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The aquatic plants *Salvinia* (Salviniales) and *Limnobiophyllum* (Arales) from the Late Miocene flora of Sośnica (Poland)

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ABSTRACT. Fossil free-floating aquatic plants of *Salvinia mildeana* Goeppert (a water fern of the Salviniales) and *Limnobiophyllum expansum* (Heer) Kvaček (Arales) are described from the Late Miocene of Sośnica, Poland. The *S. mildeana* vegetative remains are associated with dispersed megaspores here determined as the *S. intermedia* Dorofeev complex. Characteristics of other megaspores of this complex are summarised based on translations of Russian, Ukrainian and German literature. Other megaspores assigned to the section *Salvinia* sensu Dorofeev (with elongate ellipsoidal shape and conical to pyramidal apices) are briefly discussed. Megaspores of the *S. intermedia* complex from Sośnica are compared and contrasted with those of *S. cerebrata* Dorofeev ex Nikitin using SEM and TEM. *S. cerebrata* was assigned to a different section (*Cerebrata*) by Dorofeev and it occurs in situ in plants of *Salvinia reussii* Ettingshausen from the Early Miocene of Bilina, Czech Republic. The megaspores differ in shape, ornament, surface structure and perine ultrastructure and the potential systematic value of these characteristics is emphasised. Spores linked with vegetative remains in reconstructed fossil plants provide an indication of the former biodiversity and variability of *Salvinia*. The extinct species *S. reussii* and *S. mildeana* both possess the submerged system (=dissected leaf) bearing in part root-like and inflated segments, the latter characteristic no longer represented in the modern genus. The whole fossil plants show the existence of extinct species of *Salvinia* and the extinct genus *Limnobiophyllum* in aquatic vegetation as recently as the Late Miocene in Europe. Associated plant assemblages at Sośnica are briefly reviewed and the palaeoecology of *Salvinia* and *Limnobiophyllum* in ancient wetland floras is discussed.

KEY WORDS: aquatic plants, megaspores, leaves, Salviniales, Arales, Late Miocene, Europe

CONTENTS

INTRODUCTION

ANCIENT WETLAND FLORAS

Fossils whose nearest living relatives are wetland plants are very abundant in the fossil record (e.g. Mai 1985, 1995, Collinson 1988, 2001, Collinson et al. 1993b, in press, Cevallos-Ferriz et al. 1991). In many cases facies association and taphonomic considerations, as well as morphological features (e.g. aerenchyma, heterophylly), and, more rarely, rooting in situ, conclusively demonstrate the wetland habitat of the ancient plants (e.g. Collinson 1983, 1988, in press, Cevallos-Ferriz et al. 1991). Because of their abundance these fossils have provided excellent examples of morphological change through time (e.g. Mai 1985) which have considerable potential for evolutionary and phylogenetic analyses. These wetland fossils are also significant for interpretation of ancient lacustrine, marsh and swamp communites and ecosystems, their spatial and temporal succession and evolution, and their response to global environmental change (e.g. Mai 1985, 1995, Collinson 1983, 1988, 1990, 1992b, 2000a, Collinson & Hooker 2000, Collinson et al. 1993a, Cevallos-Ferriz et al. 1991, Boulter et al. 1993, Hubbard & Kvaček 1998, Kvaček 1998, McIver & Basinger 1993). In this paper we provide an overview and new data on an important Late Miocene wetland flora from Poland.

SIGNIFICANCE OF RECONSTRUCTED AQUATIC PLANTS

The Late Cretaceous and Cenozoic plant fossil record typically consists of isolated organs such as wood, leaves, fruits, seeds, flowers and pollen. Rarer reconstructed whole plants are particularly important because they provide a more extensive suite of characters on which to base phylogenetic and ecological interpretations. They may reveal developmental stages, and information on plant habit. If they are found rooted in situ this gives unequivocal evidence of their habitat (see commentaries in Collinson 1990, 2000b). In cases when fertile specimens are available, whole plants also enable detailed comparisons with modern relatives.

Although there is an extensive fossil record of free-floating aquatic plants (see above) there are relatively few whole or reconstructed examples. These include the Maastrichtian and Palaeocene floating rosette plant *Quereuxia* (=*Trapago*) and similar fossils, a dicotyledon of uncertain family affinity (Stockey & Rothwell 1997, McIver & Basinger 1993); the floating monocotyledon *Limnobiophyllum* of the Arales (Stockey et al. 1997, Kvaček 1995, 1998, in press, McIver & Basinger 1993 (under the name *Spirodela*)); a *Pistia* like plant (McIver & Basinger 1993, Stockey 2000); the liverwort *Ricciopsis* (Hoffman & Stockey 1997); the rooted to free floating dicotyledon *Elephantosotis* of uncertain affinity and the monocotyledons *Hydrochariphyllum* and *Stratiotiphyllum* from the Early Miocene of Bilina (Kvaček 1998, in press); and a number of water ferns of the genera *Azolla*, *Salvinia* and *Hydropteris* (Collinson 1991, in press, Rothwell & Stockey 1994). In this paper we document two associated aquatic whole plants, *Salvinia mildeana* and *Limnobiophyllum expansum*, from the Late Miocene Poznań Formation at Sośnica, Poland in context of related fossil records. Besides the taxonomic treatment we add palaeoecological setting of the associated plant assemblages.

THE SOŚNICA LOCALITY

The locality of Sośnica is situated near Wrocław in Lower Silesia in the southernmost part of the Tertiary Polish-German Depression. The geological characteristics of the area and the locality in Sośnica were described by Stachurska et al. (1973) and Dyjor et al. (1998). The plant fossils occur in the grey clay of the Flamy Clay Horizon in the upper part of the Poznań Formation. The age of the deposits at the top of the horizon with plant remains is Late Miocene, an equivalent of Pontian in the stratigraphic scheme of Paratethys, based on palynology and regional geological correlation (Dyjor et al. 1998).

THE SOŚNICA FLORA

The fossil flora from Sośnica in Lower Silesia was described in a monograph by Goeppert (1855). This monorgaph was the first in the world of a Miocene fossil flora comprising many well-preserved impressions of leaves, fruits, seeds, flowers and inflorescences. The first list of plant fossils from Sośnica (Goeppert 1852) named nearly 130 taxa of vascular plants. The comprehensive monograph

(Goeppert 1855) contained the descriptions and illustrations of 128 higher plant taxa, including two of Pteridophyta: *Salvinia mildeana* Goepp. and *Hymenophyllites silesiacus* Goepp. A few years later, Goeppert (1862) revised a number of fossil taxa from the flora of Sośnica, considerably reducing the number of taxa. Schlechtendal (1897) studied selected plant taxa (*Liquidambar*, *Pterocarya*, "*Porana*"). Later revisions and identifications of new taxa were summarised by Kräusel et al. (1919) and Kräusel (1920a, b, 1929).

Reyman (1956) identified fossil wood of *Glyptostroboxylon tenerum* (Kraus) Conwentz and Micek (1959) reported fruits and a fragmentary leaf of *Eucommia europaea* Mädler. Jähnichen et al. (1984) and Jähnichen (1990) made further additions to the flora of Sośnica concerning *Palaeocarya macroptera* (Brongn.) Jähnichen, Friedrich & Takáč (Juglandaceae) and *Amentotaxus gladifolia* (Ludwig) Ferguson, Jähnichen & Alvin (Taxaceae), respectively. *Persea speciosa* Heer (Lauraceae), mentioned by Raniecka-Bobrowska and Czeczott (1958), is not represented at Sośnica because the cuticular analysis of the only preserved specimen established its affinity with *Salix* (H. Walther pers. comm., 2000). Stachurska et al. (1973) published palynological results from the sediment which contained macro-remains of plants from a clay pit of the brick-kiln at Sośnica.

Renewed investigation of the flora of Sośnica was initiated in 1981 (Łańcucka-Środoniowa et al. 1981). Subsequent revisions include Fagaceae (Walther & Zastawniak 1991), Betulaceae (Zastawniak & Walther 1998), *Trapa* (Wójcicki & Zastawniak in press), and many taxa based on leaves (Zastawniak et al. 1996). The present paper is a continuation of this series.

MATERIAL AND METHODS

Fossil specimens which are the object of this study come from two collections. The older one, from 1852, is Goeppert's original collection housed in the Geological Museum of the Institute of Geological Sciences of the University of Wrocław (MGUWr). Other specimens, collected between 1954 and 1973, belong to the collection of the Władysław Szafer Institute of Botany of the Polish Academy of Sciences in Kraków (KRAM-P), and these are both specimens preserved in the form of impressions and compressions of plants. The plant fragments in the light-cream coloured clay are mostly brown or black if plant tissues are preserved. Dispersed megaspores studied herein (KRAM – P 54/725) were washed out from the grey clay intercalations, occurring within the Flamy Clay Horizon, close to the type level of the leaf impression flora (Łańcucka-Środoniowa et al. 1981). For scanning electron microscopy (SEM) and transmission electron microscopy (TEM) they were first cleaned in hydrofluoric acid. They were attached to SEM stubs using Bostik on a cover glass, coated with gold in a polaron sputter coater and examined under a Philips 501B SEM. All three specimens studied under SEM were subsequently removed from the stub using acetone and embedded in Spurr resin. Sections 60 μm thick were cut with a diamond knife using a Reichert Jung ultracut microtome. Sections were stained with uranium acetate/lead citrate, mounted on grids with support films and examined using a Philips EM 301S TEM. All specimens were cut in a near median longitudinal plane. The illustrations herein are therefore directly comparable with those in our previous work (e.g. Collinson 1991, 1992a, Van Bergen et al. 1993, Batten et al. 1998, Batten & Collinson 2001).

THE AQUATIC PLANT *SALVINIA*

CLASSIFICATION

The modern genus *Salvinia* Seguier includes about ten species distributed in the Old World (except SE Asia-Australasia) and in the New World north to the southern United States. The genus is placed in the monotypic family Salviniaceae T. Lestiboudois (Brummitt 1992). Azollaceae and Salviniaceae can be considered distinct monotypic families united into one order Salviniales (Kramer & Green 1990). Recent cladistic analyses of modern ferns, based on morphological and molecular evidence, place *Salvinia* and *Azolla* as sister taxa within a well-supported monophyletic clade, itself a sister group to Marsileaceae, uniting all the heterosporous ferns in one monophyletic clade (Pryer 1999). Fossil whole plants such as the extinct *Hydropteris* (Rothwell & Stockey 1994), with distinctive characters, have proven controversial, but significant, for evaluating relationships within heterosporous ferns (Pryer 1999). Similarly, fossil whole plants can potentially contribute to phylogenetic studies of modern genera. *Azolla* is known from a number of fossil whole plants in the Palaeocene to Miocene (Collinson 1991, 1996, 2001). Furthermore, *Azolla* megaspores and microspore massulae (from whole plants and dispersed) are increasingly being shown to carry systematically informative diagnostic characters when studied with SEM and TEM (e.g. Batten & Collinson 2001). However, far less is known about ancient *Salvinia* whole plants or their spore structure and this paper makes a preliminary contribution to addressing this imbalance.

FOSSIL RECORD OF *SALVINIA*

Salvinia-like foliage (some specimens with the submerged leaf in addition to the surface floating leaves) is widespread in the fossil record (Shaparenko 1956, Collinson 2001). In contrast, fertile plants are very few, with one example from each of the Maastrichtian of Mexico, Eocene of the United States, Eocene of France and Miocene of Sakhalin and Bohemia (Collinson 1991, 2001, Fotyanova 1963, Weber 1973, Bůžek et al. 1971). Only in the last example have the attached sporocarps of these plants yielded information on spores. Jain and Hall (1969) noted that abundant dispersed megaspores and massulae (named *S. aureovallis* Jain & Hall) occurred in the American Eocene Golden Valley Formation as do the plants named *S. preauriculata* Berry (Berry 1925) some of which have sporocarps preserved. However, although no other *Salvinia* occur in this formation, the spores have not been found in organic attachment or particularly close association with the plants. Permineralised material from the ?latest Cretaceous / earliest Palaeogene Deccan Intertrapean Series in India includes megaspores, massulae and some associated vegetative material (Collinson 2001, discussion in Nambudiri & Chitaley 1991). There is only one record of whole fossil fertile *Salvinia* plants from which sori, megaspores and microspore massulae are known in organic connection. This is *S. reussii* Ettingshausen from the Miocene of Bohemia which yields megaspores named *S. cerebrata* P.A. Nikitin ex Dorofeev (Dorofeev 1955b, Bůžek et al. 1971, Bůžek & Konzalová 1979, Collinson 1991, Rothwell & Stockey 1994).

Compression fossils of dispersed megaspores and microspore massulae (and, more rarely complete sori) of *Salvinia* recovered by sieving techniques are also widespread in the fossil record (Collinson 2001). Batten and Kovach (1990) and Kovach and Batten (1989) list 39 named species. Almost all these records are Eocene or younger and they become most common in the Neogene in Europe and Eurasia. Cretaceous specimens formerly identified as *Salvinia* are now re-identified as *Azollopsis* (see also discussion in Collinson 1991). The oldest records are therefore specimens from Palaeocene/Eocene transitional strata (Collinson 2000b) of southern England which include *Salvinia cobhamii* Martin (Martin 1976) and new material (sori, megaspores and microspore massulae) from St. Pancras and Cobham which may be conspecific (Collinson 1992a, Van Bergen et al. 1993). Microspore massulae (*Salvinia exigua* (Dijkstra) Kempf) have also been identified in Palaeocene/Eocene transitional strata of the Netherlands (Batten & Collinson 2001).

Łańcucka-Środoniowa (1958) drew attention to the “double taxonomy” in use for fossil *Salvinia* where species were based on either dispersed megaspores or on leaves. This situation can only be improved by discoveries of spores with plants. In the absence of direct organic connection, documentation of associated spores and vegetative plants provides the best evidence for reconstruction of “whole” fossil *Salvinia* plants. In this paper we document *S. mildeana* Goeppert plants in association with megaspores of the *S. intermedia* Dorofeev complex.

