a special form of the fairly polymorphic *B. borysthenica*.

The taxonomy of *B. byelorussica* T.V. Yakub. (Yakubovskaya 1978) is not clear and is complicated by the fact that this species includes fossil seeds of *Brasenia* from two collections of evidently different age.

The seeds of *B. holsatica* are rather polymorphic in size (1.8–3.5 × 1.7–3.0 mm) and shape and separate into two morphotypes, previously described by Szafer (1925) as two independent extinct species. Detailed morphological and biometric investigations of fossil *Brasenia* seeds from numerous sites of last Interglacial in Belarus include the exposure Samostrzelniki studied by Szafer, showed a regular decrease in seed size between the lower and the upper parts of the sections where *Brasenia* seeds are reasonably abundant. Broad, oval seeds with a comparatively thin testa and infrequent surface tubercles, more often preserved at the base of the seed, dominate in the lower part of interglacial sediments, which as a rule correspond to the beginning of interglacial climatic optimum (Pl. 1, figs 2–3).

The other morphotype, which usually becomes dominant in the middle and especially in the upper interglacial layers, has narrower, oval or oviform seeds with a raised distinct isolated top and high cap as well as a thicker, stout testa (Pl. 1, fig. 1).

POTAMOGETON

As a rule, not only are the numerous *Potamogeton* species represented in each interglacial flora of Europe, but its fossil remains can also be very abundant. The overwhelming majority of these are contemporary European species, but some extinct ones may also be found in such floras. The most interesting of these are related to present-day East-Asiatic species such as *P. maackianus* A. Benn., *P. manshuriensis* A. Benn., *P. digynus* Wall., *P. friery* A. Benn. These created a few relatively independent phylogenetic lines of the genus *Potamogeton*. One distinct evolutionary line of this genus consists of four different extinct species closely resembling *P. maackianus* A. Benn. These include the Pliocene-Pleistocene species *P. praemaackianus* Wieliczk. (Velichkevich 1975), the Byelovezhian (Ferdinandovian, Cromerian) species *P. sarjanensis* Wieliczk. (Velichkevich 1979), the Alexandrian (Mazovian, Holsteinian) species *P. goretskyi* Dorof. (Dorofeev 1986) and the Neopleistocene (Eemian-Vistulian) species *P. sukaczevii* Wieliczk. (Velichkevich 1982). Each of these very clearly exhibits the essential diagnostic features of the species and differs distinctly from all the other species of this group.

The endocarps of *P. praemaackianus* Wieliczk. are large (2,5–3,4 × 2,3–2,5 mm) thick, angular in shape, with a massive keeled lid and large cone-shaped stalk directed sidelong down, with a relatively short, usually raised shoulder and small but conspicuous central depression (Pl. 1, figs 26–31).

The endocarps of *P. sarjanensis* Wieliczk. are more streamlined in shape, with a broad sloping shoulder, relatively thin style, centrally positioned, usually with a thickened stigma. The lid is slightly keeled, sometimes deeply depressed. The sides are strongly convex, with a small central depression and a deep cavity (Pl. 1, figs 23–25).

In comparison with both species described above, the endocarps of *P. goretskyi* Dorof. are massive, with a sigmoid or angular ventral margin; the lid is broad, slightly keeled, more frequently lacking a crest; the style is short, thick, ventrally positioned. The sides are irregular convex, with a small central depression and a big, stout basal wart curved outwards (Pl. 1, figs 21–22).

The endocarps of *P. sukaczevii* Wieliczk. are rather variable in their basic diagnostic features, but are always slightly flattened, with a strongly convex ventral margin in its upper part, sometimes with fragments of mesocarpal tissue in the middle part of the ventral margin and at the apex of endocarp. The lid is broad, slightly bent, keeled, with a large, thick and high crest. The big, conspicuous nipple in the base of the lid often preserved. The top of the lid does not reach the base of the style but the shoulder is usually narrow and false, being formed from the endocarp edges fused together and covered by an awl-shaped spine of the crest. The style is rather long, thick, centrally positioned or displaced to the ventral margin. The sides are flattened, with a small deep cavity or hole in the centre and with an arched shallow furrow extending along the dorsal margin and large basal wart in the base. The stalk is often very stout, long, cone-shaped (Pl. 1, figs 19–20).

The endocarps of contemporary *P. maackianus* A. Benn. come nearest to the fossil endocarps of the latter species but are thicker and having a less convex ventral margin without mesocarpal tissue fragments. The lid is short, deeply depressed with virtually no crest, the more thick style is ventrally positioned, the shoulder, if present at all, is small, false, and the furrow along the dorsal margin is more frequently inconspicuous.

