Acta Paleobot. 36 (1): 79–95, 1996

FOSSIL *POTAMOGETON* SPECIES OF MIZERNA*

FELIX YU. VELICHKEVICH[1] and MARIA ANNA LESIAK[2]

[1] Institute of Geological Sciences, Academy of Sciences of Belarus, Zhodinskaya Str. 7, 220141 Minsk, Belarus
[2] W. Szafer Institute of Botany, Polish Academy of Sciences, ul. Lubicz 46, 31–512 Kraków, Poland

ABSTRACT. A taxonomic revision of the genus *Potamogeton* has been carried out. Endocarps of the genus have been examined in fossil material from Mizerna (Pliocene-Pleistocene). Fossil collections from Belarus and another eastern part of Eurasia have also been studied and compared. The morphology of the endocarps has shown new features which supplement the taxonomic diagnosis of the species. Descriptions and plates of the endocarps of 18 species are given. Comparison of each species from Mizerna with available fossil or contemporary material has been made. 10 extinct species and 3 distinct groups of the genus *Potamogeton* have been distinguished.

KEY WORDS: *Potamogeton,* endocarps, extinct species, type collections, flora, Mizerna, Belarus, Pliocene, Pleistocene

INTRODUCTION

The famous Neogene flora of Mizerna investigated and described by W. Szafer (1954) retains its very important significance to the present day. This flora was obtained from an approximately 30 m thick layer of sediments which originated during the long period from the Middle Pliocene to the Lower Pleistocene. A few developmental vegetation stages corresponding to climatic change and varying palaeogeographical conditions were distinguished by W. Szafer. It should be stressed that a gradual cooling of the climate in the Late Cenozoic resulting in several glacial and interglacial periods might already have begun in the Pliocene or Upper Miocene, a supposition supported by several modern investigations (Zuchiewicz 1983). There is no evidence of sudden climatic change at the end of the Pliocene/Pleistocene in Europe. Cooling phases revealed in the floristic composition of fossil floras were present in different stages of the Pliocene, so the proper and precise establishment of the Pliocene/Pleistocene boundary has still been difficult and the subject of much discussion (Szafer & Oszast 1964, Oszast 1970, Zuchiewicz 1983, Stuchlik 1987).

During recent stratigraphical investigations on the Neogene and Pleistocene in Europe have developed considerably. On the basis of available palaeobotanical materials obtained from sedimentary sequences a large number of new stratigraphical units, clearly and unequivocally connected, have been established (Gurskyi & Levkov 1977, Friis et al. 1978, Gregor 1990, Sadowska 1990, Lindner et al. 1995).

The flora of Mizerna collected from outcrops and borings during several years of field work contained approximately 200 taxa of cryptogamae and phanerophyta and is considered to be one of the richest Pliocene-Pleistocene floras in Europe. In the light of modern scientific investigations the study of this flora should continue to provide information about the history of the flora in the late Cenozoic and the development of contemporary members of European vegetation.

W. Szafer distinguished water plants as important markers in relation to climatic changes. Among all water plants the genus *Potamogeton* was singled out to show its stratigraphic significance (Szafer 1954, p. 199–201). From studying over 1500 specimens, Prof. Mądalski established the existence of 16 recent

* This work has been possible thanks to a scholarship and financial support from the Kasa im. J. Mianowskiego (Fundacja Popierania Nauki) of Poland given to the senior author in 1996.

European species of *Potamogeton* derived from 7 complexes of Mizerna (Mizerna I – Mizerna IV) (Szafer 1954, p. 108, Tab. 20). Several years later Prof. M. Łańcucka-Środoniowa became the first person to pay attention to Mądalski's incorrect identifications of species and stressed the necessity of *Potamogeton* revision.

This work has been done by the two authors in this paper during 1995–96 with financial support obtained by F. Yu. Velichkevich from the Kasa im. J. Mianowskiego, Warsaw.

The recent family Potamogetonaceae comprises about 100 species of aquatic herb widely distributed in fresh and brackish water. The fruits are usually apocarpous formed from 1 – 4 drupes or more rarely nutlets. The endocarps are laterally flattened and characterized by dorsal germination valvae and a central depression on each side. There is a single campylotropous seed in each nutlet. Fossil endocarps of *Potamogeton* are common in the Tertiary floras of Europe and Asia, the earliest being recorded from the late Lower Eocene of southern Europe (Friis 1985).

MATERIAL AND METHODS

All fossil endocarps of *Potamogeton* obtained during 1949, 1960–1962 from the flora of Mizerna and stored in sets in boxes at the Museum (coll. no. KRAM-P 15/RW) of the Palaeobotanical Department have been examined. The materials from borings a, 1, 2, 4, 5 and from outcrops marked as: hole above gravels, outcrop, peat next to a new bridge – July 1961, wall above Koprocz stream and Mizerna 1961, bottom level have been considered and thoroughly studied. Additionally, new material has been examined obtained from a geological boring at Mizerna Nowa made in 1979, when 101 samples taken of regular intervals from the first 38 m of Neogene deposits of gravels, clays, sandy clays and sands were subjected to palaeobotanical analysis. For carpological analysis 53 samples from a 20.5 metre section of the profile (17.5–38.0 m) at intervals of 10–25 cm were examined. In these samples only a few, single endocarps of *Potamogeton* were found. In total, over 2000 well preserved specimens, excluding fragments, were studied. On the basis of this material 18 species, of which 10 are extinct, have been identified. The material was compared with contemporary and fossil endocarps from the eastern collections belonging to F. Yu. Velichkevich. In the case of difficult taxa examples from the type collection of species used for comparision are presented in Plates 1–3. In describing endocarps the following some publications have been used: Aalto 1970, Dorofeev 1986, Velichkevich 1982 and Cappers 1993–1994 from which a few terms have been borrowed. To improve the descriptions and morphological nomenclature the authors have added some features establishing a full set of distinct endocarp features (Fig. 1).

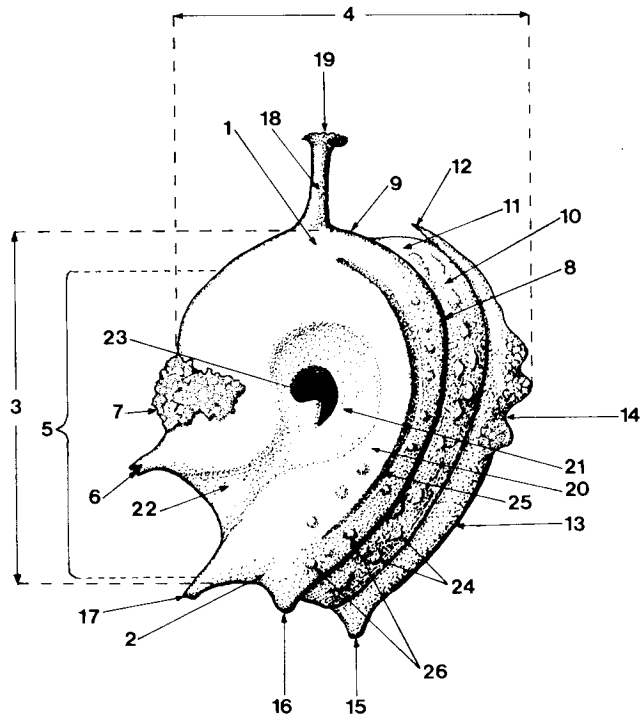


Fig. 1. *Potamogeton* fossil endocarp pattern: morphological characters and terms used in the description: 1 – apex, 2 – base, 3 – length, 4 – width, 5 – ventral margin, 6 – ventral spine (or bulge), 7 – fragments of mesocarp, 8 – dorsal margin, 9 – shoulder (distance between top of lid and base of style), 10 – lid (germination valve), 11 – top of lid, 12 – spine of lid, 13 – keel of lid, 14 – crest (crispate or plate-like), 15 – nipple of lid, 16 – basal wart, 17 – stalk, 18 – style, 19 – stigma, 20 – side, 21 – central depession, 22 – mouth of central depression 23 – cavity, 24 – tubercles, 25 – furrow, 26 – fringes

Dry endocarps were stuck with glue on holders, mounted on a specimen ring, coated with gold in an ion sputter-coating unit Jeol, IFC-1100 and then examined and photographed using a Tesla-BS-301 SEM. Some specimens were also examined under a light microscope.

