Acta Palaeobot. 40(2): 139–151, 2000

Aquatic plant communities at the Cretaceous-Palaeogene boundary in north-eastern Russia

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ABSTRACT. Several aquatic plants from the Rarytkin Formation (late Maastrichtian-Danian, Koryak Upland, north-eastern Russia) are described. In that time aquatic communities of freshwater vascular plants (macrophytes) comparable by structure and diversity with modern water ecosystems began to form. An analysis of life forms of aquatic plants makes it possible to reconstruct their probable distribution in water bodies. The Rarytkin aquatic ecosystems appear to differ from modern ones by weaker development of such ecological groups as inshore aquatic “grasses” and submerged plants with long stems and dissected or entire leaves. Because aquatic macrophytes can absorb nutrients more intensively than algae, thus preventing excessive eutrophication, the regulation of nutrient contain during a year was probably one of the most important consequence of development of aquatic macrophytes communities. In addition, rich and dense aquatic vegetation increased primary productivity in aquatic ecosystems and created both a food source and many new biotopes for insects, fish and other animals.

KEY WORDS: aquatic plants, Cretaceous-Palaeogene boundary, north-eastern Russia

INTRODUCTION

Aquatic and amphibious herbaceous plants appeared in the initial stages of angiosperm diversification already in the Early Cretaceous (Krassilov 1989). However, during the Cretaceous up to the Maastrichtian, freshwater macrophytes, particularly angiosperms, were rare in the floras. The continental deposits of northeastern Russia contain an almost complete sequence of floras from the Upper Jurassic up to the Palaeogene. In this sequence through the Cretaceous 12 stages of evolutionary development have been recognized (Samylina 1974, 1988, Herman & Lebedev 1991, Golovneva 1994a). In these floras various species of *Equisetum* were the only widespread plants connected with aquatic environments. Water ferns and lycopods were not represented. Among flowering plants only a few species of aquatic macrophytes were recorded. Small, round peltate floating leaves of *Nelumbites* aff. *minimus* Vachr. were found in the Toptanian flora of the Late Albian (Samylina 1976). Floating rosettes of leaves of *Quereuxia angulata* (Newb.) Krysht. are known from the Cenomanian Arkagala flora (Samylina 1988), from the Coniacian Kaiwajam flora and the Campanian Verkhnebystrinsk flora (Herman & Lebedev 1991). In Gornorechensk flora of the middle Maastrichtian two new species of *Quereuxia* (*Q. rotundifolia* Golovn. and *Q. flabellata* Golovn.) appeared (Golovneva 1991, 1994a). The diversity of aquatic plants increased significantly in the late Maastrichtian-Danian Rarytkin flora, which yielded more than 9 species (Golovneva 1994a). In this time aquatic communities of vascular freshwater plants comparable by structure and diversity to modern aquatic ecosystems began to form. Investigation of the aquatic plants of the Rarytkin flora enables us to reconstruct one of the initial aquatic communities dominated by angiosperms and is important for palaeoecology, because the subsequent development of such communities led to remarkable changes in freshwater ecosystems and influenced considerably the evolution of the respective faunas.