QUATERNARY FLORAS AND STRATIGRAPHY OF BELARUS

The new stratigraphical scale of the Quaternary was previously created in Belarus on the basis of recent materials of a complex of biostratigraphical methods but primarily palaeobotanical investigations (Velichkevich *at al.* 1996). The scale is based on the principle of succession in the development of the Pleistocene Interglacial epoch fossil biota. Stage-by-stage development of natural complexes suggests a single-optimum composition of each interglacial period. In accordance with the new scale, the lower chronostratigraphical boundary of the Quaternary is established near the upper part of the palaeomagnetic episode of Olduvai (approximately at the level of 1.8 mln years ago). The Quaternary of Belarus in its new understanding includes the iceless period of the Eopleistocene and Glaciopleistocene containing the Meso- and Neopleistocene. The lower boundary of the Glaciopleistocene is established somewhere in the deposits of the first continental glaciation (Narev), and the location of the Neopleistocene lower boundary moves down to the floor of the Dnieper (Saale) horizon.

Eopleistocene sediments are not sufficiently widespread in Belarus and adjacent regions, therefore seed complexes of this age are not numerous. The fossil floras of the most ancient (Korchevian) Interglacial reflected forest vegetation of the coniferous type, which was unlikely to have created a continuous cover and had a mosaic distribution. A characteristic complex of plants of this time is represented by *Azolla interglacialis* Nikit., *Scirpus* (*Schoenoplectus*) *kreczetoviczii* Wieliczk., *Stratiotes goretskyi* Wieliczk., *Caulinia antiqua* T.V. Yakub., *Aldrovanda zussii* T.V. Yakub. At the same time as the forest zone species, the herbaceous flora of this Interglacial includes representatives of steppe communities and numerous plants of open and wet habitats.

The floras of two successive Interglacials – Byelovezhian and Mogilevian – are alike in their composition and collection of exotics. The forest communities include a large group of coniferous and broad-leaved tress and shrubs: *Pinus*, *Picea*, *Larix*, *Juniperus*, *Quercus*, *Tilia*, *Acer*, *Fraxinus*, *Sambucus* etc. A type collection of exotics in these floras is as follows: *Brasenia borysthenica* Wieliczk. s.s, *B. borysthenica* var. *dvinensis* Wieliczk., *Caulinia macrosperma* Wieliczk., *Stratiotes brevispermus* Wieliczk., *Aldrovanda borysthenica* Wieliczk., *Potamogeton sarjanensis* Wieliczk., *Pilularia borysthenica* Wieliczk. etc. The Mogilevian interglacial floras show a distinctly specific character due to the presence of *Carpinus betuloides* Wieliczk., *Caulinia lithuanica* Rishk., an original form of *Brasenia* etc.

The Alexandrian (Holsteinian) interglacial floras reproduce the forest communities with dominant dark-coniferous tree species: *Abies alba* Mill., *Taxus baccata* L., *Picea* sect. *Omorica*, *P. abies* (L.) Karst. Remains of broad-leaved trees are typical only to deposits of the climatic optimum of this interglacial, however, the proportion of the nemoral element at that time was considerably smaller than in floras of other interglacials. The Alexandrian Interglacial is characterised by the following group of exotic plants: *Aracites interglacialis* Wieliczk., *Aldrovanda dokturovskyi* Dorof., *Caulinia goretskyi* Dorof., *Myriophyllum spinulosum* Dorof., *Potamogeton dvinensis* Wieliczk., *P. goretskyi* Dorof., *Brasenia borysthenica* var. *heterosperma* Wieliczk.

The largest group of the Pleistocene fruit-seed floras was formed during the younger (Muravian, Eemian) Interglacial. On the territory of Belarus and neighbouring countries more than 120 such floras have been studied by the palaeocarpological method. Floras of this age are characterised by the abundance of *Brasenia holsatica* (Web.) Weberb. seeds and the remains of numerous broad-leaved trees and shrubs.

CONCLUSIONS

A considerable increase in the specific variety of the genera *Brasenia* and *Potamogeton* in the Pleistocene should not be regarded as fortuitous, since a very similar picture is observed in a few other genera of water plants

(*Aldrovanda*, *Caulinia*, *Nymphaea*) of the European flora. Frequent and strong climatic fluctuations, associated with alternation of glacial and interglacial stages, influenced the rate of evolutionary processes in some of those taxa which showed a high ability to adapt to the environment. In the interglacial floras, the water and water-mire plants were represented by groups of more or less isolated populations which developed in different, relatively independent directions. In each glacial period, the water and water-mire plants of the European plain flora were, as a rule, subject to destruction over a large part of their distribution. These species could then regenerate in the next interglacial stage, spreading from small isolated populations which might remain somewhere in the periphery of their ranges and, naturally, retained only a part of the species genotypes. Such species could thus be restored in a significantly changed state and give rise to a new taxa of intra-specific or even specific ranks. In Palaeobotany as well as in Palaeontology in general the limits of fossil species are highly indistinct, so it is very difficult to confirm that all new taxa described from the Pleistocene floras are actual species, but the systematic and stratigraphic independence such taxa is unquestionable. The discovery and detailed examination of taxa having a narrow stratigraphical range is very important not only for the history of the Quaternary flora but also for stratigraphy. These taxa were used as the basis for the dating of interglacial floristic complexes and for detailed stratigraphical subdivision of Pleistocene sediments.