TERMINOLOGY

Gross morphology of *Salvinia* plants is unique among ferns (e.g. Bonnet 1955, Croxdale 1978, 1979, 1981). The plant is rootless, bearing on stems groups (previously interpreted as whorls) of three leaves, two floating and one submerged. The submerged leaf was also interpreted as a branching system (Bonnet 1955). The leaf is highly dissected and usually petiolate. We employ the term “segment” for individual parts of this system, instead of “leaflet” (Croxdale 1981) because in the submerged system in *S. reussii* and some other more species, there is no regularity of arrangemnt and no rachis, to which individual leaflets would be attached (a similar case in angiosperms is seen e.g. in *Utricularia*). The segments are simple or divided, either root-like, or inflated, or fertile, branched, simple or reduced. The latter corresponds to “sporocarpophore”, i.e. a fertile part of the leaf (Bůžek et al. 1982).

Terminology of the spore wall in the heterosporous ferns varies amongst authors. To facilitate comparison with previous electron microscope studies on fossils we follow the terminology used by Collinson (1991, 1992a), Batten (Batten et al. 1998) and Batten & Collinson 2001). In the spore wall (sporoderm) the exine (megaspore proper) is overlain by a perine (perispore) which itself can be subdivided into one or more layers (e.g. endo and exoperine). The terms exine and perine were applied in the same manner by Kempf (1971). However, Tryon and Lugardon (1991) use the terms exospore (equivalent to exine herein) and epispore (the outer wall equivalent to perine herein) because they emphasise that the outer layer in heterosporous ferns differs in development and is not equivalent to the perispore in homosporous ferns.

SYSTEMATICS OF *SALVINIA* FROM SOŚNICA

Polypodiophyta

Salviniaceae T. Lestib.

Salvinia Séguier

Salvinia mildeana Goeppert

Figs 1–5

1855 *Salvinia mildeana* Goeppert, p. 5, Pl. 1 figs 21–23

? 1859 *Salvinia formosa* Heer, p. 156, Pl. 145 figs 13–15

? 1954 *Salvinia formosa* Heer; Hantke, p. 41, Pl. 1 figs 8–14

? 1957 *Salvinia formosa* Heer; Nötzold, p. 77, Pl. 1 figs 2–3

1981 *Salvinia mildeana* Goeppert; Łańcucka-Środoniowa et al., p. 108, Pl. 1 fig. 8

1996 *Salvinia mildeana* Goeppert; Zastawniak et al., p. 858, Pl. 282 figs 7a, b

1998 *Salvinia* cf. *mildeana* Goeppert; Krenn, p. 176, Pl. 1 fig. 5

Lectotype. Specimen MGUWr 725p/1, Fig. 1: 3 (Goeppert 1855, Pl. 1 fig. 21)

Paralectotype. Specimen MGUWr 718p, Fig. 1: 4 (Goeppert 1855, Pl. 1 fig. 22)

Material. Goeppert's collection: MGUWr 652p (det. R. Kräusel), 662p/1–4, 718p – paralectotype (Goeppert 1855, Pl. 1 fig. 22), 725p/1 – lectotype (Goeppert 1855, Pl. 1 fig. 21), 725p/2. New collections: MGUWr 1037p/2 (det. W. Micek in 1966, unpubl.), 1570p/1,2, 1875p, 1889p, 2285p, 2456p, 2513p, KRAM-P 54/624–629, 54/631, 54/632, 54/634–54/641, 54/645, 54/648, 54/650, 54/651, 54/654, 54/1057, 54/1061, 54/1063; 40 specimens with vegetative plant remains, mostly floating leaves.

Emended diagnosis. Plants bearing submerged leaf dissected into filiform as well as inflated ultimate segments like in *S. reussii* Ett., but the latter much narrower (2 mm max.) and in groups of two to three at most. Root-like segments also less branched. Floating leaves elliptical-elongate, keeled, maximum length typically less than 20 mm, venation consisting of meshes, those quadrangular bearing as a rule 4 tubercles.

Associated megaspores (assigned to the *Salvinia intermedia* complex)

Material. KRAM-P 54/725 15 specimens. (Figs 6, 7: 1–5; 8: 1, 3, 5, 7, 9).

Megaspores ellipsoidal, most of the body smooth, very finely perforate under the SEM; base finely tuberculate-wrinkled, apex tuberculate in lower part, exoperine with discontinuous perforate boundaries to the vacuoles.

We are unable to identify these megaspores with certainty to any of the previously named similar species prior to a full SEM and TEM survey of those species which is beyond the scope of this work. We introduce the term *S. intermedia* complex for the group of currently named species with characteristic morphology and similar to the Sośnica spores (see Tab. 1 and discussion below).

Description of Sośnica vegetative remains

Fragmentary free-floating rootless herbs consisting of thin main axes, mostly torn apart, bearing on nodes at intervals of probably less than 10 mm two floating opposite entire leaves with keel-like, and submerged system (leaf) dissected into simple or divided root-like segments and 2–3 slightly inflated ultimate segments ("floats"), all arising from the same node (Fig. 1: 1, 7; 2). Fertile segments unknown. Floating leaves, mostly recovered as detached, entire, rounded to elliptical to elongate, varying in size, 5–16 mm wide (mean 10 mm of 35 readings) and 8–17 mm long (mean 12 mm of 33 readings). On the lower leaf side there is a keel-like, widely attached, triangular petiole showing several forking veins, about 4 mm long (Fig. 1: 6). Leaf venation pin-

Table 1. Comparison of megaspore morphology within the *Salvinia intermedia* complex

Species/locality	Size (in mm)	Shape	Apex	Middle	Base
S. intermedia complex Not assigned to species Sośnica, Late Miocene	0.51–0.59 × 0.31–0.34 (small, not fully developed specimens excluded)	ellipsoidal, straight, sometimes bent with one side inflated, equatorial part thin-walled in places, maximum width near middle	rounded, flaps broadly triangular, slightly more than 1/3 but much less than 1/2 of the spore length, lower part of flaps with distinct tubercles and sometimes wrinkles	smooth, almost without sculpture, with depressions of various form and size, slight indication of stellate area on one specimen	rounded to broadly acute, at the very base sculpture slightly coarser than on the middle with faint tubercles and wrinkles
S. rhenana Kempf (1971) Weilerswist, Rhineland, Pliocene	0.55–0.69 × 0.34–0.50 (small, not fully developed specimens excluded)	spindle-shaped, with maximum width in equatorial region, equatorial part inflated and thin-walled	acute, flaps greater than 1/3 of spore length, wrinkled, slightly tuberculate	nearly without sculpture, depressions of various forms and sizes not primary structures	narrow, rounded to acute, the same tuberculate and wrinkled surface as the apex
S. intermedia Dorofeev (1955b) (non P. A. Nikitin), Odessa, Bolshoi Fountain, Late Miocene to Pliocene	0.6–0.8 × 0.4–0.5 some 0.2–0.4 × 0.15	ellipsoidal to broadly spindle-shaped, slightly flattened at both ends	bluntly acute, a neck delimits the flaps from the body, tuberculate-wrinkled	smooth or slightly wrinkled (illustration Pl. 2, fig. 2 shows stellate area and depression not mentioned in the description)	bluntly acute, tuberculate-wrinkled
"*S. intermedia*" sensu Dorofeev (1955c), Strashnyi Gorge and Demidovo, Middle-Late Miocene	0.45–0.65 × 0.25–0.30	ellipsoidal, sides inflated	acute, finely wrinkled or finely tuberculate	smooth or slightly wrinkled (illustrations Pl. 1, figs 2–4 show stellate areas and depressions not mentioned in the description)	acute, almost always finely wrinkled or finely tuberculate
S. petri Dorofeev (1987a), Prisk, Tomsk region, Pliocene	0.51–0.7 × 0.3–0.4	ellipsoidal to elongate, regular, slightly inflated (sometimes on one side) sometimes slightly indented, rarely ovoidal or obovoidal, bent	pyramidal, long flaps trigonal and cordate without ears, smooth	smooth, rarely scultpured in obovate specimens, stellate areas not distinct, depressions still deep, but radial ridges very indistinct, only those, which are longitudinal, are more distinct	slightly or strongly narrowed to acute and not well distinguished from the body, rarely rounded, smooth
S. aspera Dorofeev (1987a), Belyj Yar, Tomsk region, Oligocene	0.49–0.56 × 0.3–0.37	ellipsoidal to obovoidal, straight to slightly bent, maximum width in middle or upper half	very distinct, small flaps with tapered ears and depressed centers, surface uneven, tubercles not large or small, very closely compact	flat or scabrate, due to fine tubercles, rarely specimens with low tubercles and fine pits, few specimes have hints of stellate areas	rounded, rarely narrowed and scarcely differentiated, surface little more roughly scultpured than the middle with tubercles or wrinkles
S. ovata Dorofeev (1987b), Izakovka, Omsk region, Late Miocene	0.49–0.68 × 0.37–0.45	mostly ovoidal with very inflated sides, widest in lower half or middle	conical but small, hardly differentiated, flaps slightly uneven or with rare large tubercles on the margins and 2–3 short ridges in the middle at the base	surface lightly sculptured, depressions small, radial wrinkles very indistinct	rounded or in a few specimens with a small protrusion, sculpture faint, fine tubercles and wrinkles

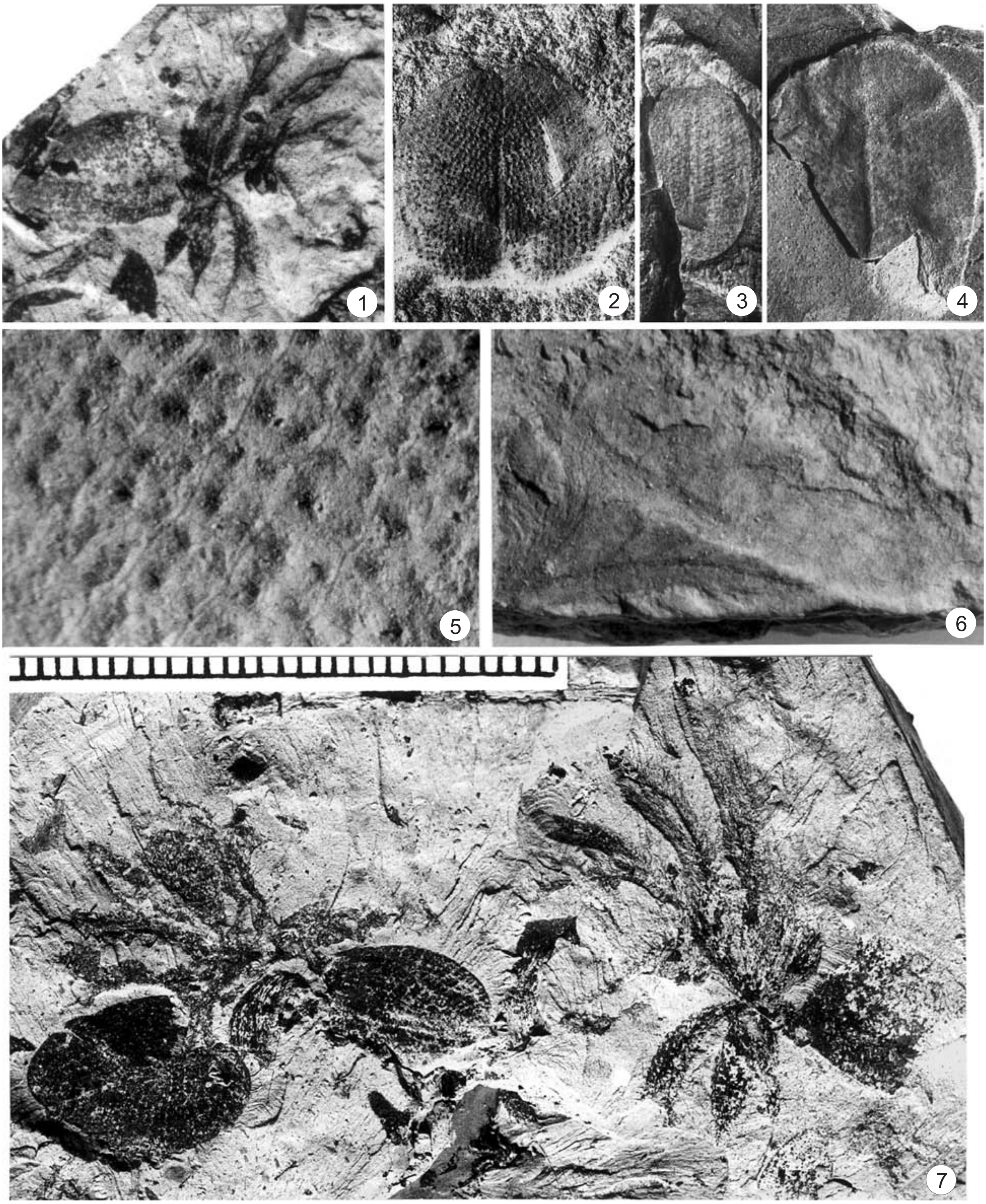


Fig. 1. *Salvinia mildeana* Goeppert, Sośnica: **1** – plant impression with one floating leaf and submerged segments bearing filiform and inflated segments, KRAM-P 54/640/I, × 2, **2** – floating leaf strongly tuberculate, MGUWr 725p/2. × 2, **3** – lectotype, MGUWr 718p, Goeppert 1855, Pl. 1 fig. 22, × 3, **4** – paralectotype, MGUWr 725p/1, Goeppert 1855, Pl. 1 fig. 21 (specimen damaged), × 3, **5** – detail of Fig. 1: 2, showing arrangement of tubercles within areolae, × 20, **6** – floating leaf in side view showing keeled petiole, MGUWr 662p/1, × 7, **7** – two detached plants with floating leaves and submerged segments bearing filiform and inflated segments, KRAM-P 54/627, × 3

nate-reticulate (Fig. 3: 1, 4). Primary vein thick and straight at the base, and thin and zig-zag in the upper part. Delicate lateral veins, approx. 10 at each side of the primary vein, diverging from it at a right or slightly obtuse angle at the base, at 55° in the central