MATERIALS

Fossil plant remains were collected from deposits of the upper part of the Rarytkin Formation, in the Gornaja River basin and along the right bank of the Anadyr River (Fig. 1). The Rarytkin Formation is exposed in the northeastern part of the Rarytkin Ridge (Koryak Upland, north-eastern Russia) and is about 2000 m thick. It consists of cyclically bedded sandstones, shales, and coal and represents lacustrine, paludal, and fluviodeltaic deposits of a large flood-plain. The Rarytkin Formation contains two plant assemblages, which represent different stages of evolutionary development: a middle Maastrichtian Gornorechensk flora and a late Maastrichtian-Danian Rarytkin flora. (Golovneva 1994a,b). The Rarytkin flora comprises more than 60 species and is dominated by several species of *Trochodendroides, Corylus beringiana* (Kryst.) Golovn., *Metasequoia, Glyptostrobus* and *Mesocyparis*. Such plants as *Taxodium*, *Platanus raynoldsii* Newb., *Quercus groenlandica* Heer, *Arthollia, Rarytkinia, Celastrinites, Nyssa, Platimelis, Beringiophyllum, Vitis* and *Ginkgo* are less abundant. Ferns are represented by *Onoclea* and *Coniopteris*. The remains of aquatic plants of the Rarytkin flora are preserved as impressions mostly in fine-grained grey siltstone or sandstone, mixed with terrestrial plants or in finely laminated coaly shales. All specimens are housed in the Komarov Botanical Institute (St. Petersburg), collection number 967. On the basis of remains some aquatic plants have been reconstructed (Fig. 2).

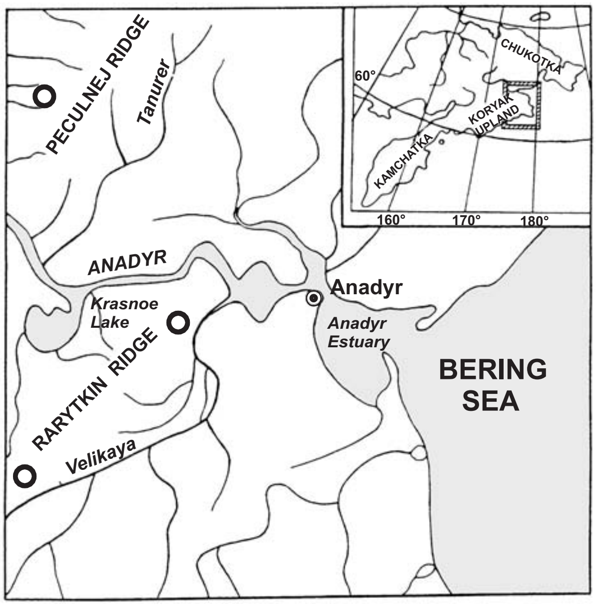

Fig. 1. Map showing the location of the Maastrichtian-Danian deposits of the Rarytkin Formation. Insert: location of study area in north-eastern Russia

DESCRIPTION OF AQUATIC PLANTS

Haemanthopyllum cordatum Golovn.

Pl. 1, fig. 13; Fig. 2B

1987 *Haemanthopyllum cordatum* Golovneva, p. 1127, pl. 1, figs 1, 2, 4, 5, pl. 2, fig. 2.
1994a *Haemanthopyllum cordatum* Golovneva, p. 121, pl. 64, figs 1–4, 10, 12.
1997 *Haemanthopyllum cordatum* Golovneva, pl. 9, figs 2, 6, text-fig. 4.

This is a rooted rosulate plant with petiolate ovate submersed leaves (Golovneva 1994a, 1997). Leaves of *Haemanthophyllum* Budantsev are characterized by (1) very thin and delicate leaf blades, 4–18 cm length, with entire margin, cordate base and rounded apex; (2) a large number (13–25) of longitudinal acrodromous veins; (3) three adjacent, usually thickened median veins traceable along the whole leaf blade or in the distal part alone; (4) fairly dense, about 7–18 per 1 cm of the leaf length, cross-veins traversing the primary veins at 30°–40° in the central part of the leaf and almost at right angle near the margin; (5) thin higher order venation between the cross-veins, usually forming 2–3 rows of polygonal areolae. The latter character is usually only occasionally preserved in small areas of the better-preserved leaf impressions.

