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POTAMOGETON SUKACZEVII WIELICZK. IN THE NEOPLEISTOCENE FLORAS OF POLAND, BELARUS AND LITHUANIA*

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ABSTRACT. The extinct species *Potamogeton sukaczevii* Wielicz., characteristic of the Neopleistocene floras of Belarus and adjacent areas, has been found for the first time in Poland. The present site extends the known range of this species significantly south-westwards. This is the last of the whole group of extinct species bearing affinity to very remote east-Asiatic forms; towards the end of the Neogene and all through the Pleistocene it was widely distributed throughout eastern Europe. At the site Horoszki Duże in the valley of the Czyżówka stream (eastern Poland) endocarps of *P. sukaczevii* occur only in the Early Vistulian part of lacustrine sediments, though in Belarus this species is more frequently encountered in interglacial deposits.

KEY WORDS: *Potamogeton sukaczevii* Wieliczk., fossil endocarps, Eemian Interglacial, Early Vistulian interstadials

INTRODUCTION

The remains of a *Potamogeton* species, unknown to the European flora, were first published by Dorofeev (1963) from the Eemian (Muravian) Interglacial floras of Belarus and the Smolensk Province of Russia. He described some specific endocarps of this species from six sites under the name of the contemporary Far Eastern species *P. oxyphyllos* Miq. (Miki 1961). However, it was found later that *P. maackianus* A. Benn. (Velichkievich 1973), now widespread in Korea, Japan and the Russian Far East, is more closely related. Later studies of the Pleistocene floras from eastern Europe showed that some endocarps similar in shape are encountered not only in the Neopleistocene floras but also in older interglacial floras; these, however, belong to various extinct species more or less related to *P. maackianus*. They include the Pliocene-Pleistocene species *P. praemaackianus* Wieliczk. (Velichkevich 1975), Ferdynandovian (Byelovyezhskiy, Cromerian) species *P. sarjanensis* Wieliczk. (Velichkevich 1979), the Mazovian (Alexandrian) species *P. goretskyi* Dorof. (Dorofeev 1986) and *P. sukaczevii* Wieliczk. (Velichkevich 1982), which is known from the Neopleistocene.

It is an interesting fact that its remains are recorded not only in sediments of the last interglacial but also in the older interstadial of the Early Vistulian. It is noteworthy that the type of this species was described from the Early-Vistulian part of the Cherikov profile on the river Sozh in eastern Belarus. The westernmost sites of this species have hitherto been known only from the valley of the river Nemen in the territory of Belarus and Lithuania (Velichkevich 1982). Finding it at the site Horoszki Duże in eastern Poland lets us hope for new finds from the Neopleistocene sediments of the valleys of the rivers Bug and Vistula.

DESCRIPTION OF THE SITE

The site Horoszki Duże lies in the valley of the stream Czyżówka in southern Podlasie (Fig. 1). The lacustrine sediments from this site were first submitted to expert palynological analysis by Bitner (1954) and on this basis were referred to the Eemian Interglacial (then termed the Younger or Mazovian II Interglacial). No analysis of plant macrofossils was