SYSTEMATIC DESCRIPTIONS

Potamogeton tataricus Dorof. et Wieliczk.

Pl. 1, figs 1–4

1986 *Potamogeton tataricus* Dorof. et Wieliczk., Dorofeev; p. 36, Figs. 12, 1–9.

Material. Coll. KRAM-P no /15 RW/ 1a, 2, 45–52a, 8a, 64a, b, 70: 576 endocarps.

Description. The endocarps are fairly large, 2.2–2.8 mm long and 1.7–2.4 mm wide. They are obovate and asymmetrical. The ventral margin is strongly convex in the 2/3 and straight or concave in the basal 1/3. The dorsal

margin is uniformly convex, semicircular with a broad and slightly keeled lid. Sometimes, in the upper part of the lid, a small crest has been preserved and at its base small warts are visible. The pointed top of the lid falls short of the style base leaving a small shoulder. The style is centrally positioned, fairly thick and long and usually inclined towards the dorsal margin. The stalk is short and blunt, with a broad and cuneate base. The sides are convex, with a small and deep central depression. The endocarp walls are thick with their surface small-celled, mainly dark brown, mat or slightly lustrous.

Comparison. The endocarps of the *P. tataricus* type collection from the Middle Pliocene flora of Rybnaya Sloboda in Tataria agree with those described above. (Pl. 1, fig. 4), except that they are slightly narrower, possess a less convex ventral margin and a narrower, crevice-like central depression. Besides, some of the endocarps of the Tataria collection have a small, but distinct shoulder. The other species from the same group (*P. tertiarus* Dorof., *P. praemackianus* Wieliczk. and *P. sarjanensis* Wieliczk.) show considerably greater differences from the species described above and point to a more distant relationship within the genus.

Potamogeton obtusatus Dorof.

Pl. 1, figs 5–9

1986 *Potamogeton obtusatus* Dorof., Dorofeev; p. 97, Fig. 50, 1–10.

Material. Coll. KRAM-P no /15 RW/ 3d–67: 244 endocarps.

Description. The endocarps are medium sized, 2.0–2.5 × 1.6–1.9 mm, obovate and flat. The ventral margin is slightly convex to nearly straight or somewhat sigmoid, with a rouned edge and furnished with a ventral bulge in the lower part. The dorsal margin is falcate or nearly semicircular. The lid has an entire or crispate crest. The top of the lid is adpresseed to the style, or more frequently separated from it by a small shoulder which is sometimes absent. The style is thin, filamentous and very rarely preserved. The stalk is tubercular, poorly differentiated and often absent. The sides are flat or concave with a broad, shallow central depression extending to the ventral margin in the form of a mouth. The endocarp walls are fairly thin to thick. The surface may be even, rough, mat or slightly lustrous.

Comparison. The endocarps of the type collection from the Middle Pliocene flora of Kholmech, Belarus (Pl. 1, figs 8, 9) completely match the ones studied in size and shape but differ by having a more conspicuous plate-like and crispate lid crest. The endocarps of the contemporary *P. obtusifolius* Mert. et Koch show considerably greater differences from those described. Thus, for example, the fossil endocarps of the latter species from the Mazovian interglacial flora of Minichi in the southwestern region of Belarus (Pl. 1, fig. 10) are larger, with convex sides, fringed lid crest and conspicuously prickled stalk. The *P. obtusus* Dorof. endocarps described from the Upper Pliocene of the Tambovskaya area (Dorofeev 1986) are very similar to *P. obtusatus* in several important diagnostic features; the differences between them having principally biometric significance. It should be stressed that *P. obtusatus* was the only species present at least till the Eopleistocene in Belarus, then, in the Middle Pleistocene, *P. obtusifolius* Mert et Koch appeared (Velichkevich 1982).

Potamogeton squamatus Dorof.

Pl. 1, figs 12–14

1986 *Potamogeton squamatus* Dorof., Dorofeev; p. 94–96, Fig. 49, 11–18.

Material. Coll. KRAM-P no /15 RW/ 3a–75a: 593 endocarps.

Description. The endocarps are small, 1.8–2.1 × 1.4–1.8 mm, fairly stable in size but variable in shape: from semicircular or obovate to oval or nearly orbicular. The elongate and obovate forms are the most characteristic. The ventral margin is slightly convex, arched or somewhat sigmoid, keeled at the edge, sometimes with a small, ventral spine in the middle part. The dorsal margin is semicircular, with a narrow and crested lid whose pointed apex reaches the base of the style. Over the greater part of the lid the crest is preserved, being slightly broader towards the apex, but not reaching the top of the lid. The style is short, thick, ventrally positioned, often absent. The stalk is small but usually conspicuous, cuneate in cross-section, inserted laterally towards the base. The sides are flat or slightly sunken, with an inconspicuous central depression. There is sometimes a small, rolled thickening

along the lid which terminates in a nipple at the base. The walls are fairly thin to stout. The surface is fairly smooth, but sometimes slightly rugose, light-brown and mat; under greater enlargement it is inconspicuously celled.

Comparison. The type collection endocarps from the Middle Pliocene flora of Daumantay in Lithuania vary in shape, and on average they are smaller, but one can find among them specimens completely identical to those described above (Pl. 1, fig. 14). Dorofeev, the author of the species, included it in the *P. obtusifolius* group but we disagree: *P. squamatus* has no feature in common with *P. obtusifolius* Mert. et Koch. There are some similarities between *P. squamatus* and the Ukrainian *P. sarmaticus* Maemets (Dorofeev 1986, Fig. 55, 57–58), although its relationship with other contemporary *Potamogeton* species is unclear.

Potamogeton cf. ***aculeatus*** Dorof.

Pl. 1, figs 15–20

1986 *Potamogeton aculeatus* Dorof., Dorofeev; p. 90, 92, Fig. 46, 3–16.

Material. coll. KRAM-P no 15/RW/ 4b, 40a: 5 endocarps.