Revision of the presently available fossil evidence showed that the genus *Haemanthophyllum* Budantsev was widespread in the vast territories of northern Eurasia and North America from the Maastrichtian to the Miocene. Besides *H. cordatum*, we can distinguish four species of *Haemanthophyllum*: *nordenskioldii* (Heer) Boulter & Kvaček with elliptical float-

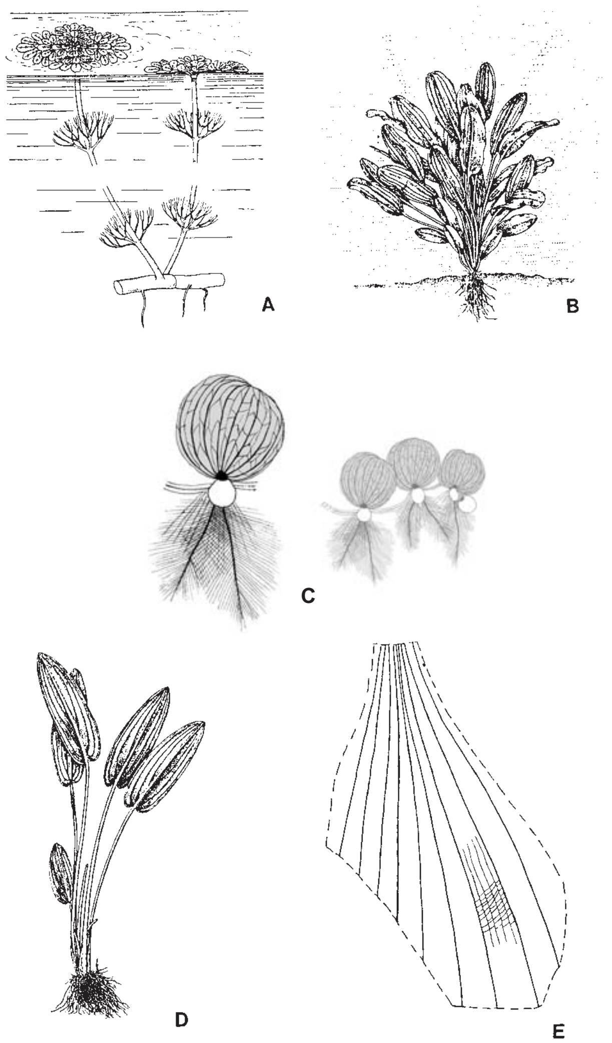

Fig. 2. Reconstruction of some aquatic plants from the Rarytkin flora. **A** – *Quereuxia angulata* (Newb.) Krysht. (after Samylina 1988), **B** – *Haemanthophyllum cordatum* Golovn., **C** – *Limnobiophyllum* sp. (after Kvaček 1995 modified), D, E – *Ottelia*-like plant: **D** – reconstruction, **E** – venation of leaf, × 0.5

ing and submersed leaves from the Palaeocene of Spitsbergen; *H. kamtschaticum* Budantsev with large (up to 35 cm long) cordate leaves from the Palaeocene and Eocene of Kamchatka (Budantsev 1983); *H. zhilinii* (Pneva) Golovn. with elliptical leaves from the Oligocene-Miocene of Kazakhstan and *Haemanthophyllum* sp. with ligulate leaves from the Eocene of Ireland (Boulter & Kvaček 1989). Fragments of *Haemanthophyllum* leaves, similar with *H. nordenskioldii*, were found in Danian deposits of the Amur region (Krassilov 1976) and in Palaeocene deposits of Alaska (Spicer et al. 1994). Leaves resembling *H. kamtschaticum* were found in the Palaeocene deposits of the Fort Union and Ravenscrag Formations in the North America (Brown 1962, McIver & Basinger 1993). Up to now *H. cordatum* is the most ancient species of the genus.