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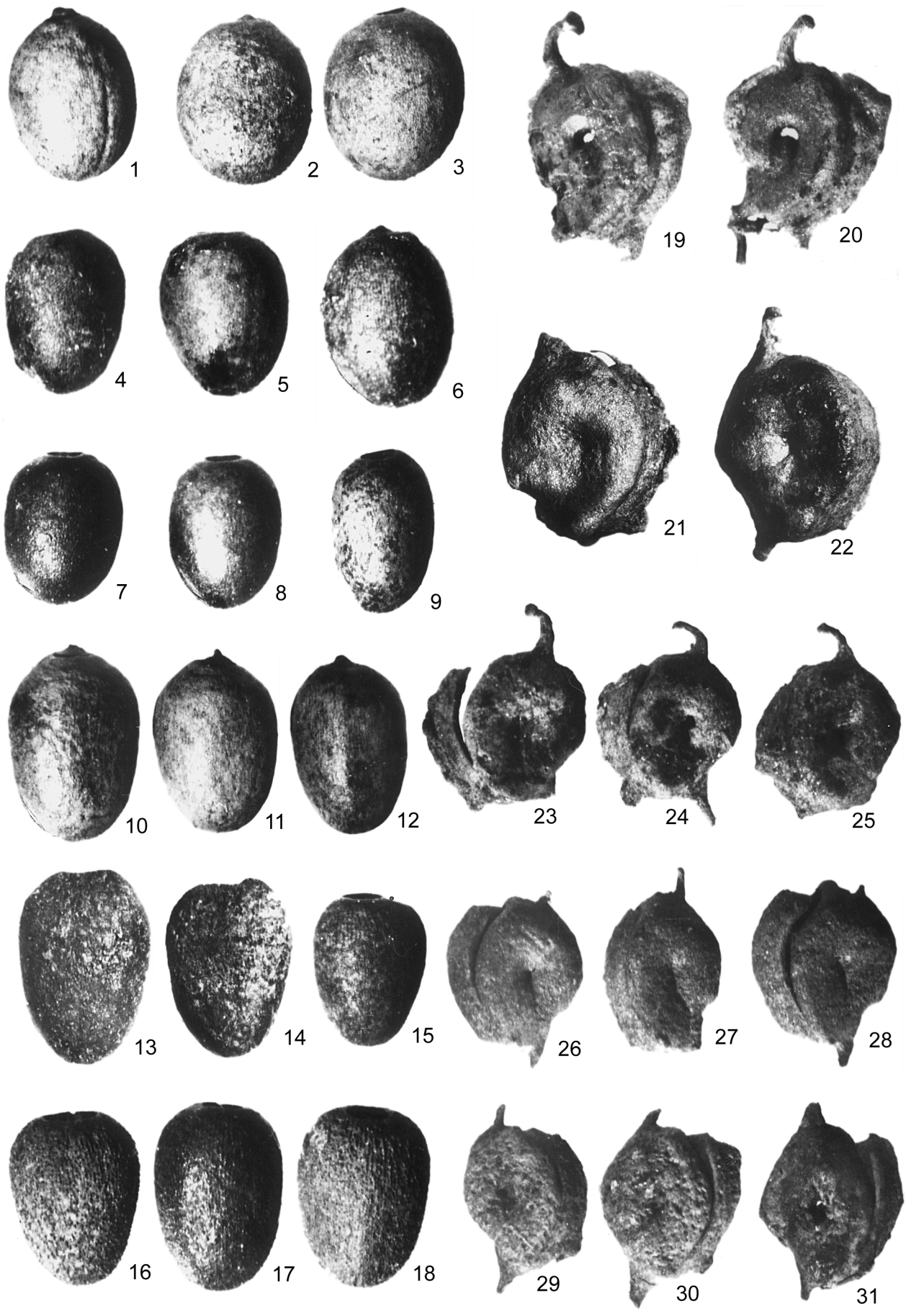
PLATE

Plate 1

1–18. *Brasenia*, seeds, ×11: 1–3 – *B. holsatica* (Web.) Weberb., Bogatyrevichi; 4–6 – *B. borysthenica* var. *nemenensis* Wieliczk., Prinemanskaya; 7–9 – *B. borysthenica* var. *heterosperma* Wieliczk., (7–8 – Verkhov'e-2, 9 – Ruba); 10–12 – *B. borysthenica* var. *dvinensis* Wieliczk., Smolenski Brod; 13–15 – *B. borysthenica* Wieliczk. s.s, Nyzhninsky Rov; 16–18 – *B. tanaitica* Dorof., Kholmech

19–31. *Potamogeton*, endocarps, ×11: 19–20 – *P. sukaczevii* Wieliczk., Cherikov; 21–22 – *P. goretskyi* Dorof., Prinemanskaya; 23–25 – *P. sarjanensis* Wieliczk., Obukhovo; 26–31 – *P. praemaackianus* Wieliczk. (26–28 – Verkohv'e-2, 29–31 – Dvorets)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