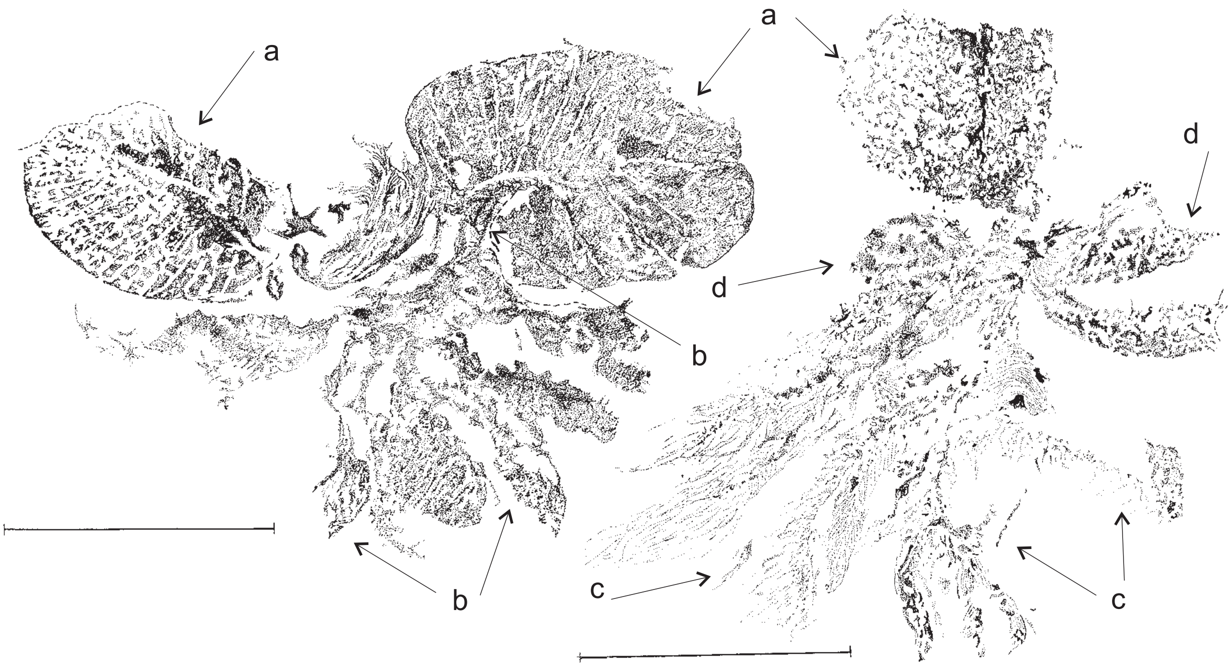


Fig. 2. *Salvinia mildeana* Goeppert, Sośnica. Drawing of detached plants shown in Fig. 1: 7: **a** – floating leaves, **b** – keel-like petiole, **c** – root-like hairy segments, **d** – inflated segments (scale bar 10 mm)

part and at 45° in the upper part. They are usually zig-zag. Between them simple inter-secondary veins are visible; together with veins of the 3rd order these form rows of quadrangular or hexangular areoles, gradually diminishing in size towards the leaf margins. In some specimens sometimes traces of papillas in the form of 4 tubercles and/or hollows per areole can be seen on the surface (specimen MGUWr 718p, 725p/2 – Fig. 1: 2, 3, 5). In other specimens only tiny rounded meshes of aerenchyma (MGUWr 1875p – Fig. 3: 5) are evident. Rarely the underside is seen to be covered with simple trichomes (MGUWr 1037p). Similar trichomes are also spread over submerged organs (KRAM-P 54/640), which are represented by simple root-like segments (Fig. 1: 7; 2; 3: 6) and slender inflated narrow spindle-shaped segments, usually in groups of two (or three) attached to the node (Fig. 1: 1, 7; 2). The latter are slightly inflated, thin-walled, aerenchymatous, and show an areolate surface in a similar manner to the leaf reticulation, but without tubercules (Fig. 3: 2). The tips of the inflated segments form hairy projections. All specimens are sterile, most are detached single leaves, rarely plant fragments with axes.

Description of associated megaspores (assigned to the *Salvinia intermedia* complex)

Previous work

Megaspores were originally determined as *Salvinia* cf. *aspera* Dorofeev and *Salvinia* sp. microsporangium by Łańcucka-Środoniowa et al. (1981). However, the determination was changed to *Salvinia intermedia* Nikitin ex Dorofeev and *Salvinia* sp. (Łańcucka-Środoniowa unpubl., Kraków Palaeobotanical Museum Catalogue). We have re-examined the fifteen specimens currently housed in the Kraków collection (KRAM-P 54/725) but there are no microsporangia or microspore massulae amongst these specimens. We have located three megaspores which appear to be fully developed (Fig. 6: 1–3, 5, 6) and 12 megaspores which may be underdeveloped, immature or aborted (being smaller or having very distorted, not fully inflated, shapes). We have re-examined one of the former (Fig. 6: 3–10) and two of the latter (Fig. 7: 1, 3, 4) by SEM and TEM. It is possible that some of the smaller underdeveloped spores might have been previously misinterpreted as massulae by Łań-

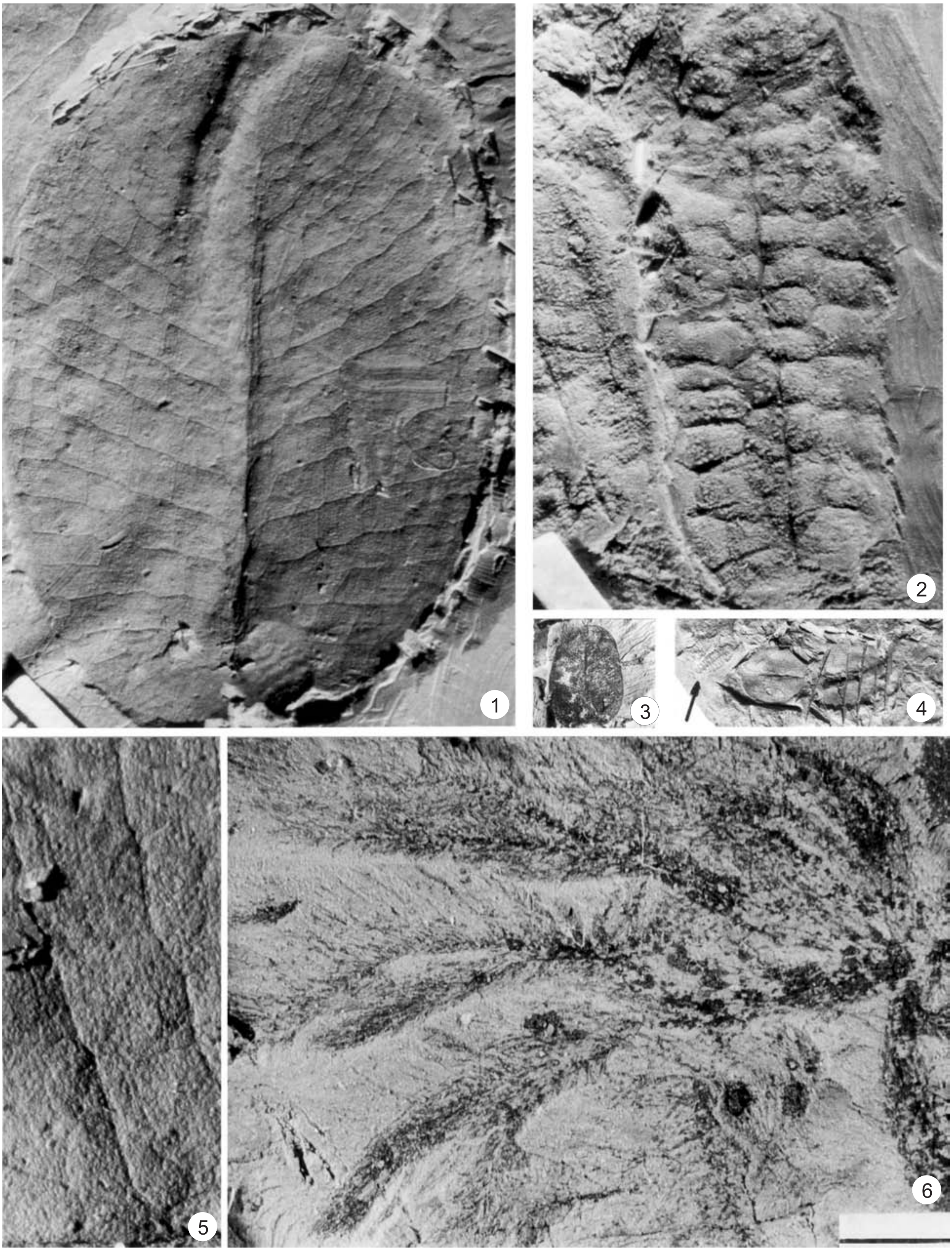


Fig. 3. *Salvinia mildeana* Goeppert, Sośnica, **1** – floating leaf impression showing venation and aerenchyma, MGUWr 1875p, × 5, **2** – inflated segment, detail of Fig. 3: 4, KRAM-P 54/625, × 13.3, **3** – carbonised floating leaf, MGUWr 1037p, × 1.4, **4** – a pair of floating leaves and detached inflated segments (arrow), KRAM-P 54/625. × 1.5, **5** – aerenchyma within areoles, detail of Fig. 3: 1, × 13.6, **6** – submerged divided filiform hairy segments, detail of the specimen shown in Fig. 1: 7, × 7

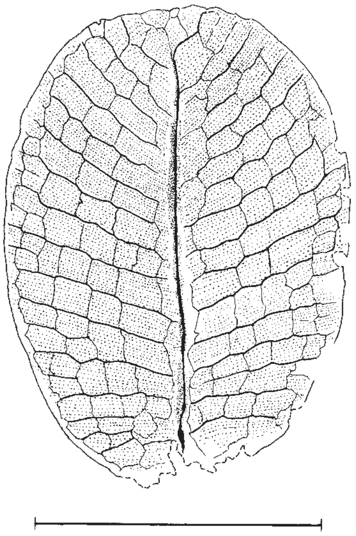


Fig. 4. *Salvinia mildeana* Goeppert, Sośnica. Drawing of detached floating leaf shown in Fig. 3: 1 with clearly visible venation (scale bar 10 mm)

cucka-Środoniowa. Illustrations of *Salvinia reusii* are included for contrast with a very different megaspore morphology to be discussed later (Fig. 7: 6–10; 8: 2, 4, 6, 8). A comparative table (Tab. 1) is provided of the megaspores from Sośnica with those of previously described similar species.

Morphology and ultrastructure of Sośnica megaspores

Megaspores elliptical, straight, sometimes bent with one side inflated; length 0.51–0.59 mm, width 0.31–0.34 mm (based on three fully developed specimens – Fig. 6: 1–3, 5, 6); the twelve small or not fully developed specimens (excluded e.g. Fig. 7: 1–4). Maximum width approximately in the centre of the spore. The apex rounded, with three broadly triangular flaps, which occupy slightly more than one third, but much less than one half of the spore length. Flaps distinct from the spore body, but with no delimiting neck or collar (Fig. 6: 1–3, 5). Tubercles, and sometimes wrinkles, distinct on the lower part of the flaps at the junction with the spore body, but indistinct or lacking in the apical part of the flaps (Fig. 6: 4; 7: 2). Detailed surface sculpture seen in SEM coarsely wrinkled and coarsely perforate (Fig. 6: 10). Middle part of spore (upper part of spore body), smooth, almost without sculpture (Fig. 6: 1–3, 5, 8), or with few small tubercles in patches, but never covering the entire middle part of the spore (Fig. 7: 1, 2). The middle part of the spore also shows depressions of various form and size (Fig. 6: 1–3, 5, 6) and slight indication of stellate areas, with slight ridges radiating from depressions, on one developed specimen (Fig. 6: 2) and one small specimen (Fig. 7: 1, 2). Detailed surface sculpture seen in SEM very finely wrinkled to scabrate, also very finely perforate with two size classes of perforations (Fig. 6: 9). Base rounded to broadly acute (Fig. 6: 1–3, 5, 7). On the very base sculpture is slightly coarser than the middle area with faint tubercles and wrinkles (Fig. 6: 7), much less distinct than those of the apex.