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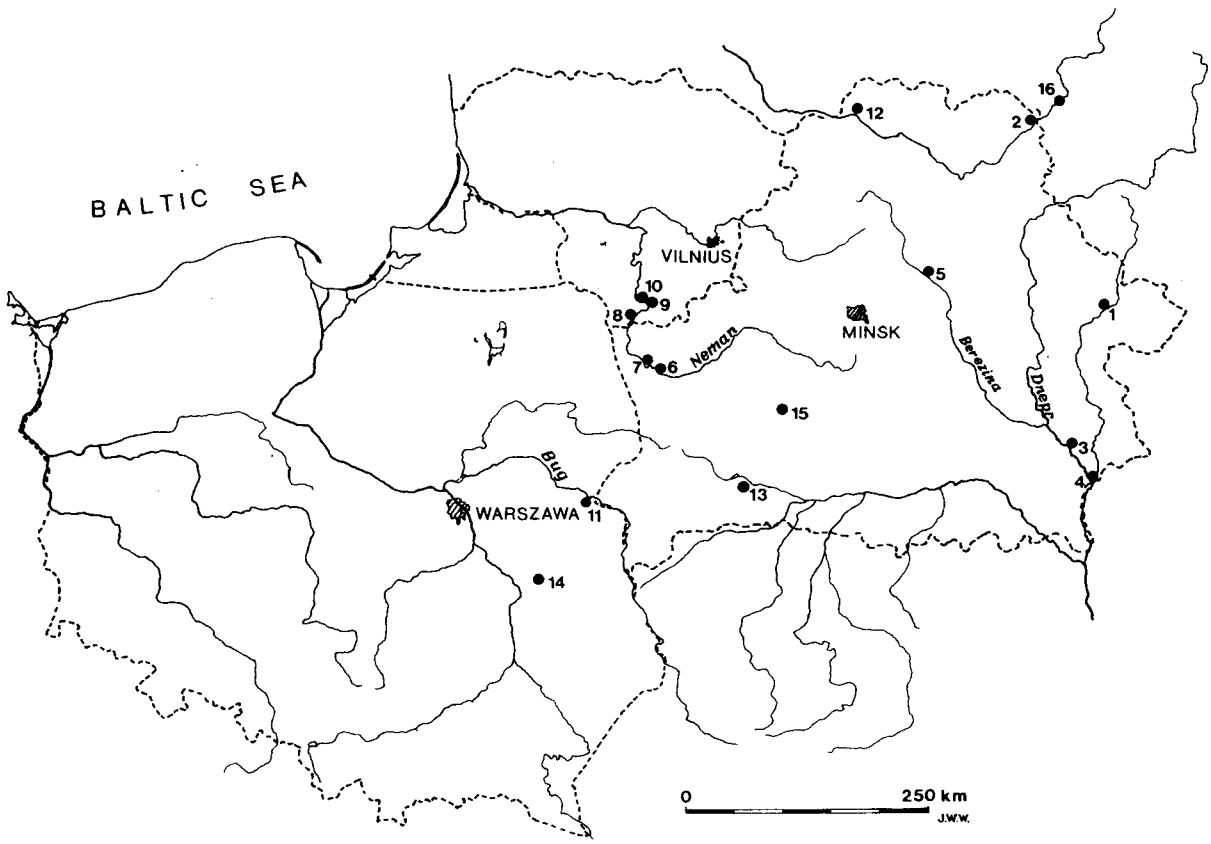

Fig. 1. Location of the sites discussed in the text; Eemian (Murava) Interglacial and Early Vistulian: 1 – Cherikov, 2 – Cherny Bereg, 3 – Borkhov Rov, 4 – Loyev, 5 – Murava, 6 – Knyazhevodtsy, 7 – Komotovo, 8 – Lishkyava, 9 – Yanyonis, 10 – Nyatesos, 11 – Horoszki Duże, 16 – Panfilovo; Ferdynandovian (Belovezha, Cromerian) Interglacial: 12 – Obuchovo, 13 – Motol, 14 – Ferdynandów; Mazovian (Alexandrian, Holsteinian) Interglacial: 15 – Minichi

carried out because of the fragmentary nature of the profile (op. cit.). A later reinterpretation of Bitner's pollen diagram by Mamakowa (1989) enabled her to distinguish two interstadials of the Early Vistulian (Brörup and Odderade) in the top part of the deposits.

In order to undertake a new study at Horoszki Duże aiming at detailed palaeobotanical and stratigraphic analyses of these sediments a 24-metre-thick profile was drilled. Sands with gravel and pebbles (up to 7 cm in diameter – eroded moraine?) formed the bottom part of the lacustrine sediments, overlaid by a series of sand and silts. From a depth of 16 m, the following organogenic deposits occur: calcareous gyttja, bituminous shales, peats, and silts varying in shaliness and claying. This series is covered by a layer of sands one metre thick. The site lies beyond the maximum extend of the Last Glaciation. Palynological and palaeocarpological analyses of the part of the profile representing the Late Warta Glacial, Eemian Interglacial, Early and Middle Vistulian were carried out.