Description and comparison. The lengths of the three entire endocarps are 2.5, 2.6, 2.7 mm respectively and one endocarp without a lid is 2.3 mm long. In size they completely agree with the specimens of the type collection from the Middle Pliocene flora in Daumantay, Lithuania (Pl. 1, fig. 20). Moreover, the endocarps described are similar in several features to the *P. aculeatus* type. These characters are: the flattened shape, lid structure, presence of some short or long processes on the lid surface and at the sides along the dorsal margin, lack of a shoulder, the presence of a deep and arched furrow (nearly a cavity) on the sides and other less important ones. But the shape of the ventral margin differs significantly from that of *P. aculeatus*: the type endocarps have a slightly convex ventral margin with a spine or bulge in the middle part, but the endocarps of Mizerna have a ventral margin with a strongly pointed lower part and a narrow upper part which protrudes forward. The studied endocarps are not numerous and are partially deformed, so the above mentioned differences could be caused by fossilization or erosion. The endocarps are characteristic to the extent that they cannot be confused with those of any other *Potamogeton* spp. group. It is most likely that *P. aculeatus* occurs in the flora of Mizerna, because the other species from the same group (*P. antiquus* Dorof. and *P. grisczenkoi* Dorof.) differ considerably greater from those described above.

Potamogeton peregrinus Dorof.

Pl. 1, figs 21, 22; Pl. 2, figs 1–4

1986 *Potamogeton peregrinus* Dorof., Dorofeev; p. 53–55, Fig. 23, 1–12

Material. Coll. KRAM-P no 15/RW/ 1d, 4a, 52b, 58b–64c: 76 endocarps.

Description. The endocarps are medium sized, 2.2–2.5 × 1.8–2.2 mm, oval and flat. The ventral margin is unevenly sigmoid, rounded at the edge, sometimes with a mesocarpal excrescence originating from the central depression. The dorsal margin is uniformly convex, cordate to semicircular in shape. The lid is broad, keeled, with a small, plate-like crest. The pointed top of the lid reaches the base of the centrally positioned, small and thick style that is seldom preserved. The stalk is very small, often absent. The sides are flat or slightly sunken, with large cavity in the middle. The dorsal margin is rolled with a prominent wart at the base. The surface is smooth, fine-celled, mat and grey-brown. The walls are moderately thick.

Comparison. The endocarps of the type collection from the Upper Pliocene flora of Lipetska area are very variable in size and shape, but many of them very closely resemble those described. The endocarps of Mizerna differ in having more uniform size and shape, a thinner and more fragile style, a somewhat inconspicuous stalk and a smaller lid crest. The other related species from this group: *P. rossicus* Dorof., *P. lepidus* Dorof. and *P. mendymensis* Dorof. are similar in endocarp pattern to those described above but differ considerably in size and shape, wall thickness and perforation and slightly in other less important features.

Potamogeton compressoides Dorof.

Pl. 2, figs 5–9

1986 *Potamogeton compressoides* Dorof., Dorofeev; p. 84, Fig. 41, 1–10

Material. Coll. KRAM-P no 15/RW/ 7a, 23c, 30a–74: 26 endocarps.

Description. The endocarps are large, 2.3–2.9 × 1.5–2.3 mm, obovate or nearly semicircular, inflated and thick. The ventral margin is slightly inclined in the upper part, only rarely is it convex. The lower part of the ventral margin is straight or somewhat folded, sometimes with a ventral bulge. The lid is keeled, with remnants of a plate-like or fringed crest. The top of the lid reaches the base of the style, sometimes leaving a very short shoulder. The style is prickly, centrally positioned or sometimes somewhat ventrally displaced. The stalk is very small, inconscpicuous, situated laterally and obliquely inserted at the base. The sides are convex or slightly flattened with a small cavity opening at the ventral margin above the ventral spine. Some of the endocarps, probably slightly immature, are flatters, thin-walled, with a large central depression.

Comparison. The endocarps studied agree completely in their size, shape and other details with the endocarps of the type collection from the Upper Pliocene flora of the Ranino Tambovskaya area in Russia (Dorofeev 1986). The endocarps of the contemporary species *P. compressus* L., for example from the Eemian flora of Nizhnaya Boyarshchina from the west of the Smolensk area in Russia, are larger, longer, with a pointed base and distinct stalk and they are furnished with a crispate lid crest, thick style and large, arched central depression (Pl. 2, figs. 10, 11).

Potamogeton pseudoacutifolius Dorof.

Pl. 2, figs 12–15

1986 *Potamogeton pseudoacutifolius* Dorof., Dorofeev; p. 88, Fig. 45, 11–18

Material. Coll. KRAM-P no 15/RW/ 4c, 21c, 22d, 54, 57a, 66b: 16 endocarps.

Description. The endocarps are fairly large, 2.0–2.7 × 1.6–2.2 mm, obovoid and thick-walled. The ventral margin is convex, sometimes almost keeled, with a large spine in the middle or slightly below, folded at the edge. The lid is broad, keeled, with a crispate or plate-like crest and sometimes tubercles and fringes are also visible. The top of the lid usually reaches the base of the style, rarely leaving a small shoulder. The style is prickly, centrally or ventrally positioned, but more often absent. The the stalk is tiny and somewhat inconspicuous. The sides are inflated, convex, with a large central depression opening into a mouth at the dorsal margin above a bulge; sometimes tubercles can be seen along the ventral margin. The walls are thick and their surface is uniformly rough and dark to light brown.

Comparison. The type collection endocarps from the Middle Pliocene flora of Kholmech, Belarus, agree with ours for the most part, but they have more tubercles on the sides, a larger ventral bulge, a more distinct stalk and a crispate lid crest. The endocarps of *P. acutifolius* Link from the Middle Pleistocene flora of Minichi, Belarus, are larger, furnished with a prominent crispate lid crest, slightly convex ventral margin and inflated sides (Pl. 2, figs 16, 17). The more recent endocarps of *P. acutifolius* Link are fairly large, shorter and wider than the fossil ones, having a slightly crispate lid crest and nearly smooth sides, without a central depression.

Potamogeton cf. ***pliocenicus*** Dorof.

Pl. 2, fig. 19

1966 *Potamogeton pliocenicus* Dorof., Dorofeev; p. 48, Pl. 1, Figs. 21–24, designat. typi omissa

1986 *Potamogeton pliocenicus* Dorof., Dorofeev; p. 53, Fig. 24, 12–16

Material. Coll. KRAM-P no 15/RW/ 40b: 20 endocarps.

Description. The endocarps are medium sized, 2.1–2.4 × 1.6–1.8 mm, flat, thin-walled, poorly preserved. The ventral margin is slightly convex or sigmoid, folded and acute at the edge. The stalk is small or completly absent. The dorsal margin is somewhat arched and the lid is broad, keeled, often with a short, plate-like crest. The top of the lid does not reach the style base, leaving a small, somewhat raised shoulder. The style is usually broken with its base ventrally positioned. The sides are flat or sunken, they are thickened and protrude at the edge, and they have a broad central depression or cavity. The surface is rough, sometimes bearing remnants of the mesocarp, mat and dark brown.

Comparison: Many extinct, predominantly the Pliocene species of *Potamogeton,* separated by Dorofeev into the Perfoliatus group have similar endocarps. There is an evident resemblance between this group and our studied endocarps and, additionally some specific features (size and shape, wall thickness, lack of spines or tubercles) which allow us to include

them in the Middle Pliocene species *P. pliocenicus* Dorof. which was widely distributed in the south of the Ukraine and Russia.

Potamogeton cf. ***heterocarpus*** Dorof.

Pl. 2, figs 20, 21; Pl. 3, fig. 1

1986 *Potamogeton heterocarpus* Dorof., Dorofeev; p. 53, Fig. 25, 1–10

Material. Coll. KRAM-P no 15/RW/ 3c, 8c, 9b, 10c–26c, 36c: 27 endocarps.