Ultrastructure of megaspore wall seen in TEM shows two layers, an inner exine and an outer perine (Fig. 8: 1; 9: 2, 4). Exine approximately 3 mm thick (Fig. 8: 1), increasing in thickness on the flaps (Fig. 9: 2). Exine with porous central zone occupying most of the thickness with narrow non-porous inner and outer surfaces (Fig. 8: 7). Perine in the equatorial zone 13–17 mm thick (Fig. 8: 1) extending to 67 mm thick at the base and up to 86 mm thick across the flaps (Fig. 9: 2). Perine with two major zones (Fig. 8: 1), inner endoperine, approximately 2 mm thick, consisting of separated narrow filaments, mostly perpendicular to the exine surface (Fig. 8: 1, 5, 7). Outer exoperine of convoluted, folded, undulating narrow filaments, surrounding vacuoles of different sizes (Fig. 8: 1, 3, 5). In the perine of the spore body there are large vacuoles up to 4 mm in diameter (Fig. 8: 1, 3, 5) but smaller vacuoles around 1 mm in diameter tend to occur towards the inside and the outside. The innermost exoperine can be totally lacking in vacuoles in places. In the perine of the flaps, very large vacuoles are present, up to 10 mm in diameter (Fig. 9: 1, 2). In the thinnest portions of the wall, nearest to equatorial depressions (Fig. 9: 2, 4), the vacuoles may be absent (Fig. 9: 5). The vacuole boundaries are discontinuous in section (Fig. 8: 1, 3, 5) and SEM shows them to be perforate (Fig. 7: 5). The perine outer surface is also discontinuous (Fig. 8: 1, 3) and even in the middle zone of the spore the surface is very finely perforate and wrinkled (Fig. 6: 9). Between the flaps the broken remnant of the gula surrounding the trilete laesurae can be seen (Fig. 9: 1 centre, Fig. 9: 3 left). It is separated from the flaps by a narrow slit (Fig. 9: 3) and, although only a small part is preserved, it is identical in

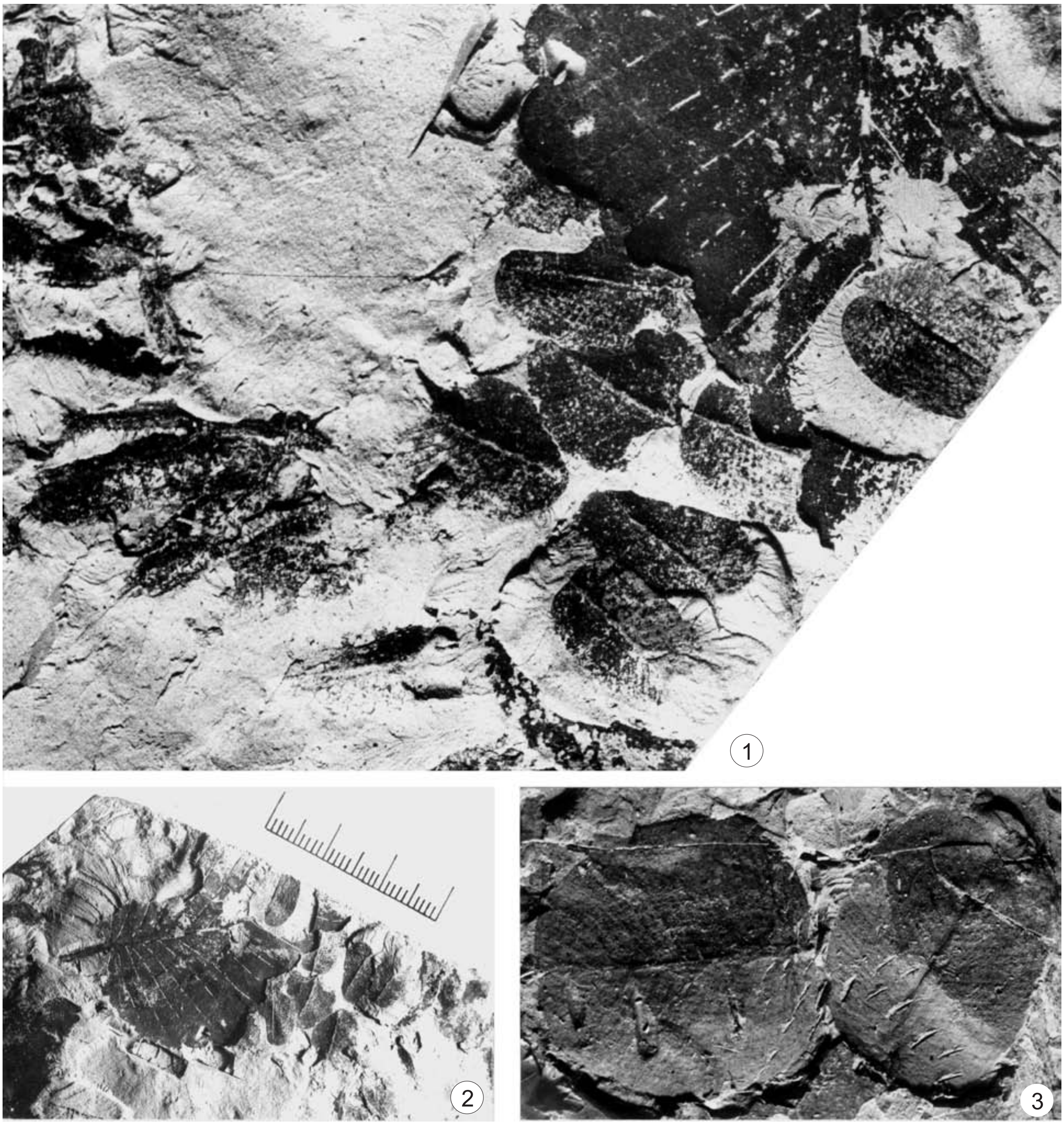


Fig. 5. *Salvinia mildeana* Goeppert, Sośnica, **1** – bedding plane covered by floating leaves, inflated segments together with a leaf fragment of *Ulmus carpinoides* Goepp., KRAM-P 54/639, × 3, **2** – the same specimen, × 1, **3** – a pair of floating leaves, KRAM-P 54/624. × 3

structure to those illustrated by Kempf (1971) for other species of *Salvinia*.

DISCUSSION OF VEGETATIVE REMAINS

In vegetative traits *Salvinia mildeana* resembles *Salvinia reussii* Ettingshausen emend. Bůžek, Konzalová & Z. Kvaček (Bůžek et al. 1971), which is distributed mainly in the Late Oligocene (fertile specimens in Germany – H. Walther pers. comm.) and Early Miocene of Europe (Bůžek et al. 1971). Both species have in common vegetative features of the plant body (leaf form, venation, inflated segments), of which *S. mildeana* is more reduced. It is tempting to consider both as a single evolutionary lineage with *S. mildeana* a derived descendent. However, according to the megaspore morphology they represent two sections in sense of Dorofeev (1963, 1987b). The plants of *Salvinia mildeana* are slender and surely more delicate (Tab. 2). Some samples show

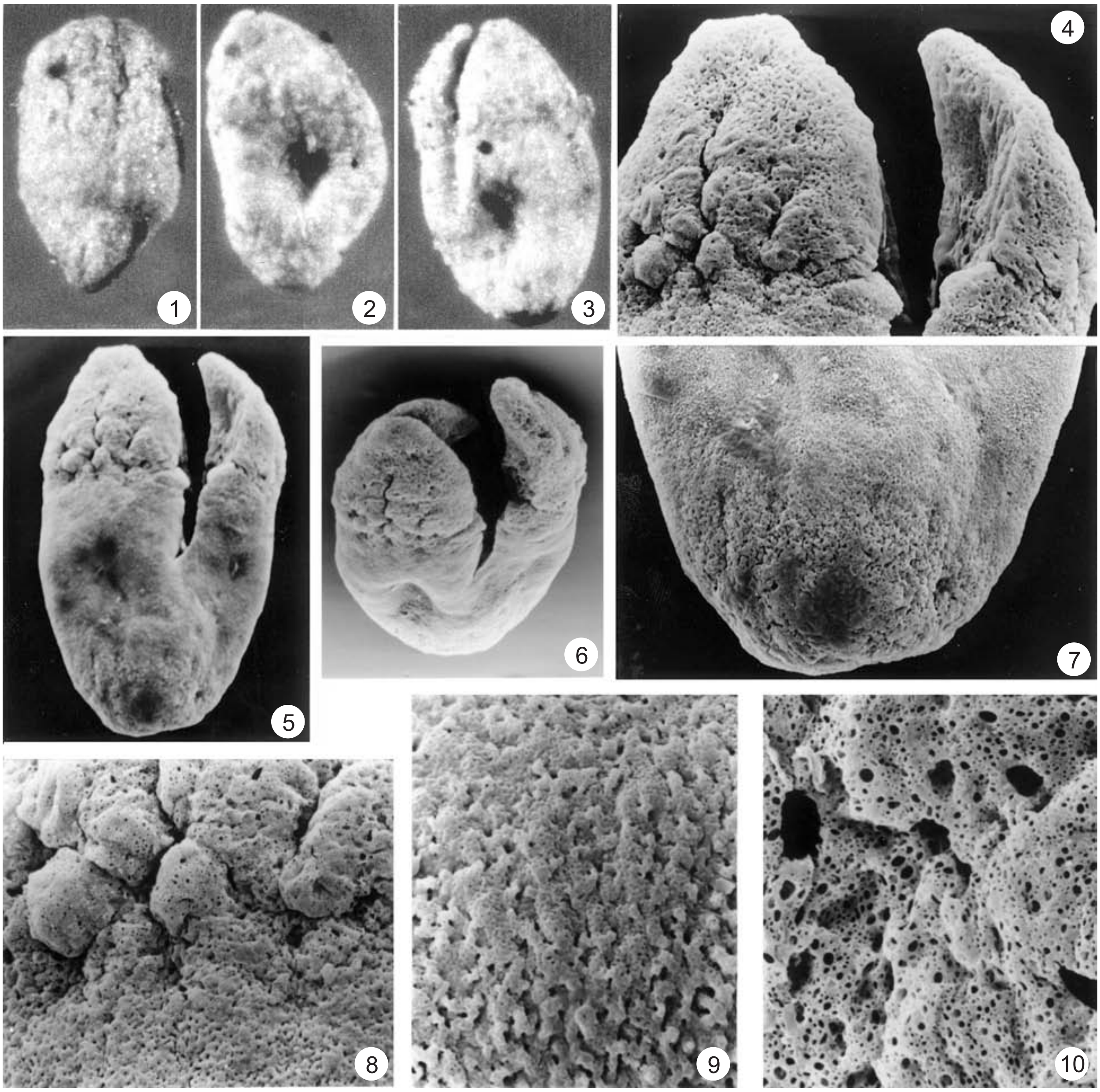


Fig. 6. Megaspores of the *Salvinia intermedia* complex from Sośnica, **1–3** – light micrographs of three fully developed megaspores, KRAM-P 54/725, × 80, **2** – shows slight indications of stellate areas, **4–10** – SEM of the megaspore from Fig. 6: 3, **4** – detail of the apex, × 200, **5** – lateral view, × 100, **6** – apical view × 100, **7** – detail of the base, × 200, **8** – detail of junction of apical flaps and spore body from fig. 6: 4, × 400, **9** – fine structure of the surface in the middle of the spore with two size classes of perforations, × 1600, **10** – surface structure near the middle of the apical flaps, × 1600

that leaf remains of both species covered whole bedding planes (Fig. 5: 1) and probably formed the same "carpets" on the water surface as do *Salvinia* species today. Inflated segments (floats), so large in *Salvinia reusssi*, were less significant in the Late Neogene, because *S. mildeana* plants did not have massively branched submerged systems like those in *S. reussii*, and hence they were much lighter. Among recent representatives of *Salvinia* with similar heavily branched submerged systems to those in *S. reussii* the function of the inflated segments was taken over by inflated petioles (e.g. *S. oblongifolia* Mart.). No remains of spores or sporangia have been observed within inflated segments in the fossil samples studied. In contrast, in *S. reussii*, sporangia are found in sporocarps on fertile branched segments. We support the reconstruction in Collinson (1991) and we disagree with the interpretation of Rothwell and Stockey (1994) for *S. reussii* that inflated segments would

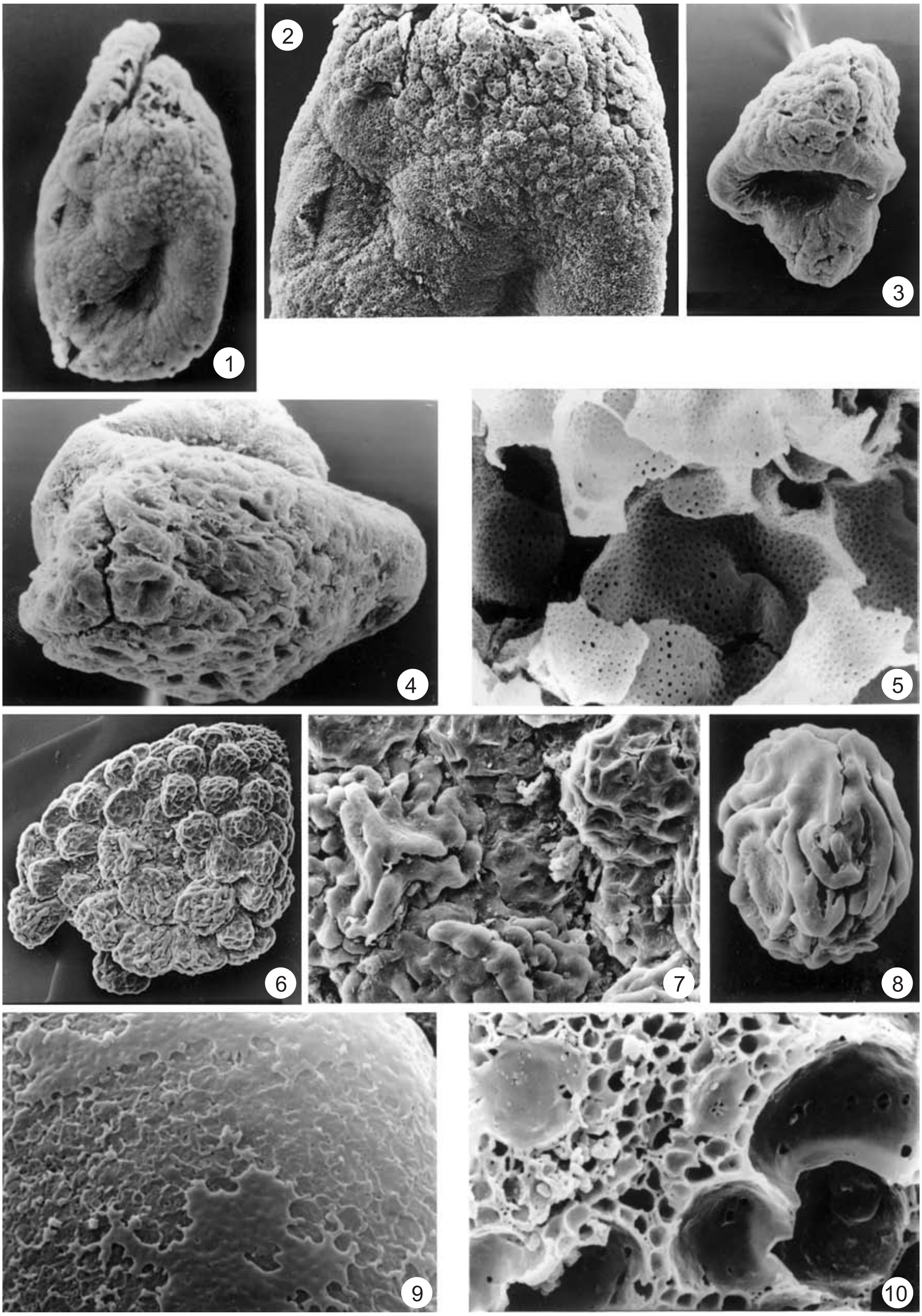


Fig. 7. 1–5 – megaspores of *Salvinia intermedia* complex from Sośnica, KRAM-P 54/725, **6–10** – sorus and megaspores of *Salvinia cerebrata* Nikitin ex Dorofeev from Bilina (M.E. Collinson collection). **1** – small megaspore with slight indication of stellate area and few tubercles on part of the middle of the spore, × 100, **2** – detail from Fig. 7: 1 of the junction of the apical flaps and spore body showing small tubercles, × 200, **3–4** – lateral (3) and apical (4) views of underdeveloped specimen with distorted shape, × 100 and × 200, **5** – detail of slightly broken apical flap from Fig. 7: 1 showing perforate boundaries of exoperine vacuoles, × 1600, **6** – amphisporangiate sorus, massulae towards the top, megaspores towards the base, × 30, **7** – detail of Fig. 7: 6 showing massula (right side) and apical view of megaspore (left side), × 100, **8** – lateral view of megaspore, × 100, **9** – fine detail of surface of ridge/fold on megaspore, × 3000, **10** – fractured exoperine showing continuous boundaries to vacuoles, × 6500 (all SEM)