Originally *Haemanthophyllum* Budantsev was assigned to the Amaryllidaceae on the basis of leaf venation similarities with some extant species of the genus *Haemanthus* L. (Budantsev 1983). Further studies of leaf venation in *Haemanthophyllum*, and comparison with various extant monocotyledons, has led us to conclude that this fossil genus is closely related to *Aponogeton* L. (Golovneva 1987, 1997). The modern monotypic family Aponogetonaceae is native to tropical Africa, south-eastern Asia and northern Australia, with its centre of distribution in Madagascar (Tomlinson 1982). The genus *Aponogeton* L. consists of aquatic plants with submersed, floating and partly aerial leaves. Prevailing among them are submersed lanceolate or ligulate leaf forms with typically 7–9 (rarely 11–13) longitudinal veins. In *Haemanthophyllum* there are 11–25 longitudinal veins and wider, elliptical or ovate leaf forms prevail. These characters provide a distinction between *Haemanthophyllum* and *Aponogeton*. The density of cross-veins in *Haemanthophyllum* is commonly somewhat higher than in *Aponogeton*. The leaves of *Haemanthophyllum* have also been compared with extant representatives of the Alismataceae and Potamogetonaceae, which have a similar habit. Plants of these families differ considerably from *Haemanthophyllum* in the characters of the primary and higher order venation (Golovneva 1997).

The earliest reproductive structure assigned to Aponogetonaceae was reported from the Early Cretaceous of South America (Selling 1947), but the material was not properly described. Unfortunately, no reproductive organs comparable to those of *Aponogeton* were found in association with *Haemanthophyllum* leaves. The earliest remains of *Aponogeton* leaves came from the Late Oligocene of Kazakhstan (Zhilin 1974, Andreev 1991). Thus, *Aponogeton* was widespread in the past, not only in the tropics, but also in extratropical areas. The joint occurrence of *Haemanthophyllum* and *Aponogeton* near the Eocene-Oligocene boundary in the same region can be regarded as additional confirmation of the close relationship between these genera.

Limnobiophyllum scutatum (Dawson) Krassilov

Pl. 1, fig. 12

1875 *Lemna (Spirodela) scutata* Dawson, p. 329, pl. 16 figs 5, 6.
1878 *Carpites verrucosus* Lesquereux, p. 305, pl. 60 fig. 3.
1942 *Carpites verrucosus* Lesquereux; Dorf, p. 157, pl. 17 fig. 7.
1949 *Lemna (Spirodela) scutata* Dawson; Bell, p. 82, pl. 63 figs 1, 3, pl. 67 fig. 1.
1962 *Hydromystria expansa* auct. non (Heer) Hantke; Brown, p. 52, pl. 16 figs 1, 3, 8–11.
1973 *Limnobiophyllum scutatum* (Dawson) Krassilov, p. 110, pl. 23 figs 46–61.
1976 *Limnobiophyllum scutatum* (Dawson) Krassilov, p. 52, pl. 12 figs 1–12.
1977 *Porosia verrucosa* (Lesq.) Hickey, p. 114, pl. 54 figs 1–4.
1993 *Carpites verrucosus* Lesquereux; McIver & Basinger, p. 55, pl. 49 figs 1–3.
1993 *Lemna (Spirodela) scutata* Dawson; McIver & Basinger, p. 31, pl. 17 figs 1–5.
1994a *Limnobiophyllum scutatum* (Dawson) Krassilov; Golovneva, p. 120, pl. 27 figs 4–6.
1995 *Limnobiophyllum scutatum* (Dawson) Krassilov; Kvaček, p. 51, text-fig. 1.
1997 *Limnobiophyllum scutatum* (Dawson) Krassilov; Stockey et al., p. 356, text-figs 1–42, 45.