FOSSIL MATERIAL

At the site Horoszki Duże endocarps of *Potamogeton sukaczevii* have been found only in the part of the profile which is acknowledged on the basis of palynological studies to represent the first interstadial of the Early Vistulian (at a depth of 9.42–13.10 m). This was a period of the development of forests, birch at first (with *Betula alba* and *B. humilis*) followed by taiga-type boreal forests with *Pinus cembra* or *P. sibirica*, *Picea* sect. *Picea* and *Larix*. Remains of *Potamogeton sukaczevii* have not been found in deposits of the Eemian Interglacial, nor in other interstadials of the Early and Middle Vistulian. Its endocarps were accompanied by macrofossils of other species of *Potamogeton*: *P. praelongus* Wulf., *P. compressus* L., *P.* cf. *obtusifolius* Mert. et Koch, *P. pussilus* L., and many aquatic and marsh taxa: *Caulinia flexilis* Willd., *Nuphar pumilum* (Timm.) DC., *Myriophyllum alterniflorum* DC, *Batrachium* sp., *Eleocharis palustris* (L.) Roem. et Schult., *E. ovata* (Roth) Roem. et Schult., *Menyantes trifoliata* L., *Scheuchzeria palustris* L. and others.

The endocarps from Horoszki Duże were compared with those from all the Eemian and Early Vistulian sites in Belarus and in the southern regions of Lithuania. In order to show the most characteristic morphological features of *Potamogeton sukaczevii*, its endocarps were also compared with the endocarps of the present-day East-Asiatic species *P. maackianus* and

with older species of this genus from Mazovian (Alexandrian) and Ferdynandovian (Byelovyezhskiy, Cromerian) interglacial floras.

SYSTEMATIC PART

Potamogeton sukaczevii Wieliczk.

Pl. 1 figs 1–15, Pl. 2 figs 1–5

Description. The endocarps are large (2.5–3.1 × 2.0–2.6 mm), wide obovate and thick. In its upper half or over two-thirds of its length the ventral margin is straight or slightly concave, passing into the broad base of the thick conical pedicel, sometimes with remains of the stalk at the end. Fragments of the spongy tissue of the mesocarp are as a rule preserved in the middle part of the ventral margin. The lid is broad, thick, slightly bent, with a small blunt keel, which sometimes bears fragments of a high, thick crest and – in its lower part – a large nipple. The upper part of the lid does not reach the base of the style, but a true shoulder is rare. More frequently, the shoulder is found to be false, being formed of the endocarp edges grown together, covered by a thin, awl-shaped spine of the lid. The style is placed centrally, more rarely shifted sidewards, fairly thick, straight or bent. The lateral side is lightly convex, with an insignificant central depression and a through aperture. An arched furrow extends along the thickened dorsal margin of the endocarp and pronounced basal warts occur in the base on either side. The walls are thick and durable. The thin-cellular surface is yellowish or brown in colour, with a light oily reflex.

Comparison. The endocarps of the type collection are more variable as regards dimensions (2.7–3.5 × 2.2–3.3 mm). They have a plate-like crest on the lid, better-preserved fragments of spongy tissue on the ventral margin and on the lateral sides along the dorsal line. They mostly lack a shoulder or have a small false one. Among the several hundreds of endocarps of the type collection there are many specimens absolutely identical to those described from Horoszki.

The endocarps of *Potamogeton sukaczevii* from other Neopleistocene floras of Belarus (Komotovo, Knyazhevodtsy, Cherny Bereg, Murava, Borchov Rov), Lithuania (Yanyonis, Nyatiesos, Lishkyava) and western Russia (Panfilovo, Ryasna, Nizhnyaya Boyarshchina), despite some morphological variation, exhibit the essential diagnostic features of the species very well and differ distinctly from all the other species of this genus. The diversiformity of the endocarps of *P. sukaczevii* is above all connected with the intraspecific variability of this species in the area of its occurrence (valleys of various rivers). No doubt, their morphology has also been influenced by entirely abiotic factors namely the lithology of the sediments, their chemical composition, compactness, etc. For instance, the endocarps from strongly compacted lacustrine sapropelites (Pl. 1 figs 9–11, Komotovo) are more flattened and angular than those from peat (Pl. 1 figs 14–15, Murava) and humic sands (Pl. 2 figs 1–2, Knyazhevodtsy). Some conditions under which plant remains persisted in the sediment are able to enhance or to suppress the morphological features of the fossil endocarps to a certain degree and thus to create additional difficulties in their exact determination.