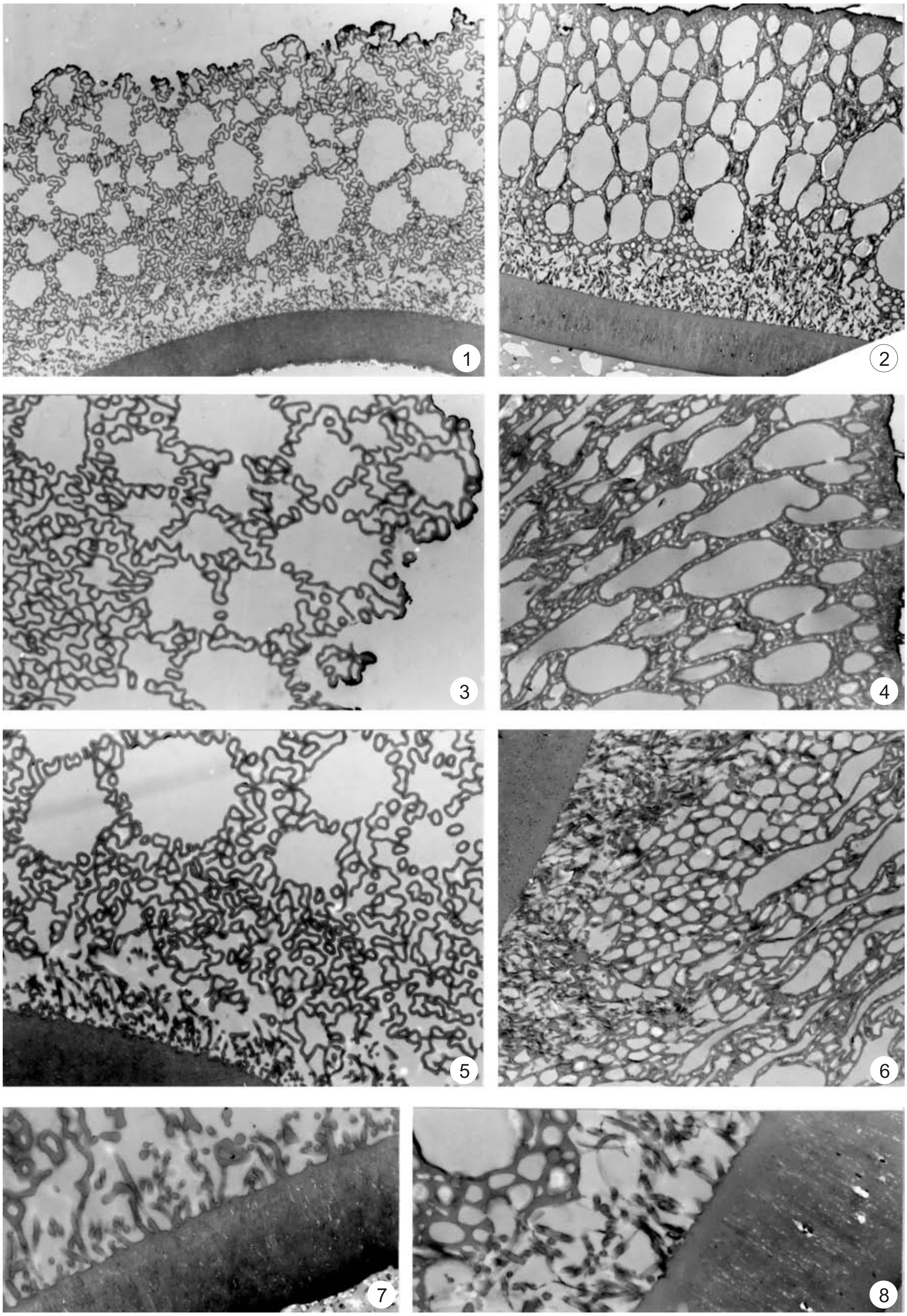


Fig. 8. Comparison of the megaspore wall ultrastructure between *Salvinia intermedia* complex from Sośnica (1, 3, 5, 7 – the specimen shown in Fig. 6: 3–10) and *Salvinia cerebrata* from Bilina (2,4,6,8 M.E. Collinson collection). Note especially the discontinuous boundaries of exoperine vacuoles in the former and continuous boundaries in the latter, **1–2** – entire megaspore wall, exine at base, thin black line on outer surface is gold coating from SEM study, × 3000, **3–4 –** detail of outer part of exoperine, × 6000, **5–6** – detail of inner part of exoperine, and endoperine (exine at bottom left in 5 and top left in 6), × 6000, **7–8** – detail of exine and endoperine, × 10 000, (all TEM)

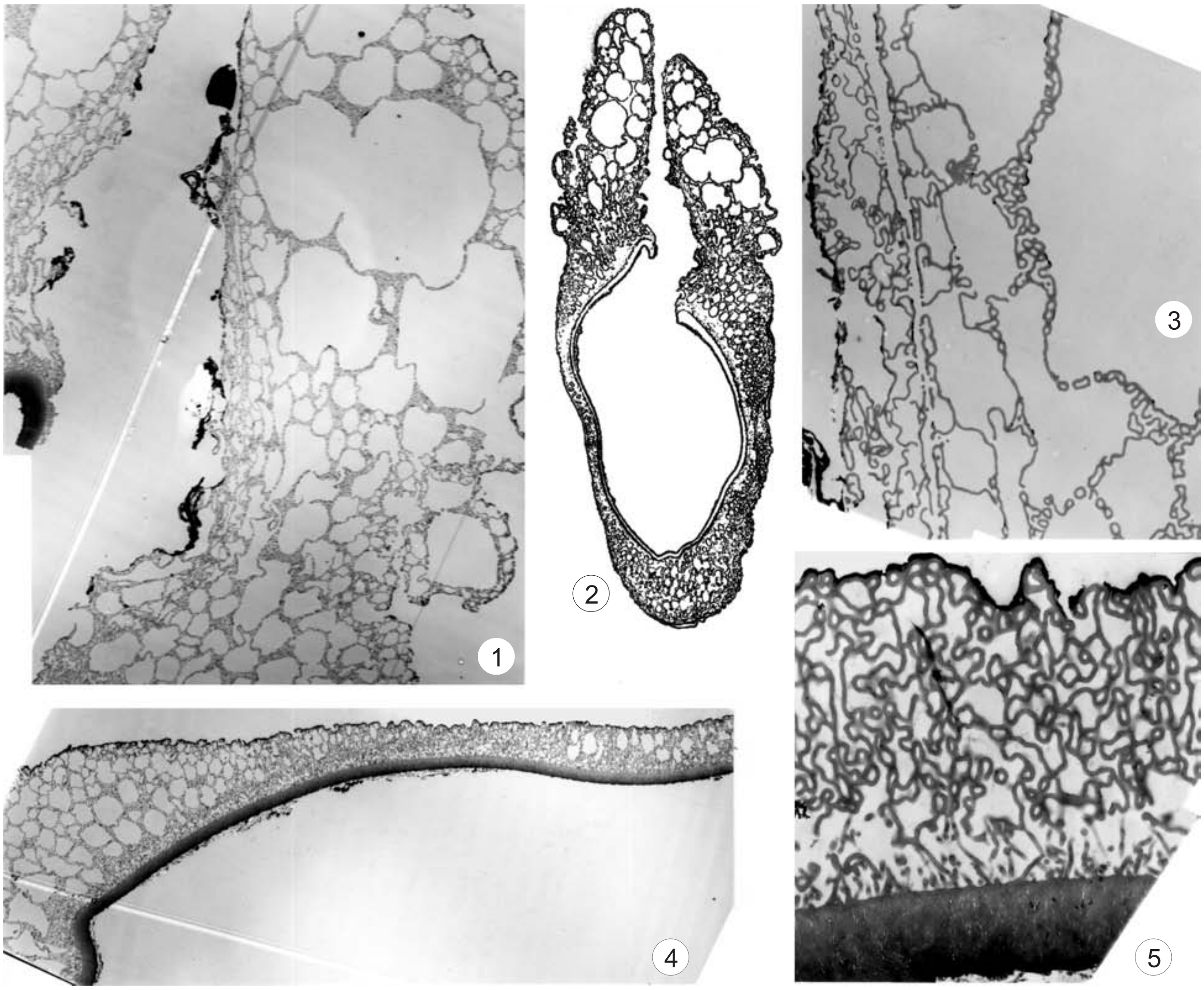


Fig. 9. Megaspore of *Salvinia intermedia* complex from Sośnica from Fig. 6: 3, **1** – detail of apical flaps and small remnant of gula (center left), × 750, **2** – median longitudinal section of the entire spore, × 150, **3** – detail of Fig. 9: 1, gula at left separated from flap by a thin slit, × 6000, **4** – detail from Fig. 9: 2 showing variation in thickness of megaspore wall, × 750, **5** – detail of thinnest area of megaspore wall showing absence of exoperine vacuoles, × 3000 (all TEM)

represent sporocarps. Solitary small rounded bodies, which we have observed on the bedding planes of some samples from Sośnica (KRAM-P 54/650, 54/625), may in fact be poorly preserved remains of dispersed sporangia but, due to oxidation, there is no information about the spore content.

The *S. oblongifolia*-type of leaf surface pattern sensu Shaparenko (1956) with typically four tubercles per areole, shared by *S. mildeana* and *S. reussii*, is not a reliable diagnostic trait at the species level and thus the wide concept of *S. mildeana*, as employed by many authors (e.g. Shaparenko 1956, Fotyanova 1963, 1988), cannot be maintained. Like in the case of the *S. natans*-type of foliage (*S. sunschae* Palibin, *S. kryshtofovichiana* Shaparenko, *S. natanella* Shaparenko), also the *oblongifolia*-type was obviously differentiated over Eurasia into independent taxa. Unfortunately, all Asiatic and most European occurrences have not been so far correlated with taxa based on megaspores, even in cases of fertile specimens (e.g. *S. neurolaqueta* Fotyanova 1963) or associated megaspores (e.g. Kirchheimer 1928). Foliage alone, particularly if fragmentarily preserved, is difficult to be safely identified at the species level.

Even not knowing the associated megaspores we consider probably conspecific with *S. mildeana* Goepp. s.s. the following records in Europe in view of conformable morphology of floating leaves:

Salvinia formosa Heer s.s. (Middle Miocene, Sarmatian of Schrotzburg, Germany, cf. Florin 1940, Hantke 1954, Nötzold 1957) – we dis-

Table 2. Comparison between populations of *Salvinia reussii* Ettingshausen (Bilina Mine) and *Salvinia mildeana* Goeppert (Sośnica)

Character	*Salvinia reussii*	*Salvinia mildeana*
size of floating leaves in mm	8–30 × 10–45	5–16 × 8–16
shape of leaves	ovate oval (rounded) – elongate oval	mostly oval
petiole	broadly keeled	broadly keeled
venation areoles	mostly quadrangular, typically with four tubercules	mostly quadrangular, typically with four tubercules
submerged system	strongly branched, up to 100 mm long, two segments under the node bearing inflated segments	about 10 mm long with segments bearing root-like or inflated segments
inflated segments ("floates")	regularly developed, one segment bearing 2 to several floats, typically 5–15 mm long and 2–5 mm wide	one segment bearing 2–3 floats, typically 8 mm long and 2 mm wide
fertile segment	branched, sporocarps widely spaced	?
sporocarps	amphisporangiate (sometimes with only microsporangia)	?
megaspore species	*Salvinia cerebrata* in situ	*Salvinia intermedia* complex associated
megaspore section sensu Dorofeev 1963, 1987b	*Cerebrata*	*Salvinia*
megaspore shape	more or less equiaxial, globose, apex turbinate to flattened	elongate, ellipsoidal, apex conical
megaspore ornament	convoluted or wavy, sometimes fusing, broad ridges or folds	discrete tubercules and wrinkles on lower part of apical flaps, fine wrinkles on base, smooth in middle
megaspore surface	ridge surface brightly shining, continuous, not perforate, even under high magnification EM	even when appearing smooth under LM surface is actually finely wrinkled and perforate under high magnification EM
megaspore ultrastructure	exoperine vacuole boundaries and outer surface continuous	exoperine vacuole boundaries and outer surface discontinuous, perforate

agree with the arguments by Florin (1940) that in *S. mildeana* the areoles (Segmente sensu Florin) are nearly flat (vs. domed in *S. formosa*) and that the two species differ in "mehreren anderen morphologischen Markmalen", because these differences may be due to different preservation. The size range of floating leaves at the type locality Schrotzburg slightly exceed (11–22 mm long, 8–13 mm wide – Nötzold 1957) that indicative of *S. mildeana*, the submerged root-like segments are longer and no inflated ultimate segments have been observed (Hantke 1954). Information on co-occurring megaspores is badly needed to corroborate the identity with *S. mildeana*. Other records identified as *S. formosa* fall partly within the variation of *S. reussii* (e.g. from North Bohemia – Bůžek et al. 1971, Kvaček & Hurnik 2000), or represent so far doubtful entities (see Florin 1940).