Limnobiophyllum Krassilov is a free-floating rosette usually with two rounded subopposite leaves of unequal size, basally continuous, with numerous simple and branched roots on a reduced main stem. The rosettes are borne on stolons, on which they are spaced 1–4 cm apart (Fig. 2C). At present two species are recognized – *L. scutatum* (Dawson) Krassilov (end of the Cretaceous to the Oligocene of North America and Palaeocene of East Asia and Spitzbergen) and *L. expansum* (Heer) Kvaček (Miocene of Europe). The genus is most common in the Palaeocene. The morphology and anatomy of *Limnobiophyllum* have been studied in detail by Krassilov (1973), Kvaček (1995) and Stockey et al. (1997). The leaves of *Limnobiophyllum* are suborbicular or reniform with entire-margins, well-developed aerenchyma. The initial leaves, which are the largest in each rosettes, reach 1–3 cm across and have campylodromous venation consisting of 9–14 primaries, among which irregular reticulate veins of higher orders can be observed. The second and subsequent leaves are significantly smaller, thickened and more or less tuberculate with a smooth border. The venation on small leaves is usually weakly impressed. Stockey et al. (1997) studied the anatomical structure of leaves, male flowers and pollen.

Only small single leaves about 6–8 mm across have been found in the Rarytkin Formation. Some palaeobotanists considered these leaves to be remains of other taxa because of the sharp differences between them and the first large leaves. Hickey (1977) placed them in a separate genus *Porosia* typified by *Carpites verrucosus* Lesquereux. McIver and Basinger (1993) followed Lesquereux (1878) and considered such leaves as seed remains. Kvaček (1995) suggested that single thicker tuberculate rootless bodies might represent turions or winter buds filled with nutrient reserves, which sank to the bottom, as contemporary *Lemna* sp. and their allies do. The distinction between putative turions and small rosette leaves is, however, not a clear one, because such features as thickness, prominence of tubercules and size are variable, and a gradual transition between large leaves with impressed venation and small thickened tuberculate ones can be observed.

Using the cuticular characters of single small leaves, Krassilov (1973) suggested that *Limnobiophyllum* is close to the Araceae, and may thus represent an intermediate link between the Araceae and the Lemnaceae. Krassilov's opinion was endorsed by Kvaček (1995) on the basis of more complete material and a detailed comparison with *Pistia* (Araceae) and *Spirodela* (Lemnaceae). Using cladistic analysis Stockey et al. (1997) suggested that *Limnobiophyllum* together with *Pistia* and Lemnaceae represent a monophyletic group, and in consequence *Limnobiophyllum* was included by these authors in the family Lemnaceae *sensu lato*. Therefore, any similarity of *Limnobiophyllum* to the Hydrocharitaceae (*Hydromystria*, *Limnobium*) is only superficial.

Quereuxia angulata (Newb.) Krysht.

Pl. 1 figs 1, 3; Fig. 2A

1861 *Neuropteris angulata* Newberry, p. 131, pl. 3 fig. 5.
1878 *Trapa? microphylla* Lesquereux, p. 295, pl. 61 figs 16, 17a.
1930 *Trapa microphylla* Lesquereux; Hollick, p. 109, pl. 84 fig. 4.
1935 *Trapa microphylla* Lesquereux; Berry, p. 61, pl. 19 figs 1–11.
1949 *Nymphaeites angulatus* (Newb.) Bell, p. 64, pl. 17 figs 4, 7

1953 *Quereuxia angulata* (Newb.) Kryshtofovich, p. 23, pl. 3 figs 1–11, pl. 4 figs 1–8, text-figs 3, 4.
1958 *Quereuxia angulata* (Newb.) Kryshtofovich, p. 66, pl. 13 figs 7–9.
1962 *Trapa angulata* (Newb.) R.W. Brown, p. 83, pl. 58 figs 1–12.
1993 *Trapago angulata* (Newb.) McIver & Basinger, p. 43, pl. 31 figs 1–5, pl. 32 figs 1–7, pl. 33 figs 2, 4, pl. 34 fig. 7;
1996 *Trapago angulata* (Newb.) McIver & Basinger; Stockey & Rothwell, figs 2–37.