In the modern European flora there is no *Potamogeton* species resembling *P. sukaczevii* in endocarpal structure. Endocarps of the present-day East-Asiatic species *P. maackianus* come nearest the fossil endocarps of *P. sukaczevii*, from which, however, they differ in the following characteristics: being thicker and having a less convex ventral margin, on which there are no fragments of mesocarpal tissue, with the lid pressed-in deep and hardly any crest, the thick style shifted towards the ventral margin, a small, false shoulder, if any, and a slight depression in the lateral sides instead of a through aperture (Pl. 2 figs 6–8, contemporary).

The difference between the Neopleistocene *P. sukaczevii* and the modern *P. maackianus* is relatively small, which is not surprising, as other Pleistocene species of *Potamogeton* related to *P. maackianus* also represent a similar general type of structure of endocarps but quite different combinations of essential morphological characters. Endocarps of the extinct Middle Pleistocene species *P. goretskyi* Dorof., described from the Mazovian (Alexandrian) flora of Belarus (Dorofeev 1986), are massive, angular, with an s-shaped and slightly angular ventral margin and a broad keel-like lid devoid of a crest; in the lower part of the lateral sides they have stout nipples curved outwards (Pl. 2 figs 9–10). Remains of this species are

Table 1. Affinity of the pleistocene species of *Potamogeton*

Extinct European species	Recent east-Asiatic and east-Siberian species
P. sukaczevii Wieliczk.	
P. goretskyi Dorof.	
P. sarjanensis Wieliczk.	*P. maackianus* A. Benn.
P. praemaackianus Wieliczk.	
P. dvinesis Wieliczk.	*P. distinktus* A. Benn.
P. diginoides Dorof.	*P. diginus* Wall. ex Hook
P. felixi Dorof.	*P. fryeri* A. Benn.
P. pannosus Dorof.	
P. ultimus Dorof.	*P. manschuriensis* A. Benn.
P. dorofeevii Wieliczk.	*P. sibiricus* A. Benn.
P. cf. *tenuifolius* Raf.	*P. tenuifolius* Raf.

comparatively scarce in fossil floras, but their exceptionally original shape rules out mistakes in their identification.

Endocarps of the third species, *Potamogeton sarjanensis* (Pl. 2 figs 11–15) (Velichkevich 1979), characteristic of the Ferdynandovian (Byelovyezhskiy, Cromerian) Interglacial floras of Belarus and adjoining regions are, in comparison with *P. sukaczevii* and *P. goretskyi*, irregularly round in shape, with more streamline contours; the shoulder is broad, sloping, the style situated centrally and the lid sometimes pressed-in deep. The basic diagnostic characters of this species are stable and present even in specimens from very isolated sites of fossil floras (Velichkevich 1982). Velichkevich has recently found some endocarps very similar to those of *P. sarjanensis* in an assemblage of macrofossils from the site Ferdynandów (eastern Poland), whose flora is correlated with the floras of the Byelovyezhskiy Interglacial in Belarus (Janczyk-Kopikowa 1975, 1991). In all probability, the same species occurs in the Early Pleistocene flora from Leith in the north of Germany (Gregor & Menke 1986, Pl. 2 fig. 1), but it was identified by those authors as *P. natans* L. Referring by those authors to the Tralau paper (1971) in this case seems to be incorrect, since the paper shows real *P. natans* (Tralau 1971, Pl. 3:1, fig. 8). The latest finds (Horoszki Duże, Ferdynandów, Leith) allow us hope that some extinct species of *Potamogeton* may be hidden under the names of various contemporary species in some other interglacial floras published from Europe, notably the Early and Middle Pleistocene ones.