Description. The endocarps are medium sized, 2.2–2.6 × 1.6–2.0 mm, obovate or nearly obovoid, flat. The ventral margin is convex in the middle or only in the upper part, folded at the edge, sometimes furnished with a small spine below the middle. The lid is smooth, keeled, sometimes with a small, irregular crest. The shoulder is very inconspicuous or absent. The style and stalk are not preserved. The sides are thickened, with a shallow central depression.

Comparison. The endocarps of the *P. heterocarpus* type collection from the Middle Pliocene flora of Belarus are similar in size and shape to ours but differ from them in having thinner walls, a better developed central depression and preserved style. The authors are unable to give a more precise specific identification of the Mizerna endocarps.

Potamogeton natans L.

Pl. 3, figs 2–4

Material. Coll. KRAM-P no 15/RW/ 22c, 23b, 24a, 26d, 56, 65, 69: 38 endocarps.

Description. The endocarps are medium sized, 2.0–2.4 × 1.1–1.8 mm, obovate, mainly elongate. The ventral margin is slightly convex, somewhat folded in the lower part, rounded at the base and lacking any processes. The lid is smooth, keeled, furnished in the upper part with a crest which falls short of the top of the lid. The shoulder is raised, small but conspicuous. The style is ventrally positioned, rarely preserved, the stalk inconspicuous. The sides are slightly convex, with a small but sometimes deep, arched central depression.

Comparison. The contemporary and Pleistocene endocarps of this species are larger, with more convex sides and a crested keel, but among numerically large collections one can find endocarps that completely agree with those described above (Pl. 3, figs 3, 4).

Potamogeton perfoliatus L.

Pl. 3, figs 5–7

Material. Coll. KRAM-P no 15/RW/ 6a, 24e, d, 62b: 11 endocarps.

Description. The endocarps are 2.4–2.5 × 1.7–2.0 mm, obovate and bent in the long axis. The ventral margin is slightly sigmoid, keeled or sometimes rounded. The lid is furnished with a smooth or spiny keel, the top of the lid reaching the base of the style. The ventrally positioned style has a broad base. The sides are thickened and have a small, shallow central cavity, sometimes only an arched, inconspicuous hollow. The walls are thick.

Comparison: The contemporary and Pleistocene endocarps of this species are very variable in their basic diagnostic features, closely resembling *P. natans* but differing from it in possessing thick sides, a nearly smooth lid and in the lack of a shoulder.

Potamogeton praelongus Wulf.

Pl. 3, figs 8, 9

Material. Coll. KRAM-P no 15/RW/ 57b: 1 endocarp.

Description. The endocarp is 3.1 × 2.3 mm, obovate and thick. The ventral margin is sigmoid and folded at the edge. The lid is large, keeled, with an entire-edged and plate-like crest that does not reach the top of the lid. The shoulder is very small and raised. The style and the stalk are not preserved. The sides are slightly convex, with a small, arched central depression opening into a mouth on the ventral side. The surface is finely pitted, dark brown and mat.

Comparison. Contemporary endocarps are larger, more inflated usually with convex sides and without a distinct central depression. Interglacial flora collections do include *P. praelongus* endocarps that vary in size and shape but, provided the collection is large enough, (for example from the Middle Pleistocene flora of Minichi, south-western Belarus) one can find endocarps that completely agree with our single specimen studied (Pl. 3, fig. 9). It is also possible that this specimen belongs to an extinct form of *P. praelongus* but it is impossible to be sure on the basis of a single specimen.

Potamogeton trichoides Cham. et Schlcht.

Pl. 3, figs 10, 11

Material. Coll. KRAM-P no 15/RW/ 49c: 1 endocarp.

Description. The endocarp is 1.8 × 1.5 mm, semicircular. The ventral margin is convex in the upper part, straight below and furnished with a ventral spine. The lid is slightly tubercular, flattened, with the top that reaching the base of the style. The style is centrally positioned, thin, with a thickened stigma. The stalk is absent. The sides are slightly convex, with a large shallow central depression. The walls are thick.

Comparison. The endocarps of this species differ from those of the type collection (Pl. 3, fig. 11) which are wider and possess sunken sides. However, the observed differences fall within the range of infraspecific variability.

Potamogeton ex gr. ***natans*** L.

Pl. 3, figs 12–16

Material. Coll. KRAM-P no 15/RW/ 5b, 6b, 10d: 7 endocarps.

Description. The narrow endocarps are 2.2–2.5 mm in length, deformed and curved. The ventral margin is slightly curved and rounded at the edge. The lid is keeled, rarely furnished with a crest and its top reaches the base of the style. The apex is pointed, the style thick and broken. The stalk is small but distinct. The sides are thickened, with a broad and shallow central depression possessing a small, arched cavity at its base.

Comparison. These endocarps closely resemble *P. natans* L. and *P. perfoliatus* L. in size and shape. Similar endocarps were described by Dorofeev (1986, Fig. 18; 3, 11, 12) under the name *P. pseudonatans* Dorof., an extinct species from the Middle Pliocene of the Lipetskaya area in Russia. On the basis of his description and photographs it can be seen that those endocarps are larger with convex sides and cavities and the results of any comparision between these and our few poorly preserved endocarps should be made with some reservation.

Potamogeton cf. ***rutilus*** Wolfg.

Pl. 3, figs 17–19

Material: coll. KRAM-P no 15/RW/ 47c, 52c, 58c, 64d: 58 endocarps.

Description. The endocarps are small, 1.8–2.2 × 1.2 × 1.6 mm, semicircular, elongate and inflated. The ventral margin is slightly convex, especially in the upper part, rounded at the edge and terminates the base in a prominent spiky stalk. The dorsal area is uniformly convex, with a low and slightly keeled or rounded lid whose top reaches the style base, sometimes leaving a tiny shoulder. The style is a slender, fairly long, somewhat ventrally positioned. The sides are convex, without a central depression. The walls are thick. The surface is smooth, mat, brown or almost black.

Comparison. The contemporary and Neopleistocene endocarps of *P. rutilus* Wolfg. are similar in size and shape to our studied ones but differ by being slightly smaller, narrower with a nearly straight ventral margin and a pointed or blunt apex and base. The endocarps of the extinct species of *P. palaeorutilus* Dorof. and P. *pseudorutilus* Dorof. are also smaller and wider and have differently shaped styles and the stalks.

Potamogeton ex gr. ***friesii*** Rupr.

Pl. 3, figs 20–22

Material. Coll. KRAM-P no 15/RW/ 52d, 60b: 19 endocarps.

Description. The endocarps are small, 1.6–1.9 × 1.2–1.5 mm, obovoid or obovate, inflated. The ventral margin is convex, involute at the base, rounded at the edge. The dorsal side is convex, with a broad and slightly keeled lid whose top does not reach the base of the style, leaving a small and inconspicuous shoulder. The style is short, pointed and ventrally positioned, vertical or inclined towards the dorsal margin. The stalk is short and prickled. The sides are convex, smooth or with a tiny circular or arched central depression. The walls are thick. The surface is smooth, mat and grey-brown.

Comparison. Dorofeev referred most of the features distinguished to the extinct Neopleistocene species *P. pseudofriesii* Dorof. There are reasons to believe that in the flora of Mizerna some similar extinct species from that group existed which only approximately resemble contemporary *P. friesii* Rupr.