Quereuxia angulata is a widespread aquatic dicot, recorded in Eurasia from the Cenomanian to the end of the Palaeogene and in North America from the Maastrichtian and the Palaeogene. The most complete specimens were described by Samylina (1988), McIver and Basinger (1993), also Stockey and Rothwell (1996). This species consists of floating rosettes of leaves about 10 cm across attached to vertical stems which arise from horizontal rhizomes. The floating leaves are decussate, with the upper 3–4 pairs simple, the others compound with three, five, seven or more leaflets. The vertical stems also bear whorls of highly dissected filiform submerged leaves at the nodes. The leaves and leaflets are similarly variable in shape varying from symmetrical rounded or ovate, to asymmetrical, angulate, obovate or elliptical, with a serrate margin. The venation is pinnate, craspedodromous. The secondary veins diverge at an angle 30–35 degrees and branch dichotomously, while the tertiary venation is reticulate. The secondary and higher order veins form a marginal vein.

Quereuxia leaves were first described as the fern *Neuropteris angulata* Newberry (1861) and many authors subsequently interpreted these leaf rosettes as *Trapa* remains (Knowlton 1900, Berry 1935, Dorf 1942, Brown 1962). The plant, however, differs distinctly from *Trapa* in its leaf morphology and venation pattern, features which Kryshtofovich (1953) used to establish the new genus *Quereuxia* for these leaf remains typified by *Neuropteris angulata* Newberry. McIver and Basinger (1993) created from Canadian material the genus *Trapago*, which was also typified by *Neuropteris angulata* Newberry. Therefore, the *Trapago* is a late synonym of *Quereuxia*.

Several types of fruit have been reported in association with *Quereuxia* leaves (Brown & Houldsworth 1939, Kryshtofovich 1958, Brown 1962, Samylina 1988, Golovneva 1991, 1994a), but all the putative fruits have not been found attached to leaf rosettes. Brown and Houldsworth (1939) described elliptic fruits 5–10 mm long, with an acute rostrulate apex and longitudinal grooves, from the Palaeocene Ravenscrag Formation. These fruits were found near the stem inside the rosette of leaves and for a long time were considered to be truly attached. Samylina (1988), following this reconstruction, described similar fruits from the Cretaceous deposits of Russia as the supposed fruits of *Quereuxia* under the name *Carpites kolymensis* Samyl. Re-examination of the Ravenscrag material (McIver & Basinger 1993, Stockey & Rothwell 1996) has, however, revealed a lack of organic attachment between fruits and stems. McIver and Basinger (1993) believe that these fruits belong to *Viburnum*. Elliptic fruits with two little curved spines at the apex, which occurred in association with *Quereuxia* leaves in the deposits of the Rarytkin formation, were described by Kryshtofovich (1958) as *Quereuxia aculeata* Krysht. Additional material from the same localities showed that the spines of the fruits transformed into curved horns during their maturation (Golovneva 1991, 1994a). These fruits were transferred to the genus *Palaeotrapa* Golovn. (Pl. 1 fig. 2), because they were not attached to the leaf rosettes. The assignment of *Palaeotrapa aculeata* (Krysht.) Golovn. fruits and the *Quereuxia angulata* (Newb.) Krysht. leaves to the same plant is based on the juxtaposition of these remains and on the similarity of both of them with the modern genus *Trapa*. Stockey and Rothwell (1996) recently described a solitary flower or immature fruit about 5 mm long attached by a long pedicel in the axil of a compound leaf of *Quereuxia*. Unfortunately, because of the lack of well preserved specimen the structure of the flower is not clear. Further studies are needed for a better understanding of the reproductive organs of this plant.

Sparganiophyllum multinervosum Golovn.

Pl. 1 fig. 4

1994a *Sparganiophyllum multinervosum* Golovneva, p. 120, pl. 27 fig. 7.

This species is represented by linear leaves about 6 mm wide, with blunt rounded apex, entire margins and fine parallel venation. The veins are numerous, dense, some of them (5–6) thickened. Cross-veins are not discernible.