DISCUSSION

The genus *Potamogeton* appeared in Europe towards the end of the Eocene (Chandler 1925), but from Siberia it is known from the Oligocene (Nikitin 1965). In the Neogene and particularly in the Pleistocene it became one of the most widespread groups of aquatic plants. In interglacial floras of different ages this genus may be represented by numerous species and often by a great abundance of macrofossils. The species of *Potamogeton* play an important part in appraising and establishing the stratigraphic position of fossil floras, especially Pleistocene ones.

The Pleistocene floras of Poland and Belarus developed under similar palaeogeographical conditions and, as a result, show many similarities. Joint macroscopic studies of the Mazovian Interglacial floras in Poland and the Alexandrian floras in Belarus pointed out that these floras resemble each other not only owing to the general taxonomic composition but also to the set of extinct exotic species from such genera as *Brasenia*, *Aldrovanda*, *Aracites*, *Myriophyllum* and others (Mamakowa & Velichkevich 1993a, b). This is also true of the genus *Potamogeton* from coequal interglacial floras of Poland and Belarus, which in addition to typical European species, embrace also a number of exotic species mostly with East-Asiatic phylogenetic connections.

The occurrence of *Potamogeton sukaczevii* – the last of the group of extinct species related to *P. maackianus* – in the Neopleistocene (Eemian and Early Vistulian) floras of Poland, Lithuania, Belarus and the western regions of

Russia indicates the maintenance of close connections with the East-Asiatic flora nearly all through the Pleistocene (Tab. 1). In addition to 15–17 recent European species of *Potamogeton* present in various combinations in the interglacial floras of different ages, this genus was represented in the Pleistocene of eastern Europe by an only slightly smaller number of exotic species. As a rule, these species occur at the top of the phylogenetic tree of this genus, tree, whose roots reach deep into the Neogene.

At the same time, only several extinct species showing analogous phylogenetic connections are known from older, Middle Pliocene floras of the region under study. These are, e.g. *Potamogeton borysthenicus* Dorof. from the Belorussian flora of Kholmech or *P. tataricus* Dorof. et Wieliczk. from the flora of Mizerna (Velichkevich & Lesiak 1996).

A considerable increase in the specific variety of the genus *Potamogeton* in the Upper Pliocene and Pleistocene should not be regarded as fortuitous, since a very similar picture is observed in some other genera of aquatic plants (*Brasenia*, *Aldrovanda*, *Caulinia*) of the East-European flora (Velichkevich 1982). This interesting phenomenon is most probably connected with frequent and violent climatic fluctuations, which in the Glacio-Pleistocene passed into a sequence of glacial and interglacial stages. In each period of glaciation the water and water-marsh plants of temperate floras were, as a rule, subject to destruction over a large part of their area. These species could then prevail again in a period of subsequent climatic warming in an interglacial, developing anew from small isolated populations which had been in a position to survive somewhere in the periphery of their respective ranges and, naturally, retained only part of the species genotypes. In this way a species could be restored in the area of its former range, though now in a significantly changed state. It may be claimed nearly for certain that the glacial stages of the Pleistocene many a time exerted a positive influence on the rate of evolutionary processes in some of the most plastic taxa of the water-marsh flora (Velichkevich 1994). Large, widespread Neogene species, which usually existed virtually unchanged for millions of years, in the late Pliocene yielded to small, better adapted and more variable Pleistocene species. The greater part of these relatively young species joined the modern flora, others died out gradually during the Pleistocene. The detection and detailed examination of such stenochronic species is important not only to the correct understanding of the distinctness of the Pleistocene flora but also to the biostratigraphy of Pleistocene sediments.

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PLATES

Plate 1

Potamogeton sukaczevii Wieliczk.