Salvinia cf. *mildeana* Goepp. (Late Miocene, Pannonian of Paldau, Styria, Krenn 1998) – after the inspection of the specimens at the Museum Joanneum, Graz, we are convinced that this population, even sterile, fits well within the type collection of *S. mildeana* in size range, kind of preservation and less developed submerged segments although no inflated segments have been recovered. For the rest of the records assigned to *S. mildeana*, a detailed study of the material is inevitable including attempts of correlation with megaspores in association. This is beyond the scope of the present paper.

DISCUSSION OF MEGASPORES

Many species based on megaspores have been described from the Palaeogene and Neogene. Batten and Kovach (1990) and Kovach and Batten (1989) list 39 species. According to Dorofeev (1987b) twenty one of these fall into section *Salvinia* sensu Dorofeev (Dorofeev 1963, 1987b) having an elongate generally ellipsoid shape comparable to the Sośnica specimens. *S. rhenana* Kempf (Kempf 1971) would also belong in this section on the basis of its shape. Of these spores a number differ from the Sośnica material in having strong, heavy or pronounced surface sculpture of tubercles all over the spore. These species, described by Dorofeev (1987a, b), are *S. cinerea, S. irtyshensis, S. ornata, S. rotundata, S. rugosa, S. siberica, S. tambovica, S. transcarpatica, S. tuberculata*. *S. irtyshensis* is distinct amongst this group because the tubercles are elongate. Other species, although not so strongly sculptured, differ from the Sośnica material because they are sculptured with distinct tubercles in the middle part of the spore. These include species described by Negru (1978) (except *S. crispa* – see below) and *S. clavata, S. tenera*, and *S. tanaitica* described by Dorofeev (op. cit.). *S. tanaitica* also has distinct stellate areas. Other species also differ from the Sośnica material as follows: *S. sarmatica* is broad, it has stellate areas with radiating ridges and has small tubercles all over the apical flaps; *S. crispa* Negru (Negru 1978) (= *S. miocenica* var. *crispa* Dorofeev, Dorofeev 1968) has strong prominent tubercles on the apical flaps; *S. miocenica* var. *miocenica* sensu Dorofeev (Dorofeev 1968) has large but low tubercles on the sides (corners) of the middle part of the spore; *S. ruthenica* Dorofeev (Dorofeev 1987a) has distinct tubercles all over the apical flaps; *S. trachytica* Dorofeev (Dorofeev 1987a) has rounded tubercles on the sides and small fimbriate tubercles around the stellate areas in the middle of the spore; *S. glabra* Dorofeev (Dorofeev 1987a) has a pitted surface; *S. aphtosa* Wieliczkiewicz (Velichkevich 1990) has a narrow apex with distinct separation of the apical flaps and a neck between the flaps and the spore body as well as being sometimes smooth it can have pimple like tubercles which vary in size and are more intense on the base and apex.

The remaining species are very similar to those from Sośnica and they are compared in Tab. 1 according to translations of the original descriptions. These spores all share an elongate, ellipsoidal to fusiform shape, a more or less smooth outline and surface to the middle area of the spore (upper part of spore body), and a relatively small-scale sculpture of small tubercles to fine wrinkles on the apex and base of the spore. However, all the species listed differ from the Sośnica material as follows:

S. petri apparently lacks tubercles but has longitudinal grooves or ridges on the apical flaps. These are not mentioned in the description but are shown clearly on the illustrations in Dorofeev (1987a) and in specimens (at that time assigned to *S. intermedia* but subsequently segregated) from the Prisk locality in Dorofeev (1963). We consider that the synonomy for *S. petri* in Dorofeev (1987a) should have read Dorofeev (1963) pro parte as it seems intended to include only the specimens from the Prisk locality. *S. petri* is *S. intermedia* sensu Nikitin (Nikitin 1948) and Dorofeev (Dorofeev 1955a). The material studied by Nikitin came from Kozhevnikovo on the Ob river and Dorofeev (Dorofeev 1987a) included this in *S. petri*.

S. aspera Dorofeev (Dorofeev 1987a) is typically widest in the upper part of the spore, especially well-displayed in the illustrated specimens.

S. ovata Dorofeev (Dorofeev 1987b) has inflated sides, small apical flaps, rare large tubercles on the margins of the flaps and short ridges or grooves at the bases of the flaps.

S. intermedia Dorofeev (Dorofeev 1955b, non Nikitin 1948), should be the type material of *intermedia* on the basis that this is the first figured specimen accompanied by a diagnosis, i.e. the first valid publication. (The illustration in Dorofeev 1955a was not accompanied by a diagnosis or a description). This material is from Odessa, SW Ukraine and is distinct from the material where the name *S. intermedia* was first listed (Nikitin 1948) which is from western Siberia (river Ob). Therefore, the attribution of the name *S. intermedia* Nikitin ex Dorofeev is incorrect as Nikitin's concept was different from that of Dorofeev (see also Dorofeev 1987a). *S. intermedia* has a neck or indentation which delimits the apex from the body of the spore and the illustrations show stellate areas. Both these features are lacking in Sośnica specimens. However, the distinct neck (e.g. Dorofeev 1955b, Pl. 2 fig. 3) may result from opening of the apical flaps and so this may not be a good specific character.

S. "intermedia" from Strashnyi Gorge and Demidovo (Dorofeev 1955c) requires a new name, if specifically different, because *S. intermedia* from Odessa should be the type material (see above). This population has inflated sides and a more elongate shape than the Sośnica specimens. The illustrations also indicate clear stellate areas which are lacking in Sośnica specimens.

S. rhenana Kempf (Kempf 1971) has more inflated sides than the Sośnica material.

Overall, *S. rhenana* seems to be most similar to Sośnica material differing only in the inflated sides. It is also the only species to have been studied by TEM, and spore ultrastructure is in full agreement with that of spores from Sośnica (apart from very minor differences in thicknesses of wall layers). Apart from *S. rhenana* (Kempf 1993) none of the original material of similar species has been illustrated by SEM, even for *S. rhenana* we have only two illustrations (one LM and one SEM) with which to compare the Sośnica specimens. In the time available for this project we have not been able to study the original material of any of these similar species. Mai (2000b) used SEM to figure a specimen from many which he assigned to *S. intermedia* Nikitin based on the Odessa material (=*S. intermedia* Dorofeev, Dorofeev 1955b, see above). These occurred at many Middle and Late Miocene localities in the Lusatia. The specimen differs from Sośnica specimens in having more well-developed tubercles all over the apical flaps and in a less elongate shape but it lacks the neck which is present in the original Odessa material (Tab. 1)

A full SEM and TEM survey of populations of each of the species is needed before a clear comparison can be made. Therefore we refer to the Sośnica specimens (and to the group of species listed in Tab. 2 as a whole) as the *S. intermedia* Dorofeev complex, using the name *S. intermedia* for this complex as it is the earliest validly published name for a member of this group (Dorofeev 1955b).

The spores of the *Salvinia intermedia* complex are characterized by an elongate generally ellipsoidal to fusiform shape, a smooth middle part of the spore, only slightly sculptured bases and apices, both with small tubercles or wrinkles. They may or may not have inflated sides. They may or may not have stellate areas with radiating ridges associated with depressions in the middle of the spore.

Specimens named *S. intermedia* from Rypin (Poland, Late Miocene) by Łańcucka-Środoniowa (1958) are very similar to, probably the same as, the specimens from Sośnica. They may differ slightly in the ornament on the apical flaps with the Rypin material having fewer tubercles. Confirmation must await SEM and TEM comparison of the actual material.

INFRAGENERIC DISTINCTION BASED ON SPORES

The above discussion covered spores which belong in section *Salvinia* sensu Dorofeev (Dorofeev 1963, 1987b) on the basis of spore shape. Very different spores occur in the section *Cerebrata* Dorofeev. A representative of this section is *S. cerebrata* Nikitin ex Dorofeev which is known in situ from plants of *S. reussii* (Bůžek et al. 1971, Collinson 1991) and from dispersed amphisporangiate sori (Fig. 7: 6). The key characteristics of these megaspores are contrasted with those of the Sośnica megaspores in Tab. 1. *S. cerebrata* megaspores are more or less equiaxial, not elongate, the apex is turbinate or flattened (Fig. 7: 8), the ornament consists of convoluted or wavy folds or ridges (Fig. 7: 7), the surface of the ridges is very smooth and brightly shiny (Fig. 7: 8) and has no perforations even under high magnification SEM (Fig. 7: 9). In TEM section a thin continuous, homogeneous, imperforate sporopollenin layer is evident at the outer exoperine surface (Fig. 8: 2). In TEM ultrastructure the exoperine vacuoles have continuous boundaries (Fig. 8: 2, 4, 6) and are also seen to be continuous in SEM (Fig. 8: 10). Figure 8 contrasts the TEM ultrastructure of the Sośnica megaspores with those of *S. cerebrata*.

Kempf (1971) recorded the same differences in TEM ultrastructure between *S. cerebrata* and fossil material of *S. natans* from Pleistocene and *S. rhenana* Kempf from Pliocene of Rheinland, the latter two being like the Sośnica spores. Vanhoorne (1992) also showed different exoperine ultrastructure and spore surface between *S. cerebrata* (studied by TEM) from the Tongrian (Early Oligocene) and *S. natans* (studied by SEM) from the Early Pleistocene of Belgium. The microspore massulae of *S. cerebrata* also show the same continuous perine vacuole boundaries as the megaspores (Collinson 1991, Van Bergen et al. 1993, Kempf 1971). Friis (1977) also documented the distinctive features of *S. cerebrata* megaspores and microspore massulae using SEM and TEM. Tryon and Lugardon (1991) also recorded the Sośnica-like *Salvinia* spore ultrastructure in modern *S. natans*. Therefore, spores of the *S. cerebrata* morphology, section *Cerebrata* Dorofeev, contrast strongly with those of Sośnica, *S. rhenana* and *S. natans* all of which can be assigned to section *Salvinia* sensu Dorofeev.

If these differences can be confirmed by future SEM and TEM study of other species this will enable distinction of two infrageneric groupings within spores of the genus *Salvinia*. These groupings will require typification and valid publication of the respective infrageneric taxa as this was not accomplished by Dorofeev (1963, 1987b). Alternatively, *S. cerebrata* may prove to be individually distinct in having a smooth, shiny imperforate surface on the folds, a very thin outermost homogenous exoperine layer and imperforate exoperine vacuoles with continuous boundaries. In either case the spore morphology with sculpture and ornament studied by SEM and ultrastructure studied by TEM has great potential for infrageneric distinction within *Salvinia* and for comparison with related extinct spore types.

Dispersed *Salvinia* megaspores, from Palaeocene/Eocene transitional strata of southern England, have a surface ornament of pronounced convoluted and anastomosing ridges. They are generally small (less than 400 µm), more or less equiaxial, i.e. similar in length and diameter (i.e. not elongate ellipsoidal). The perispore flaps around the laesurae are flattened or turbinate at the apex (Martin 1976, Collinson 1992a, Van Bergen et al. 1993). Preliminary SEM and TEM observations of new material (Collinson 1992a, Van Bergen et al. 1993) show that the perispore vacuolae, in both the megaspores and microspore massulae, have continuous boundaries. This is also the case for the massulae of *S. exigua* from the Palaeocene/Eocene transitional strata in the Netherlands (Batten & Collinson 2001). In all of these features this stratigraphically early material is like *S. cerebrata* (placed in sect. *Cerebrata* by Dorofeev 1968, 1987b) and unlike spores of the *S. intermedia*-complex (placed in sect. *Salvinia* by Dorofeev 1963, 1987b). This supports the suggestion by Dorofeev (1987b) that spores of the type which he placed in section *Cerebrata* were "older", which he based on the observation that they became extinct in the former USSR by the end of the Miocene.

Structural differences, like those between the continuous versus perforate surfaces and vacuoles boundaries of the *Salvinia* exoperine, are predicted by the self-assembly hypothesis for spore wall construction. Experimentally modelled self-assembly processes produced structures extremely similar to *Salvina* megaspore wall ultrastructure (Hemsley et al. 2000, Fig. 10). The fact that the two distinctive spore structures that we have observed are found within spores of distinctive gross morphology, in situ on, or associated with, distinctive vegetative organisation, shows that they belong to two natural plant species. This argues in favour of self-assembly processes under partial genetic control as suggested by Hemsley et al. (2000). *Salvinia* may prove to be an appropriate plant with which to undertake experiments on the role of self-assembly in spore wall formation.

INFRAGENERIC DISTINCTION BASED ON FOLIAGE

In a study completed in 1940 Shaparenko (1956) suggested infrageneric subdivision of extant species of *Salvinia* based on foliage. The traits he employed refer to the keel-like petiole (sect. *Carinatae* Shap.), strongly papillate laminas without keels (sect. *Papillatae* Shap.), pilose laminas without keels and papillae, and microsori including 32 spores (sect. *Pilosae* Shap.), and pilose laminas without keels and papillae, and microsori including 64 spores (sect. *Multisporae* Shap. = *Salvinia*). According to this system, several fossil records in a complete state of preservation, are mostly referable to sect. *Carinatae* (*S. reussii, S. mildeana, S. natanella, S. neurolaqueata*). Shaparenko's system is not compatible with that of Dorofeev (1963, 1987b), who divided the genus only into two sections, sect. *Cerebrata* Dorof. and *Eusalvinia* Dorof. (= *Salvinia*), because *S. mildeana* would be assigned to two sections (*Carinatae* Shap. and *Salvinia* sensu Dorofeev). In our opinion, infrageneric entities of *Salvinia* should be based on both vegetative and reproductive (mainly megaspore) traits and require further studies both of extant species (better knowledge of megaspore micro- and ultrastructure) and the fossil record.