The thin and delicate leaf blade with its rounded apex provides enough evidence for us to determine this plant as an aquatic monocotyledon. Probably, it was a rooted rosette plant with submersed ligulate leaves, but it is also possible that it could have had emergent leaves of a different type like those of modern *Sparganium* and *Sagittaria*. A similar venation pattern among modern freshwater plants commonly occurs in the submersed ligulate leaves of *Sparganium*. Most other aquatic monocotyledonous genera with strap-shaped leaves have a less dense longitudinal venation and more or less developed cross-veins. However, the relationship of *Sparganiophyllum* Golovn. to the extant genus *Sparganium* is at best putative, because the similar venation patterns of different genera with ligulate leaves can be very close; for example, the marine grass-like *Thalassia testudinum* König & Sims also has a dense venation with several thickened longitudinal veins, thin, sparse cross-veins and a similar blunt apex.

Carpolithes aculeatus Vassilevsk. & Golovn.

Pl. 1 figs 7, 8

1994a. *Carpolithes aculeatus* Vassilevsk. & Golovn.; Golovneva, p. 118, pl. 30 figs 2–4.

The isolated ellipsoidal spiny fruits are 25–30 mm long and 6–8 mm wide, with 14–17 spines. The lateral spines are 4–7 mm long and coalescing at their bases thus forming a narrow lateral wing round the fruit. The stylar spine has a length of 10–15 mm and the peduncle is 10–20 mm long. The external surface of the fruit wall is slightly ribbed and no evidence of facial spines was observed. No associated vegetative material is known.

These fruits are very similar to those of the spiny-margined species of *Ceratophyllum* L., especially *C. furcatispinum* (Herendeen et al. 1990) from the Palaeocene of North America and *C. zaisanicum* (Avakov 1962) from the Oligocene of Kazakhstan. This similarity suggests a relationship between these fossil and *Ceratophyllum*. Vegetative parts of *Ceratophyllum* are known from the Eocene (Herendeen et al. 1990), but the fruits under consideration are considerably larger (up to 5–6 times) than extant and other fossil *Ceratophyllum* fruits. Therefore we cannot assign these remains to *Ceratophyllum* with certainty and include them in the form-genus *Carpolithes* Schlotheim.

***Ottelia*-like plant**

Fig. 2D, E

In the Rarytkin flora collection there are two fragments of elliptic petiolate leaves with entire margins, attenuate apex and acrodromous venation. The leaf bases are not preserved and they range from approximately 10 to 17 cm in length. The venation consists of 7–11 primary veins arising from the base and merging at the apex. The midrib is not prominent. Between the primaries there are numerous thinner interprimaries (4–7 between each pair) which run parallel to them. The interprimaries are linked by fine transverse veins which are discernible only in certain areas of the blade. It seems that this plant consisted of a rooted rosette of petiolate submerged or partly emerged leaves. An analysis of the foliage of modern monocotyledonous taxa shows that acrodromous venation with numerous interprimaries and thin cross veins occurs among some members of the Hydrocharitaceae, such as *Hydrocharis* L., *Ottelia* Persoon and *Limnobium* Richard. Among these, *Ottelia alismoides* (L.) Persoon is most similar to the plant under discussion not only in its venation, but in its size and habit as well. An affinity of the fossil plant to the Hydrocharitaceae is very probable, but a precise determination requires additional material in a less incomplete condition.

Isoëtites Münster

Pl. 1 fig. 6

The preserved parts of the plant consists of 6–7 linear leaves up to 6–10 cm long and 2–4 mm wide, with entire margin and acute apex, stem and the lower parts of the leaves with potential sporangia are not preserved. The assignment of the specimens to the genus *Isoëtites* Münster remains is formal, because sporangia are not preserved.