Potamogeton panormitanoides Dorof.

Pl. 3, figs 23–25

1986 *Potamogeton panormitanoides* Dorof., Dorofeev; p. 107, Fig. 54, 2–8

Material. Coll. KRAM-P no 15/RW/ 59, 60a: 2 endocarps.

Description and comparison. The only two endocarps are 1.4 × 1.1 mm and 1.3 × 1.0 mm. To separate them from other species, a combination of features has to be taken into account: small size, the ventral margin that is convex in the upper part, the smooth lid with the top reaching the base of the style, the very small style and the stalk and slightly convex sides. The endocarps of an extinct Middle Pleistocene species from the Byelovezha (Ferdynandów in Poland) interglacial flora of Motol in western Belarus, are very similar to those described above. The endocarps of the contemporary *P. panormitanus* Biv.-Bern. (Finland, Aalto 1970) are comparable to ours in size but differ in their narrow, wedge-like base, more dorsally positioned style and small shoulder.

P. panormitanoides Dorof. was a characteristic species of the interglacial floras of the East-European Plain where a large number of endocarps have been found. The presence of two separate but very characteristic endocarps of *P. panormitanoides* in the flora of Mizerna considerably increases its stratigraphical range from the Middle Pliocene to the early Middle Pleistocene.

Potamogeton cf. ***coloratus*** Hornem.

Pl. 3, figs 26–28

Material. Coll. KRAM-P no 15/RW/ 11, 55b: 13 endocarps.

Description. The endocarps are small, 1.1–1.3 × 0.8–1.0 mm, obovoid or obovate, flat, without style and stalk. The ventral margin is slightly convex, slightly folded in the lower part. The lid is narrow, keeled, with its top reaching the base of the style or it leaving a tiny shoulder. The sides are flat or slightly convex, with a central cavity and shallow furrow along the lid. The surface is coal-black, mat. The walls are rather thick.

Comparison. Contemporary endocarps are larger, with a distinct style and stalk but in general they agree with those described above. The endocarps of the far-eastern *P. juzepczukii* Tzvel. (Dorofeev 1986, Fig. 55; 50–52) are similar to ours but differ in their more spherical shape, stout style and crested lid. The endocarps of the contemporary *P. polygonifolius* Pourr. are considerably larger, thicker and furnished with a shorter and wider lid bearing a small central depression or cavity (Aalto 1970, Figs. 71–72, Dorofeev 1986, Fig. 55, 53–56). The extinct species *P. coloratoides* Dorof. and *P. parvulus* Dorof. from the Upper Pliocene of Belarus are also similar in size and shape to the above, but differ from them by being more circular in shape, having thinner walls, a large cavity and the other slightly different features clearly visible on several endocarps from the type collections.

CONCLUSIONS

Our revision of *Potamogeton* has yielded much new data which cannot be related to Mądalski's previously published results (Szafer 1954). The species representation given by him from a few complexes (fossil assemblages) at Mizerna was almost completely false (op.cit. table 20). After our revision we realized that some of the collection sets named by Mądalski, and kept at the Museum, consisted of quite different species, sometimes even from different groups. Some sets, bearing the name of one species, were in fact composite. For example, in the P. trichoides set, the senior author recognized 3 completely different species, none of which was *P. trichoides*. On the basis of our present investigations only 5 species, all misidentified, have been confirmed among the 16 determined by Mądalski.

Results from the 1979 Mizerna Nowa geological boring were disappointing. Only 13 single endocarps of *Potamogeton* belonging to *P. obtusatus*, *P. squamatus*, *P. heterocarpus*, *P.* cf. *pusillus* and *Potamogeton* spp. were found in 6 out of 53 samples. Hence detailed stratigraphical investigations based on correlation with sedimentary sequences have not been possible.

By comparing the *Potamogeton* species of Mizerna with both extinct and contemporary species we can conclude that the Mizerna material separates, by age, into 3 species groups :

1. The oldest group comprises *P. tataricus*, *P. obtusatus*, *P. squamatus* and *P. aculeatus*. These are characteristic of the Middle Pliocene of Lithuania, Belarus and areas in western and central Russia. The total number of endocarps from this group, excluding *P. aculeatus*, is the greatest in the entire Mizerna collection. There are frequently 100 or more per sample. One may assume that this abundance is the result of the original laying down of the pri-

mary fossil flora assemblies which occured in the the Middle Pliocene.

2. The second group contains species described from the Middle and Upper Pliocene deposits of Belarus, Ukraine and Russia, namely: *P. peregrinus*, *P. compressoides*, *P. pseudoacutifolius*, *P. panormitanoides*, *P.* cf. *pliocenicus* and *P.* cf. *heterocarpus*. These extinct Upper Pliocene species have some relationships with contemporary ones, but each has its own specific characters. Endocarps of this group were not numerous at Mizerna, but they were observed in samples where endocarps of the first group were dominant.

3. The third and most recent group consists of endocarps of contemporary species, or species closely related to them. Often these species were described on the basis of single endocarps, so it has not been possible to determine them with certainty. In spite of this we have been able to identify the following contemporary species: *P. natans*, *P. perfoliatus*, *P. prelongus* and *P. trichoides*. Other species in this group, whose endocarps have been found, are described using modern names bearing some form of annotation such as cf.or ex gr. These species differ in some way, not only from the contemporary ones which they not resemble, but also from these of interglacial floras. The species concerned are: *P.* ex gr. *natans*, *P.* cf. *coloratus*, *P.* cf. *rutilus* and *P.* ex gr. *friesi*. They all belong to a group with small sized fruits which are taxonomically troublesome, even in contemporary floras. The slight morphological differences found in the fossil endocarps, excluding erosion, may point to incomplete species differentiation.

If we assume that, even in the oldest interglacial floras, the endocarps of properly described species were fairly similar to these of contemporary ones, we can conclude that the differentiation of the youngest complexes of the Mizerna (III/IV, IV, Szafer 1954) must have been completed at the Pliocene/Eopleistocene boundary or by the very beginning of the Eopleistocene.

ACKNOWLEDGEMENTS

The authors would like to thank Professor L. Stuchlik and Assist. Professor E. Zastawniak for allowing them to study all the fossil material from Mizerna stored at the Museum of Palaeobotany, W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow and for their encouragement during this work. Ms Z. Petri and Mr A. Pachoński are thanked for micrographs. Mr J. W. Wieser is thanked for drawing Fig. 1.

The authors are grateful to Mr Arthur Copping for correcting and improving the English text and for his helpful comments on the manuscript.

The senior author gratefully acknowledges financial support from the Kasa im. J. Mianowskiego (Fundacja Popierania Nauki) of Poland.

REFERENCES

AALTO M. 1970. Potamogetonaceae fruits. I. Recent and subfossil endocarps of the Fennoscandian species. Acta Bot. Fennica, 88: 4–85.

CAPPERS R. T. J. 1993–1994. An ecological characterization of plant macro-remains of Heveskesklooster (The Netherlands). A methodological approach. (doctoral thesis). Linders-Adremo BV, Oosterbeek.

DOROFEEV P. 1966. Pliocenovaya flora Matanova Sada na Donu. Nauka, Moskva–Leningrad, (in Russian).

DOROFEEV P. 1986. Iskopaemye *Potamogeton*. Nauka, Leningrad, (in Russian).