SALVINIA RECONSTRUCTED PLANTS

Salvinia mildeana (with spores of *S. intermedia* complex) and *S. reussii* (with spores of *S. cerebrata*) are two distinct fossil species of reconstructed *Salvinia* whole plants. More extensive studies on fossil and extant megaspore populations (using SEM & TEM) are needed to assess species level variations and to elucidate to what extent numerous Palaeogene and Neogene species named in Eurasia on the basis of megaspore morphology can be correlated with the vegetative remains. We may agree with Shaparenko (in Krishtofovich 1956) that *S. mildeana* Goeppert and *S. formosa* Heer (Heer 1859) are conspecific, although the latter is more fragmentary and without any information on attached or associated megaspores (see above). Spore characteristics documented by SEM and TEM offer excellent possibilities to distinguish fossil *Salvinia* species, and infra-generic clades (Tab. 1), whilst spores attached to, or associated with, vegetative parts provide whole plant reconstructions which enable detailed comparisons between fossil and recent species.

THE AQUATIC PLANT *LIMNOBIOPHYLLUM*

GENERIC CONCEPT AND OCCURRENCE

Two kinds of plant remains were mixed together by Krassilov (1973, 1976), when he circumscribed *Limnobiophyllum*. Originally he studied and described under this name reniform “tuberculate” bodies from the Palaeocene of Tsagayan, which he believed to represent fossil Araceae on the basis of stomata structure. However, he established *L. scutatum* (Dawson) Krassilov as a species including the type of the genus, based on leaf fossils from the early Palaeogene of North America. Hickey (1977) noticed this discrepancy and separated the tuberculate bodies in another taxon, *Porosia* Hickey [type *Porosia verrucosa* (Lesquereux) Hickey, nom. illegit. based on an illegitimate *Carpites verrucosus* Lesquereux, non (Heer) Schimper]. When dealing with *Limnobiophyllum*, Kvaček (1995) believed that both entities may belong to the same plant and explained *Porosia* as turions. Recent re-evaluation of better preserved material of *Porosia* from North America (R. Serbet pers. comm., 1996) revealed internal seed-like structure inside *Porosia* bodies, which proves that these are disseminules, although in several cases they accompany the leaves and whole plants of *Limnobiophyllum* (e.g. Joffre Bridge, Tsagayan), usually not in close association. Thus the concept of *Limnobiophyllum* had to be changed from that of Krassilov (Kvaček 1995, Stockey et al. 1997) and restricted only to foliage and whole plants. Nevertheless, some authors still continue to use the Krassilov concept (e.g. Golovneva 1994, 2000) by including *Porosia* bodies, both smooth as well as tuberculate (due to exposure of internal porose structure) into *Limnobiophyllum*.

Whole plants of *Limnobiophyllum* occur in Europe only in two places, the type locality Schrotzburg (Sarmatian – Hantke 1954, as *Hydromystria expansa* (Heer) Hantke) and at Bilina, North Bohemia (Early Miocene – Kvaček 1995, 1998, in press), in both cases in sterile state. In the latter site the plants of *Limnobiophyllum* are accompanied by seeds of *Lemnospermum* Nikitin and because of very intimate association, these may be disseminules of *Limnobiophyllum*. *Lemnospermum* is also known from Mamontova Gora, NE Siberia, probably Miocene (Nikitin in Baranova et al. 1976), the Early Oligocene to Early Miocene of Germany (Mai & Walther 1978; Mai 1999a) and Palaeocene of Joffre Bridge, Canada (Z. Kvaček personal observation), in the latter locality also accompanying *Limnobiophyllum*. In North America more localities with whole plants and isolated leaves of *Limnobiophyllum* exist in deposits of latest Cretaceous to early Palaeogene age, in one case with plants in flower (Stockey et al. 1997). Pollen in situ belongs to the spinose ulcerate morpho-genus *Pandaniidites* Elsik (Stockey et al. 1997), which is well known in the dispersed state in various Tertiary deposits in the Northern Hemisphere. So far, no record of *Pandaniidites* is available in Europe in close association with *Limnobiophyllum* remains.

FAMILY AFFINITY

Cladistic analysis carried out by Stockey et al. (1997) resolved *Pistia*, *Limnobiophyllum* and Lemnaceae as a single clade, which led the authors to suggest an emendation of the Lemnaceae sensu lato to include all three taxa mentioned above. *Limnobiophyllum* shares many important characters with the Lemnaceae including general pollen morphology (spinose, ulcerate – Stockey et al. 1997), mesophyll idioblasts, basic system of primary venation (*Spirodela polyrrhiza*), probably the seed structure (associated *Lemnospermum*), yet differs decidedly by free blades, not fused into a frond, dimorphic roots and leaves grouped in rosettes (Kvaček in press). It also differs from the Lemnaceae in pollen ultrastructure – annulate ulci, thin collumelate layer – Hotton et al. 1994, Stockey et al. 1997, M. Hesse pers. comm. 18 May 2000. Therefore, we are not confident in the new emendation of the Lemnaceae by Stockey et al. (1997) to comprise *Pistia*, *Limnobiophyllum* and Lemnaceae s.s. *Limnobiophyllum* may be derived from some extinct so far unknown fossil protoaroid, (in the sense of Krassilov and Makulbekov (1995)) during the Late Cretaceous and may have given rise to *Spirodela* by reduction process. Apomorphies of the Lemnaceae (foliage in form of "fronds", non-annulate ulci) not shared by *Limnobiophyllum*, led Kvaček (in press) to suggest a new monogeneric family for the latter. We consider that further analyses are needed to resolve the relationship of *Limnobiophyllum*.

SYSTEMATICS

Magnoliophyta

Arales

Limnobiophyllum Krassilov emend. Z. Kvaček

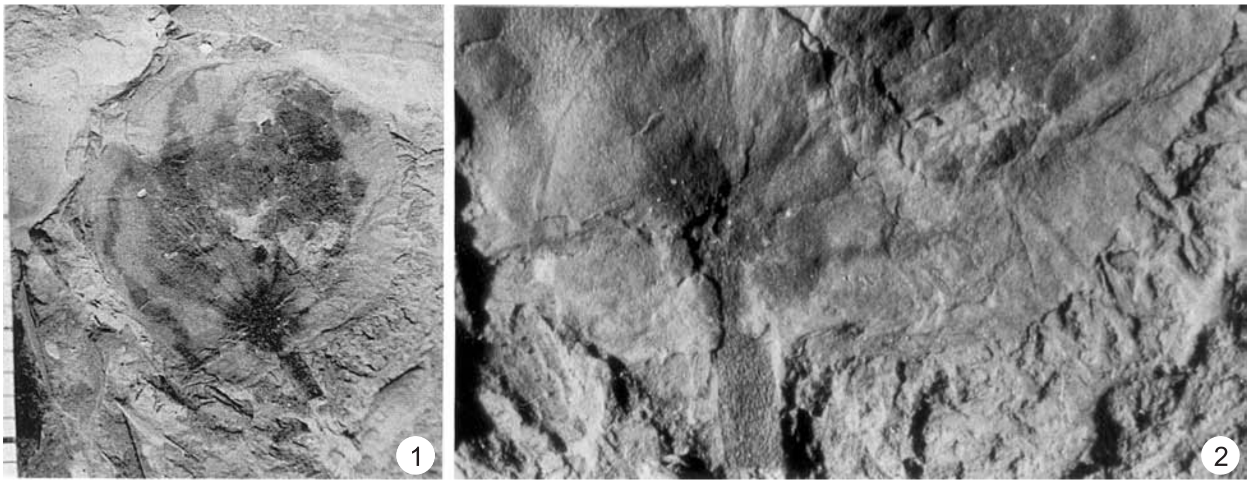
1973 *Limnobiophyllum* Krassilov, p. 110
1995 *Limnobiophyllum* Krassilov; Kvaček, p. 51

Limnobiophyllum expansum (Heer) Z. Kvaček

Fig. 10: 1, 2

1855 Cotyledo; Goepppert, p. 40, Pl. 26 fig. 46
? 1855 *Carpinus involvens* Goeppert, p. 20, Pl. 5 fig. 8
1859 *Hiraea expansa* Heer, p. 65, Pl. 121 figs 16–16b
1954 *Hydromystria expansa* (Heer) Hantke, p. 81, Pl. 14 figs 9–12
1995 *Limnobiophyllum expansum* (Heer) Z. Kvaček, p. 51, text-figs 2–6.

Material. Goeppert's collection: MGUWr



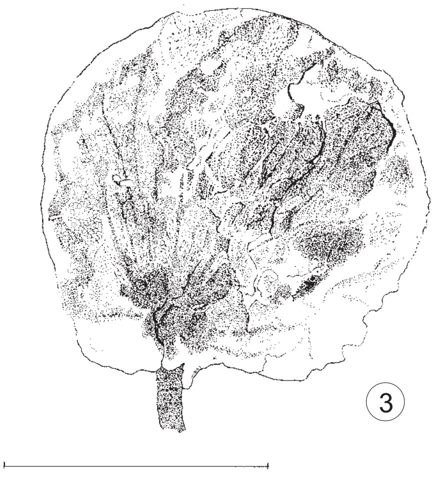


Fig. 10. *Limnobiophyllum expansum* (Heer) Z. Kvaček from Sośnica, **1** – leaf with short remnant of stolon, MGUWr 818p, Goeppert 1855, Pl. 26 fig. 46, × 3, **2** – detail of the same specimen showing attachment of stolon to leaf base, × 7, **3** – drawing of the same specimen (scale bar 10 mm)

818p/II (identified as *Hantkea* by Bůžek, unpubl.).

Description. A single fragmentary specimen from Sośnica consists of a single sessile (amplexicaul ?) rounded leaf attached to a shortened axis, from which a small remnant of a linear stolon arises. The leaf blade is circular, 15 mm across, slightly cordate (or subpeltate), the attachment point (axis) being situated ca. 2 mm inside the outline of the blade (Fig. 10). Venation is campylodromous-acrodromous, with about 9 slightly bent primaries radiating from the base and leaving only indistinct traces in the upper part of the leaf. At some places, a few secondaries are poorly visible, which form an irregular network of higher-order venation between the primaries. Elsewhere within the blade, tiny rounded meshes of aerenchyma are observable. In the upper part near the apex, dense small dots and short dark bars are visible imitating trichomes.

DISCUSSION

This is the only reliable record of *Limnobiophyllum* in the Polish Tertiary and the youngest record of the genus (see also Kvaček in press). A single specimen from Sośnica was described as "cotyledo" by Goeppert (1855). Another picture in Goeppert (1855, Pl. 5 fig. 8) showing *Carpinus involvens* Goepp. can also be suspected to represent *Limnobiophyllum*, but the blade is distorted and the specimen is missing, preventing a more precise comparison of venation. In both cases the plants have only one leaf on the central reduced axis and a fragmentary stolon, but lack remains of roots. In more complete plants known from Bilina two unequal leaves and dimorphic roots are often preserved (Kvaček 1995, 1998, in press). *L. scutatum* (Dawson) Krassilov from the Late Cretaceous to Eocene of North America (Stockey et al. 1997) and East Asia (Fedotov 1983) is very similar in its growth habit, and also solitary leaves with a fragmentary stolon are known (Krassilov 1976, Pl. 11 fig. 5, as *Hydrocharis* sp.). In many specimens of *Limnobiophyllum*, and also in that from Sośnica, aerenchyma tissue is typically preserved, but usually not over the whole blade surface, thus recalling the aerenchymatous pad on the leaf underside developed in some recent Hydrocharitaceae (*Hydrocharis*, *Limnobium*). Also dots and bar-like idioblasts can be seen in peripheral parts of the specimen from Sośnica, traits shared with the *Limnobiophyllum* plants from Bilina (Kvaček 1995).

FOSSIL *SALVINIA* AND *LIMNOBIOPHYLLUM* OCCURRENCES

Limnobiophyllum occurs either together with, or in close association with, both *Salvinia reussii* (e.g. at Bilina) and *Salvinia mildeana* (e.g. at Sośnica). The two *Salvinia* species seem to rarely co-occur and, judging according to the distribution of the *S. intermedia* complex vs. *S. cerebrata* spores the latter tend to be more characteristic of Oligocene and Early Miocene of Europe, while the former is more characteristic of the later part of Neogene. But they do overlap in time and space, particularly in the Neogene, being usually confined to separated sites (see e.g. Mai & Walther 1988, Mai 1999a).

At Sośnica, *Salvinia* remains, both leaf impressions and megaspores, are only accessory elements in the plant assemblage, which is dominated by leaf remains of arborescent plants, especially *Ulmus* and *Salix*. On the slabs bearing *Salvinia* and *Limnobiophyllum* leaves there are remains of the genera *Alnus*, *Carpinus* (leaves and an involucre), *Liquidambar*, *Salix*, *Taxodium* and *Ulmus*. On the basis of the near-living relatives, other free-floating aquatics at Sośnica include *Eoeuryale*, *Azolla*, and *Trapa* (Łańcucka-Środoniowa et al. 1981, Wójcicki & Zastawniak in press). Only *Eoeuryale* is said to be plentiful (Łańcucka-Środoniowa et al. 1981). *Limnobiophyllum* is represented by only a single specimen and *Azolla* is very rare (1–3 megaspores). Co-occurrence of these elements is not proven, although all have been found in the same level in the grey clay within the Flamy Cay Horizon (=Variegated Clay Horizon), which is interpreted to represent lacustrine deposition in the basin (Stachurska et al. 1973).