1–5. Horoszki Duże

6–8. Cherikov

9–11. Komotovo

12–13. Borkhov Rov

14–15. Murava

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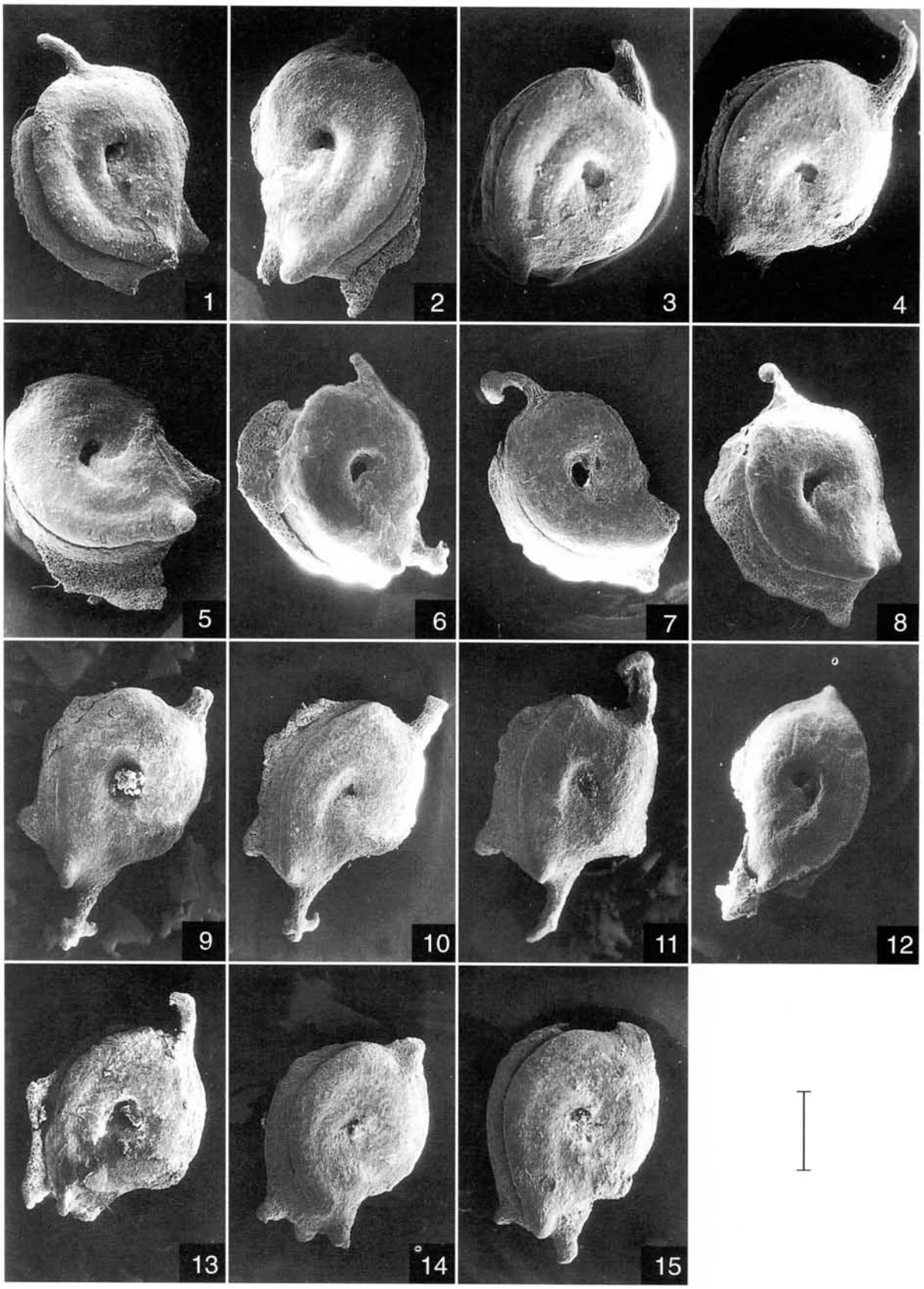
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Plate 2

Potamogeton sukaczevii Wieliczk.

1–2. Knyazhevodtsy

3–4. Panfilovo

5. Yanyonis

Potamogeton maackianus A. Benn.

6–8. Primorskiy Krai (recent)

Potamogeton goretskyi Dorof.