FRIIS E. M. 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). Det. Kongel. Danske Videnskab. Selskab, Biol. Skrifter 24(3): 1–165.

FRIIS H., NIELSEN O. B., FRIIS E. M. and BALME B. E. 1978. Sedimentological and palaeobotanical investigations of a Miocene sequence at Lavsbjerg, Central Jutland, Denmark. Danm. Geol. Unders., Arbog: 51–67.

GREGOR H.-J. 1990. European long range correlations, a new phytozonation for Neogene floras in the Tethys-Paratethys region and the problem of the salinity crisis (a computer program). In: Knobloch E. & Kvaček Z. (eds). Proceedings of the Symposium Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary, Prague, August 28th-Sept.1st, 1989: 239–254.

GURSKYI B. N. and LEVKOV E. A. (eds). 1977. Pogranichnye khorizonty mezhdu neogenom i antropogenom (Neogene and anthropogene boundary horizons). Nauka i Tekh., Minsk, (in Russian).

LINDNER L., DZIERŻEK J., LAMPARSKI Z., MARKS L. and NITYCHORUK J. 1995. Zarys stratygrafii czwartorzędu Polski; główne poziomy osadów glacjalnych i interglacjalnych oraz ich rozprzestrzenienie (summary: Outline of Quaternary stratigraphy in Poland; main glacial and interglacial horizons and their extents). Przegląd Geol., 43(7): 586–591.

OSZAST J. 1970. O wieku stożka Domańskiego Wierchu na podstawie badań palinologicznych (summary: On the age of Domański Wierch determined by palynological methods). Kwart. Geol., 14: 843–846.

SADOWSKA A. 1990. Paleofloristic changes in the Neogene of south-western Poland. In: Knobloch E. & Kvaček Z. (eds.). Proceedings of the Symposium

Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary, Prague, August 28th-Sept.1st, 1989: 223–226.

STUCHLIK L. 1987. Przegląd badań paleobotanicznych osadów plioceńskich i wczesnoplejstoceńskich Polski środkowej i południowej (summary: Review of palaeobotanical studies on Pliocene and lower Pleistocene deposits in central and southern Poland). In: Problemy młodszego neogenu i eoplejstocenu w Polsce. Materiały Konferencji Naukowej Plioceńska i eoplejstoceńska sieć rzeczna i związane z nią kompleksy osadów gruboklastycznych w Polsce. Wrocław 18–20 czerwca 1985: 53–63. Zakł. Narod. im. Ossolińskich, PAN.

SZAFER W. 1954. Plioceńska flora okolic Czorsztyna i jej stosunek do plejstocenu. (summary: Pliocene flora of the vicinity of Czorsztyn (West Carpathians) and its relationship to the Pleistocene). Prace. Inst. Geol., 11: 1–238.

SZAFER W. and OSZAST J. 1964. The decline of Tertiary plants before the maximal glaciation of the West Carpathians. Reports of the 6th Intern. Congr. on Quaternary, Warsaw, 1961, Palaeobot. sect.: 479–482.

VELICHKEVICH F. 1982. Pleystotsenovye flory lednikovykh oblastey Vostochno – Evropeyskoy ravniny. Nauka i Tekh., Minsk, (in Russian).

ZUCHIEWICZ W. 1983. Kryteria wyznaczania granicy pliocen-plejstocen. Czasopismo Geogr., 54(4): 478–495.

STRESZCZENIE

Kopalne gatunki rodzaju *Potamogeton* w Mizernej

Dokonano rewizji taksonomicznej rodzaju *Potamogeton* na podstawie endokarpów z flory plioceńsko-plejstoceńskiej Mizernej (Zachodnie Karpaty, Szafer 1954) pochodzącej z materiałów zbieranych w latach 1949, 1960–62 i 1979. Oznaczono 18 gatunków spośród których 10 należy do wymarłych. Wyróżniono 13 gatunków dotąd nie notowanych we florze Mizernej: *P. panormitanoides* Dorof., *P. aculeatus* Dorof., *P. natans* L., *P. peregrinus* Dorof., *P. obtusatus* Dorof., *P. pseudoacutifolius* Dorof., *P. compressoides* Dorof., *P. squamatus* Dorof., *P. tataricus* Dorof., *P.* cf. *heterocarpus* Dorof., *P.* cf. *pliocenicus* Dorof., *P. rutilus* Wolfg. i *P.* ex gr. *friesii* Rupr. Wyróżniono 3 grupy gatunków: środkowo-plioceńskie, górno-plioceńskie i nawiązujące do współczesnych. Nie udało się skorelować oznaczonych gatunków z wydzieleniami stratygraficznymi ani w starszych ani w nowszym, pochodzącym z 1979 r. materiale.

PLATES

Plate 1

1–4. ***Potamogeton tataricus*** Dorof., endocarps, × 45
1. Mizerna 52a, KRAM-P no 15/RW/52a/F1/5234
2. Mizerna 52a, KRAM-P no 15/RW/52a/ F2/5235
3. Mizerna 52a, KRAM-P no 15/RW/52a/ F3/5236
4. Tataria, no F4/5237

5–9. ***Potamogeton obtusatus*** Dorof., endocarps, × 45
5. Mizerna 8a, KRAM-P no 15/RW/8a/F18/5242
6. Mizerna 8a, KRAM-P no 15/RW/8a/F19/5243
7. Mizerna 8a, KRAM-P no 15/RW/8a/F20/5245
8. Kholmech, no F21/5233
9. Kholmech, no F22/5244

10–11. ***Potamogeton obtusifolius*** Mert. et Koch, endocarp
10. Minichi 1/14, no F23/5232, × 45
11. the same, fragment of lid spine, no F23/5231, × 400

12–14. ***Potamogeton squamatus*** Dorof., endocarps, × 45
12. Mizerna 10a, KRAM-P no 15/RW/10a/F9/5247
13. Mizerna 10a, KRAM-P no 15/RW/10a/F11/5249
14. Daumantay, no F12/5248

15–19. ***Potamogeton*** cf. ***aculeatus*** Dorof., endocarps
15. Mizerna 4b, KRAM-P no 15/RW/4b/F13, × 15
16. Mizerna 4b, KRAM-P no 15/RW/4b/F14, x15
17. the same, fragment of base with tubercles and lid nipple, KRAM-P no 15/RW/4b/F14/5278, × 150
18. the same, fragment of crested lid, KRAM-P no 15/RW/4b/F14/5277, × 100
19. the same, mouth of central depression, KRAM-P no 15/RW/4b/F14/5279, x 150

20. ***Potamogeton aculeatus*** Dorof., endocarp, Daumantay, no F15, × 15

21, 22. ***Potamogeton peregrinus*** Dorof., endocarps, × 45
21. Mizerna 52b, KRAM-P no 15/RW/52b/F6/5240
22. Mizerna 52b, KRAM-P no 15/RW/52b/F5/5241

Figures 15, 16 and 20 reflected light micrographs, all other figures SEM.
Scale bar equals: 1 mm (figs 1–10, 12–14, 21, 22); 0.1 mm (fig 11), 0.45 mm (fig. 18); 0.3 mm (figs 17, 19)