Limnobiophyllum is rare in the European Miocene. The richest occurrence is in the aquatic plant horizons in the Bilina mine in North Bohemia of Early Miocene age (Kvaček 1998). In the horizon 21 the most abundant occurrence is connected with masses of *Salvinia* plants and *Hydrochariphyllum*. *Salvinia* also occurs in the absence of *Limnobiophyllum*, at other levels, where it is sometimes associated with *Azolla* and *Elaphantosotis* (Kvaček 1998, in press). Of the arborescent community, *Salix, Taxodium* and *Ulmus* predominate.

The occurrence of *Limnobiophyllum* at Schrotzburg (Middle Miocene) is connected with a similar setting (Hantke 1954). It is common only in one horizon (Plant level No. 8) with *Salvinia* and many arborescent elements like *Populus, Ulmus, Liquidambar, Platanus* and *Acer*. *Salvinia* also occurs in other levels with rare, or without, *Limnobiophyllum*.

Considering *Lemnospermum* to be disseminules of *Limnobiophyllum*, its association with *Salvinia cerebrata* and the *Salvinia intermedia* complex is proven in the Early Miocene of Lusatia, Germany (core Schlabendorf-Süd KB 150/66, floristic zone VII sensu Mai – Mai 1999a). This carpological assemblage includes many more aquatic free-floating (*Lemna, Pistia, Ceratophyllum*), and rooted emergent plants (*Typha, Sparganium, Scirpus, Dulichium, Caricoidea, Spirematospermum, Butomus, Monochoria, Decodon*) in association with woody elements of the Taxodiaceae-*Nyssa* swamp forest (Mai 1999a, b, 2000a).

A single specimen of *Limnobiophyllum* has been recovered at Kreuzau in the Rhineland (Weyland 1934), a site considered of Middle Miocene age (Ferguson et al. 1998), and associated with very few specimens of *Salvinia* in sediments similar to Sośnica (Ferguson 1971). The plant assemblage is predominantly represented by riparian forest elements with very few other aquatics, e.g. *Hemitrapa* and *Stratiotes* (Ferguson et al. 1998).

The Pannonian (Late Miocene) co-occurrence of *Limnobiophyllum* and *Salvinia* at Paldau in Styria, Austria (Krenn 1998 – level H2) shows a similar flora in aquatic – riparian settings. *Salvinia* and *Limnobiophyllum* are represented by one specimen each, while the plant assemblage is dominated by *Pronephrium, Glyptostrobus, Comptonia, Myrica* and monocot foliage.

Salvinia occurs in association with "*Spirodella*" sensu Dawson (= *Limnobiophyllum* – see Stockey et al. 1997) in the Eocene of the Bighorn Basin, Wyoming (Wing 1984, Farley 1990, Davies-Vollum & Wing 1998) in pond settings in a back swamp environment of a wet distal floodplain. *Limnobiophyllum* is also found in association with *Azolla* in several Palaeocene sites in North America including deposits of oxbow lakes (McIver & Basinger 1993, Chandrasekharam 1974, Hoffman & Stockey 1994, 1997, 1999, Stockey et al. 1997). Some of these occurrences are associated with other floating aquatic plants including *Quereuxia* (=*Trapago*), a *Pistia*-like plant and *Ricciopsis* (an aquatic liverwort). Collinson (in press) summarises the fossil record of wetland communities containing associated *Salvinia* and *Azolla*.

AQUATIC PLANTS AT SOŚNICA

The remains of free-floating aquatic plants known from the flora of Sośnica include the plants *Salvinia mildeana* and *Limnobiophyllum* described herein. A few *Azolla* megaspores were also recorded (Łańcucka-Środoniowa et al. 1981) and there is excellent evidence that fossil *Azolla* were also free-floating aquatic plants (Collinson in press) but there are no whole plants at Sośnica so these megaspores may have been transported or the plants may have lived in a different setting where whole plants did not become incorporated in sediments. In addition, based on their nearest living relatives, the following fossils are also interpreted as having been produced by aquatic plants: pollen of *Butomus, Potamogeton, Sparganium*, ? *Stratiotes* and *Typha* (Stachurska et al. 1973); fruits of *Trapa silesiaca* Goeppert; a single leaf of *Trapa assmanniana* (Goepp.) Wójcicki & Zastawniak (see Wójciki & Zastawniak in press); *Eoeuryale brasenioides* Miki (seed, spine); *Sparganium neglectum* Beeby *fossilis* (fruit); *Batrachium* sp. (fruit); *Callitriche* sp. (fruit); and *Typha* sp. (seed) – Łańcucka-Środoniowa et al. (1981). The only other putative aquatic plant at Sośnica is one group of reproductive structures (specimen MGUWr 1283p), determined by Łańcucka-Środoniowa (unpubl.) as possible *Najas*. In an attempt to confirm this record M. Collinson has re-examined this specimen and studied a fragment by SEM. The individual specimens are narrowly elongate ovoid and consist of an inner translucent cuticle (tegmen or testa), with cuticle flanges marking impressions of square epidermal cells, and an outer sclerotic layer of elongate thick-walled cells (testa or fruit wall). The observed characters are insufficient to confirm the determination to *Najas*.

ASSOCIATED FOREST VEGETATION AT SOŚNICA

Most of the plant remains preserved in the clays of Sośnica originate from forest communities characteristic of the vegetation of the Late Miocene of central Europe. The so-called Cheylade “Florenkomplex” (see Mai 1995), aged 5.6 million years, is representative of this type of vegetation. According to tentative assessment based on the near-relatives autecology it comprised mesophilous deciduous or mixed forests with species composition depending mostly on the humidity of the substratum. In marshy places, in very moist sites, there were mixed forests with common *Taxodium*, accompanied by *Alnus, Carya, Leitneria, Liquidambar, Myrica, Nyssa, Pinus, Platanus, Populus, Pterocarya, Salix*, and *Ulmus* that were particularly numerous in the flora of Sośnica. In these marshy forests *Glyptostrobus* (or related Taxodiaceae = *Glyptostroboxylon*) trees would have grown. This genus was identified in the flora of Sośnica only from wood remains (Reyman 1956); the absence of traces of shoots and cones shows that the genus did not played an important role in the contemporary forests of that area. The other type of plant communities in the flora of Sośnica are mesophytic deciduous forests growing in less humid or/and more elevated sites, with a small amount of coniferous trees from the genera *Amentotaxus* and *Cephalotaxus*. Particular forest layers were formed by trees or shrubs belonging to such genera as *Acer, Aralia, Betula, Carpinus, Celtis, Distylium, Dombeyopsis, Eucommia, Fagus, Ostrya, Palaeocarya, Parrotia, Phyllanthus, Quercus, Symplocos*, and *Zelkova*. In the forests of both types there grew creepers or lianas (*Ampelopsis* and *Vitis*), and plants from the family Loranthaceae. At the forest margins or in the herb layer, there were herbaceous plants represented by fossil fruits and seeds of *Carex, Decodon, Dichostylis, Dulichium*, Gramineae, *Hypericum, Juncus, Ludwigia, Lycopus, Polygonum, Rumex, Scirpus, Selaginella*, and *Typha*. Most of these plants may have grown on the margins of a water reservoir with floating aquatic plants (see above).

The flora of Sośnica includes also the remains of plants that are supposed to have grown in drier habitats. These are genera *Tetraclinis (=Libocedrites)* and *Paliurus*, and many other so far unidentified leaf impressions, as e.g. leaflets of the type Leguminosae sensu Berger. This family is also represented by seeds and pods (Goeppert 1855).

Megafossil records document and complement the picture of vegetation of the sites Sośnica, as revealed by palynological studies (Stachurska et al. 1973). They indicate the presence of two main forest types connected with different kind of habitats. On swampy, and very wet substrate Taxodiaceae-Cupressaceae mixed forests with deciduous broad-leaved elements (*Alnus, Carya, Liquidambar, Myrica, Nyssa, Platanus, Pterocarya, Salix*) thrived. Herbaceous undergrowth was dominated by ferns, documented by higher frequencies of spores of Filicinae. The palynologically documented picture of the second type of vegetation is indicative of broad-leaved deciduous forest with diverse shrubs and climbers. Abundant pollen of such trees as *Betula, Carpinus, Engehardia, Fagus, Parrotia, Pterocarya, Quercus, Ulmus-Zelkova*, relatively frequent pollen grains of *Acer, Celtis, Juglans, Tilia* as well as trees and/or shrubs of Anacardiaceae, Aquifoliaceae (*Ilex*), Araliaceae-Cornaceae, Leguminosae, Oleaceae, Rosaceae and climbers, such as *Rhus, Parthenocissus, Smilax* and *Hedera* corroborate high diversity and richenss of these forests (Stachurska et al. 1973).

The flora of Sośnica is characterized by the domination of arctotertiary genera, while palaeotropical thermophilic elements are represented only by scarce traces of the genera *Ampelopsis, Dombeyopsis, Myrica, Smilax* and *Symplocos*. This is typical of the fossil floras of similar age in central Europe, growing in conditions of moderately warm temperate climate (Mai 1995).

CONCLUSIONS

Salvinia mildeana (with associated megaspores of the *S. intermedia* complex) and *Salvinia reussii* (with attached *S. cerebrata* megaspores, sori and microspore massulae) are two distinct fossil species of *Salvinia* (free-floating heterosporous water ferns) based on reconstructed whole plants. *S. mildeana* with associated megaspores occurs only in the Late Miocene of Sośnica, Poland but similar vegetative material occurs in the Middle and Late Miocene at Schrotzburg, Germany and Late

Miocene of Paldau, Austria. Fertile *S. reussii* plants occur only in the Late Oligocene of Germany and Early Miocene of Bilina, Czech Republic but similar vegetative material occurs in the Late Oligocene of Roumania (*S. oligocaenica* Staub, *S. ovoidea* Givulescu, Givulescu 1968) and Early Miocene of Germany (*S. macrophylla* Kirchheimer 1928, 1932). Distinguishing characteristics of these species have been presented in Tab. 1. They both differ from modern *Salvinia* in the possession of inflated segments, which probably functioned as "floats" to aid buoyancy. The inflated segments never contain spores. In contrast, sporocarps are borne on separate fertile segments. Therefore, we do not agree that these inflated segments are sporocarps as suggested for *S. reussii* by Rothwell and Stockey (1994).

S. cerebrata type megaspores and megaspores of the *S. intermedia* complex have many distinguishing features which show the potential for use of megaspore characteristics for infrageneric classification of the genus *Salvinia*. *S. cerebrata* spores are more or less equiaxial, globose, with turbinate to flattened apices and an ornament of large convoluted folds or ridges, the surfaces of which have a thin homogeneous layer of perine and are smooth and continuous, not perforate. Vacuoles in the exoperine have continuous boundaries. In contrast, *S. intermedia* complex spores are elongate, ellipsoidal, with conical apices and an ornament ranging from almost smooth to small-scale tubercles and wrinkles. Even in almost smooth parts of the spore the surface is very finely perforate and wrinkled at high magnification under SEM. Vacuoles of the exoperine have discontinuous perforate boundaries.

Structural differences, like the continuous versus perforate surfaces and vacuoles boundaries of the *Salvinia* exoperine, are predicted by the self-assembly hypothesis for spore wall construction. Their occurrence in two natural species argues in favour of self-assembly processes under partial genetic control as suggested by Hemsley et al. (2000).

Study of the Sośnica spores has shown that an SEM and TEM survey of many more of the named fossil *Salvinia* spore species, as well as the megaspores of modern species, is necessary to fully evaluate the systematic potential of spore characteristics. If confirmed by future study these distinctive characteristics will enable use of the fossil record in phylogenetic analyses of *Salvinia* and related extinct heterosporous ferns such as *Glomerisporites* and *Parazolla* (Collinson 1991, Batten et al. 1998, Rothwell & Stockey 1994). They will also provide minimum ages for synapomorphies of clades within the genus *Salvinia* and they might also prove useful for biostratigraphy of continental sequences. Preliminary results suggest that characteristics of *S. cerebrata* – type spores occur earlier in the fossil record than those of the *S. intermedia* complex or other members of section *Salvinia* sensu Dorofeev (Dorofeev 1963, 1987b). *S. cerebrata* characteristics may, therefore, represent the primitive state for *Salvinia* spores.

Limnobiophyllum is an extinct genus of free-floating aquatic plants of the flowering plant order Arales, represented by two species of reconstructed whole plants. Kvaček (in press) suggested a new monogeneric family for *Limnobiophyllum*, arguing that, although sharing some characteristics with Lemnaceae, it also differs significantly. The record from Sośnica is the youngest record of the genus, which also occurs in Europe as whole plants in the Early Miocene of Bilina (Czech Republic) and the Sarmatian of Schrotzburg (Germany).

The free-floating aquatic plants *Salvinia* and *Limnobiophyllum* co-occur with other free-floating and marginal aquatics at Bilina (Kvaček 1998, in press) and Styria, Late Miocene, Austria (Krenn 1998). At Sośnica, Late Miocene, Poland) Schrotzburg (Middle Miocene, Germany), and Kreuzau (probably Middle Miocene, Germany) *Salvinia* and *Limnobiophyllum* are closely associated, again with other aquatics. All these occurrences are associated with leaf fossils interpreted as being derived from riparian forest trees such as *Taxodium*, *Ulmus* and *Salix*. More specific statements on the Sośnica wetland plant communities would need to be linked to new collecting efforts concentrating on documenting facies associations, sedimentology and co-occurrences of fossils on individual bedding planes. A similar association of *Limnobiophyllum* with *Salvinia* or *Azolla* and other aquatics is known in the Palaeocene and Eocene of North America (Wing 1994, Collinson, in press, Stockey et al. 1997).

These reconstructed whole plants of *Salvinia* and *Limnobiophyllum* demonstrate that the former variation in the genus *Salvinia* and the order Arales exceeded that represented by the modern species and that distinct extinct species (of *Salvinia*) and genera (*Limnobiophyllum*) were present as recently as the Late Miocene. Linking distinctive spores to vegetative remains is a critical factor in providing a more natural conspectus of the diversity and variety in the history of the genus *Salvinia*. *Salvinia* and *Limnobiophyllum* were part of the free-floating component of wetland plant communities in the Early Palaeogene of North America and throughout the Miocene in Europe.

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