9–10. Minichi

Potamogeton sarjanensis Wieliczk.

11–13. Obuchovo

14–15. Motol

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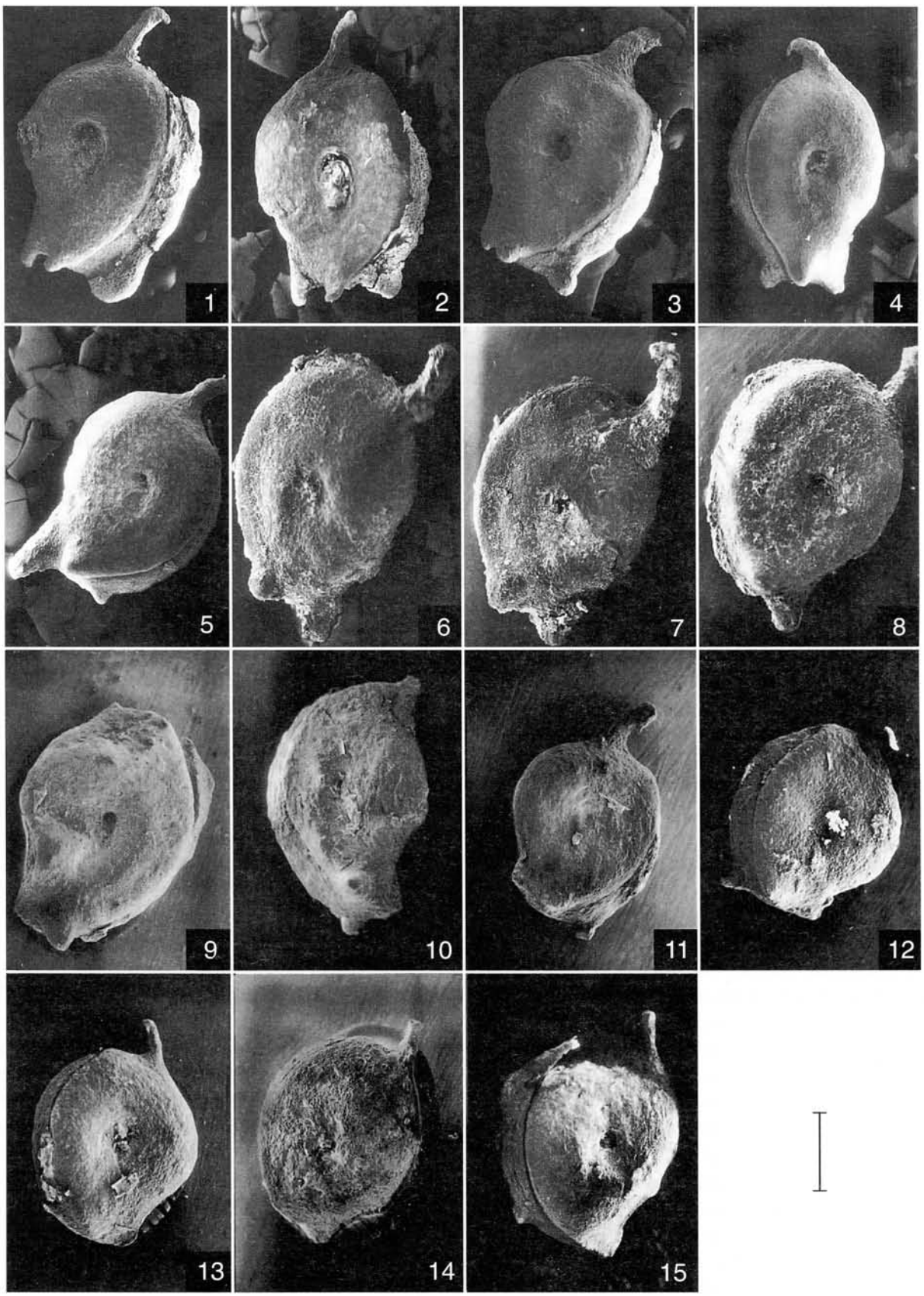
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