Phot. Z. Petri and A. Pachoński

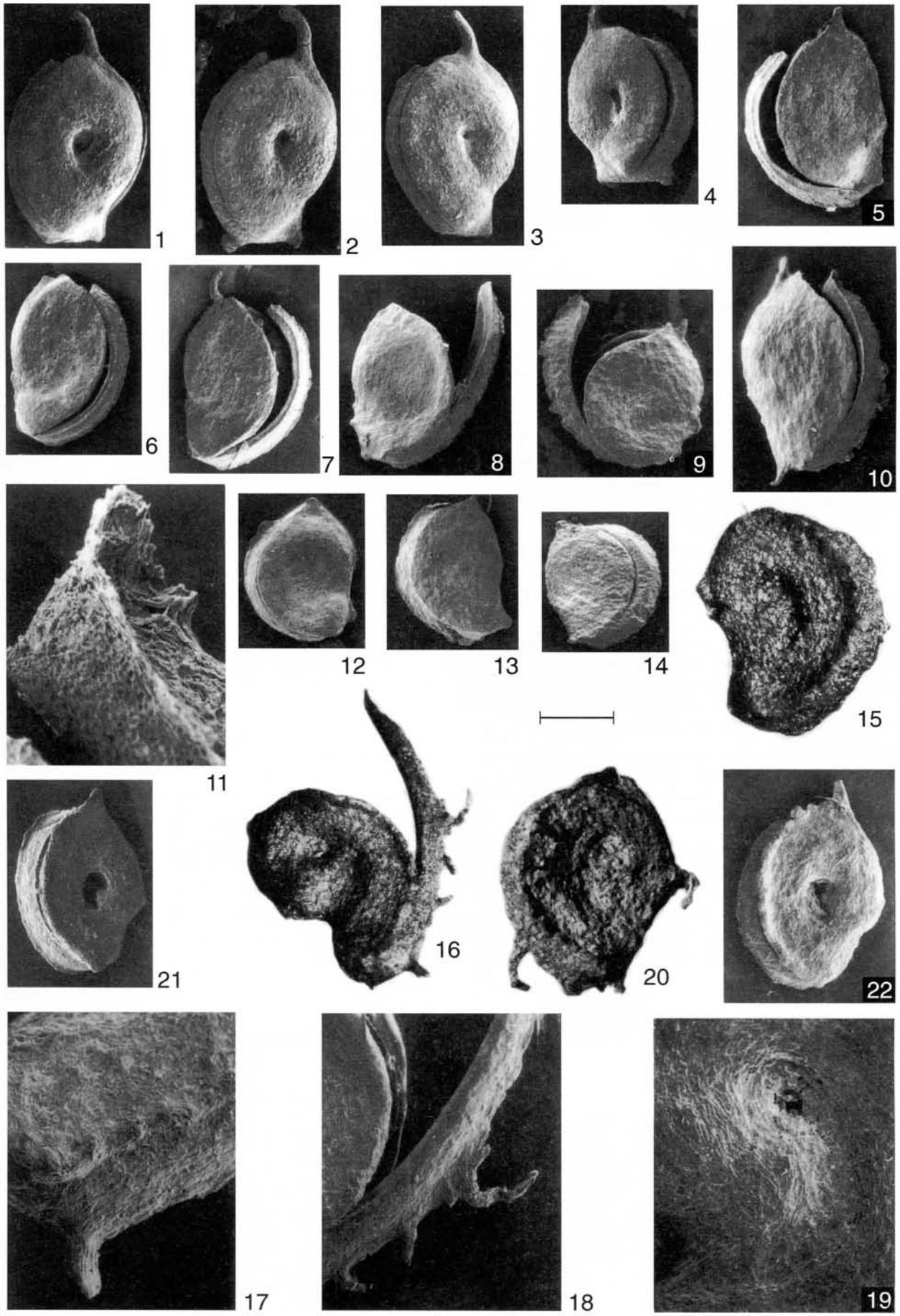

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
20
21
22
17
18
19

Plate 2

1–4. ***Potamogeton peregrinus*** Dorof., endocarps
1. Mizerna 64c, KRAM-P no 15/RW/64c/F7/5238, × 45
2. Lipetskaya area, type, no F /5239, × 45
3. the same, fragment of plate-like lid, no F /5274, × 250
4. the same, fragment of fine-celled surface, no F /5272, × 400

5–9. ***Potamogeton compressoides*** Dorof., endocarps, × 45
5. Mizerna 30a, KRAM-P no 15/RW/30a/F25/5210
6. the same, fragment of crested top of lid. Inner part of lid is clearly visible. KRAM-P no 15/RW/30a/F25/5209, × 400
7. Mizerna 30a, KRAM-P no 15/RW/30a/F26/5212
8. Mizerna 53a, KRAM-P no 15/RW/53a/F24/5215
9. Ranino, no F27/5216

10–11. ***Potamogeton compressus*** L., endocarp
10. Nizhnyaya Boyarshchina 2/17, no F28/5214, × 45
11. the same, fragment of side with distinct remains of mesocarp and fringed crest of lid, no F28/5213, × 100

12–15. ***Potamogeton pseudoacutifolius*** Dorof., endocarps, × 45
12. Mizerna 4c, KRAM-P no 15/RW/4c/F29/5211
13. Mizerna 22d, KRAM-P no 15/RW/22d/F30/ 5222
14. Mizerna 54, KRAM-P no 15/RW/54/F31/5223
15. Kholmech, no F32 /5228

16–17. ***Potamogeton acutifolius*** Link., endocarp
16. Minichi 1/16, no F33/5226
17. the same, fragment of lateral side with poorly developed central depression and crispate lid, no F33/5227, × 100

18–19. ***Potamogeton*** cf. ***pliocenicus*** Dorof., endocarps, × 15
18. Mizerna 40b, KRAM-P no 15/RW/40b/F16
19. Mizerna 40b, KRAM-P no 15/RW/40b/F17

20–21. ***Potamogeton heterocarpus*** Dorof., endocarps, × 15
20. Mizerna 22c, KRAM-P no 15/RW/22c/F46
21. Mizerna 22c, KRAM-P no 15/RW/22c/F45

Figures 18–21 reflected light micrographs, all other figures SEM.
Scale bar equals: 1 mm (figs 1, 2, 5, 7–10, 12, 13–17); 0.18 mm (fig. 3); 0.1 mm (figs 4, 6) and 0.45 mm (figs 11, 18).

Phot. Z. Petri and A. Pachoński

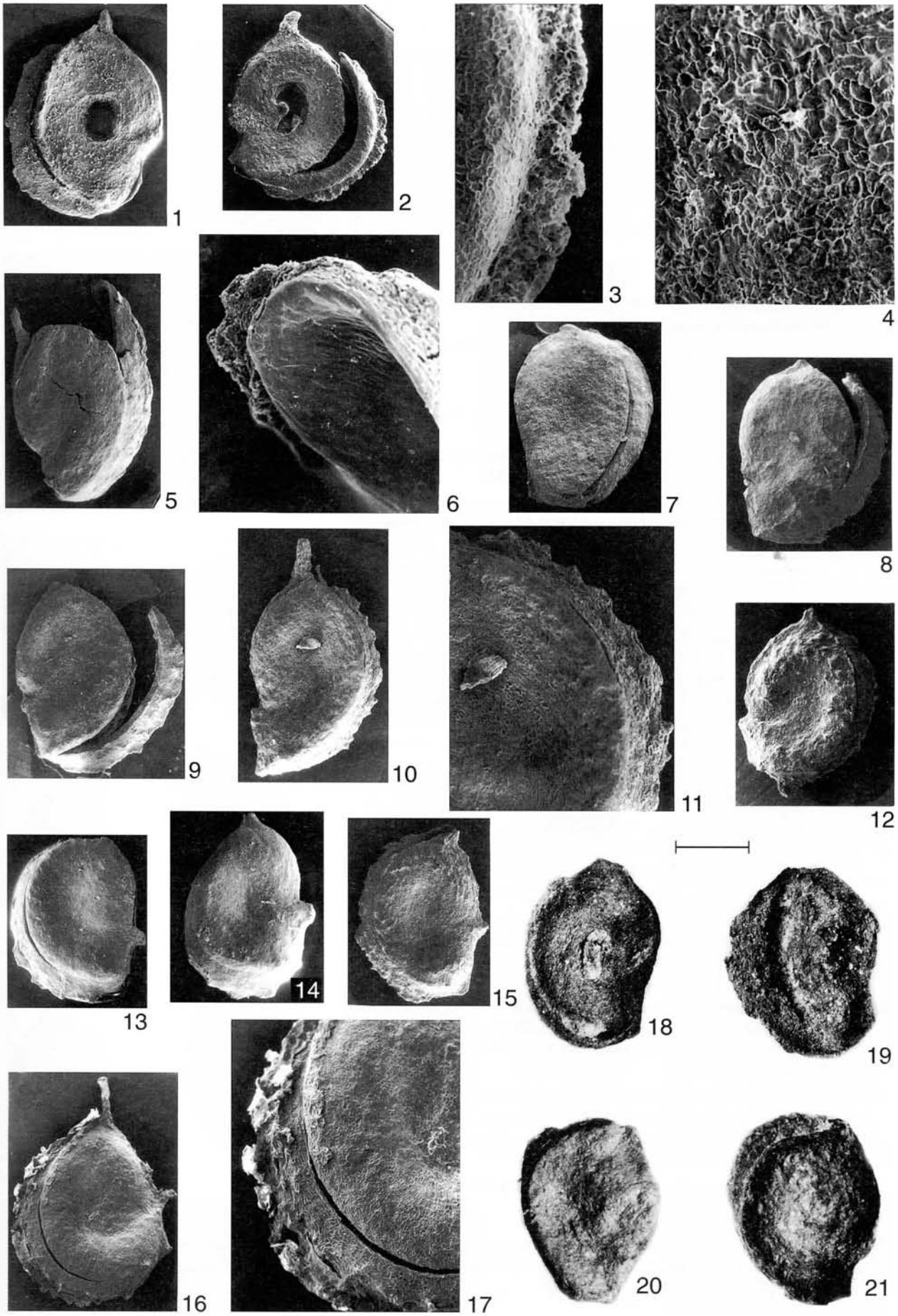

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
18
19
16
17
20
21

Plate 3

1. ***Potamogeton heterocarpus*** Dorof., endocarp, Lida, no F47, × 15

2–4. ***Potamogeton natans*** L., endocarps, × 45
2. Mizerna 22c, KRAM-P no 15/RW/22c/F38/5230
3. Minichi 24a, no F39/5224
4. Nizhnyaya Boyarshchina, no F40/5225

5–7. ***Potamogeton perfoliatus*** L., endocarps, × 15
5. Mizerna 6a, KRAM-P no 15/RW/6a/F43/
6. the same, fragment of surface with exocarp preserved, KRAM-P no 15/RW/6a/F43/5293
7. Mizerna 6a, KRAM-P no 15/RW/6a/F44

8, 9. ***Potamogeton praelongus*** Wulf., endocarps
8. Mizerna 57b, KRAM-P no 15/RW/57b/F36/5286, × 45
9. Minichi, no F37, × 15

10, 11. ***Potamogeton trichoides*** Cham. et Schlecht., endocarps, × 15
10. Mizerna 49c, KRAM-P no 15/RW/49c/F34
11. Verkhove-1, no F35

12–16. ***Potamogeton*** ex gr. ***natans*** L., endocarps
12. Mizerna 10d, KRAM-P no 15/RW/10d/F41/5229, × 45
13. Mizerna 10d, KRAM-P no 15/RW/10d/F42/5289, endocarp with seed, × 45
14. the same, lid broken open showing fragment of seed tegmen inside, KRAM-P no 15/RW/10d/F42/5291, × 100
15. the same, enlarged, the reticulate tegmen surface is clearly visible, KRAM-P no 15/RW/10d/F42/5292, × 250
16. the same, fragment of tegmen surface with thickened walls of elongate cells, KRAM-P no 15/RW/10d/F42/5290, × 1500

17–19. ***Potamogeton rutilus*** Wolfg., endocarps, × 15
17. Mizerna 64d, KRAM-P no 15/RW/64d/F53
18. Mizerna 64d, KRAM-P no 15/RW/64d/F52
19. Mizerna 64d, KRAM-P no 15/RW/64d/F51

20–22. ***Potamogeton*** ex gr. ***friesii*** Rupr., endocarps, × 15
20. Mizerna 52d, KRAM-P no 15/RW/52d/F48
21. Mizerna 52d, KRAM-P no 15/RW/52d/F49
22. Mizerna 52d, KRAM-P no 15/RW/52d/F50

23–25. ***Potamogeton panormitanoides*** Dorof., endocarps, × 15
23. Mizerna 59, KRAM-P no 15/RW/59/F58
24. Mizerna 15/133, KRAM-P no 15/RW/15/133/F59
25. Motol, no F60

26–28. ***Potamogeton coloratus*** Hornem., endocarps, × 15
26. Mizerna 11, KRAM-P no 15/RW/11/F56
27. Mizerna 11, KRAM-P no 15/RW/11/F54
28. Mizerna 11, KRAM-P no 15/RW/11/F55

29. ***Potamogeton coloratoides*** Dorof., endocarp, no F57, × 15

Figures 2–4, 6, 8, 12–16 SEM micrographs, figures 1, 5, 7, 9–11, 17–29 reflected light micrographs. Scale bar equals: 1 mm (figs 2–4, 8, 12, 13); 0.18 mm (figs 6, 15); 0.45 mm (fig. 14) and 0.03 mm (fig. 16)

Phot. Z. Petri and A. Pachoński

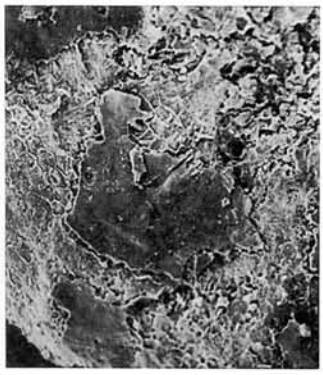

1


2


3


4


5


6


7


8


9

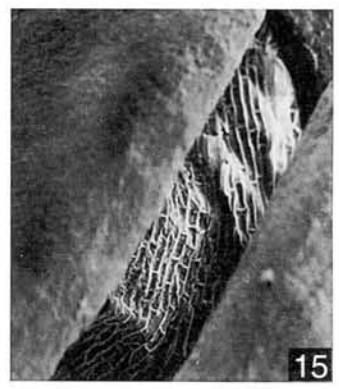

10


11


12


13


14


15


16


17


18


19


20


21


22


23

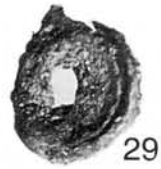

24


25


26


27


28


29