Nymphaeaceous rhizomes

Pl. 1 figs 11, 14

Among the remains of aquatic plants of the Rarytkin Formation there are some fragments of rhizomes with nymphaeaceous affinities. These up to 15 cm long and 7 cm wide and bear roots and leaf and root scars. The leaf scars are spirally arranged, orbicular to oval, 1.5–2.5 cm long, with a prominent margin. The bundle scars are orbicular, about 2 mm in diameter. The roots are 2–3 mm wide and up to 5 cm long. These remains (Pl. 1 fig. 14) show a close resemblance to the equivalent structures in the modern genus *Nuphar* L. (Nymphaeaceae). A specific determination cannot be made, because the rhizomes of different species are rather similar.

There are two other types of rhizome with root scars evenly scattered over their surface (Pl. 1 fig. 11). The root scars are about 2–3 mm in diameter with a single central bundle scar. The botanical relationship of these remains have not been ascertained.

Tall broad-leaved “grasses”

Pl. 1 figs 5, 9, 10

The Rarytkin material consists of several fragments of linear leaves, ranging in width from 0.5 to 3.5 cm, having a fine and closely spaced longitudinal venation. Such remains are usually formally classified as *Phragmites* Adanson, *Arundo* L., *Typha* L. or *Poacites* Brongniart, because graminaceous leaves have few diagnostic characters. The presence of tall semi-aquatic “grasses” is of ecological significance only, indicating a dense vegetation around the shoreline.

PALAEOECOLOGICAL AND PALAEOGEOGRAPHICAL IMPLICATIONS

The Rarytkin Formation consists of cyclically bedded sandstones, shales, and coal. The depositional setting suggests that it was a large alluvial plain with many rivers, lakes, channels and swamps providing a diversity of aquatic habitats. The remains of water plants occur in the levee facies of fine-grained sandstone and in the oxbow facies of siltstone lenses or black coaly siltstone. Large segments of the delicate leaves of hydrophytes, a predominance of floating plants and a large number of intact leaves of arboreal plants indicate that the majority of hydrophytes grew in a stagnant aquatic environment, in small ponds or oxbow lakes periodically inundated by flood-derived sediments. The preservation of so many water plants indicates that they were buried not far from where they grew.

An analysis of the life forms of aquatic vascular plants enables us to reconstruct their potential supposed distribution in the water bodies (Fig. 3). Along the shoreline might have grown horsetails and tall broad-bladed amphibious “grasses” ecologically comparable to modern *Phragmites* or *Typha*. The rhizomes of *Equisetum* were often buried in the position, in which they grew. These plants formed monodominant thickets on sandy soils. The remains of grass leaves are very rare and fragmentary. It is unlikely that these plants could have formed dense stands near the shore, as their modern counterparts do. Perhaps, their remains were transported from nearby marshes and swamps, where their requirements for light would have been better met than in the shade of trees along the margins of small ponds. Partly submerged *Ottelia*-like plants probably inhabited the shallow inshore waters. Areas situated further from the shore could have been occupied by the floating rosettes of *Quereuxia*. This plant can be considered as the ecological analogue of the modern *Trapa*, which also has superficial rosettes of leaves which are rooted with the aid of long stems which are furnished with submerged dissected leaves. The most common water depth for *Trapa* is about 30–100 cm. *Quereuxia* was the most abundant of the aquatic macrophytes in the Rarytkin flora. The fossiliferous rocks are often saturated with leaves of this plant. Probably, the rosettes of *Quereuxia* covered the entire surface of shallow ponds. *Limnobiophyllum* had free-floating rosettes of leaves and might also have formed dense mats on the water surface.

Submersed plants were represented by *Haemanthophyllum* with broad petiolate leaves and *Sparganiophyllum* with ligulate leaves. It seems that both plants had aerial flowers and were associated with shallow water. Of the two, *Sparganiophyllum* was quite a rare plant, but *Haemanthophyllum* was common. The remains of *Haemanthophyllum* are mostly preserved in coaly shales, where numerous leaf impressions are overlapping one another on the bedding planes. This plant appears to have preferred a muddy substrate with a high organic matter content.

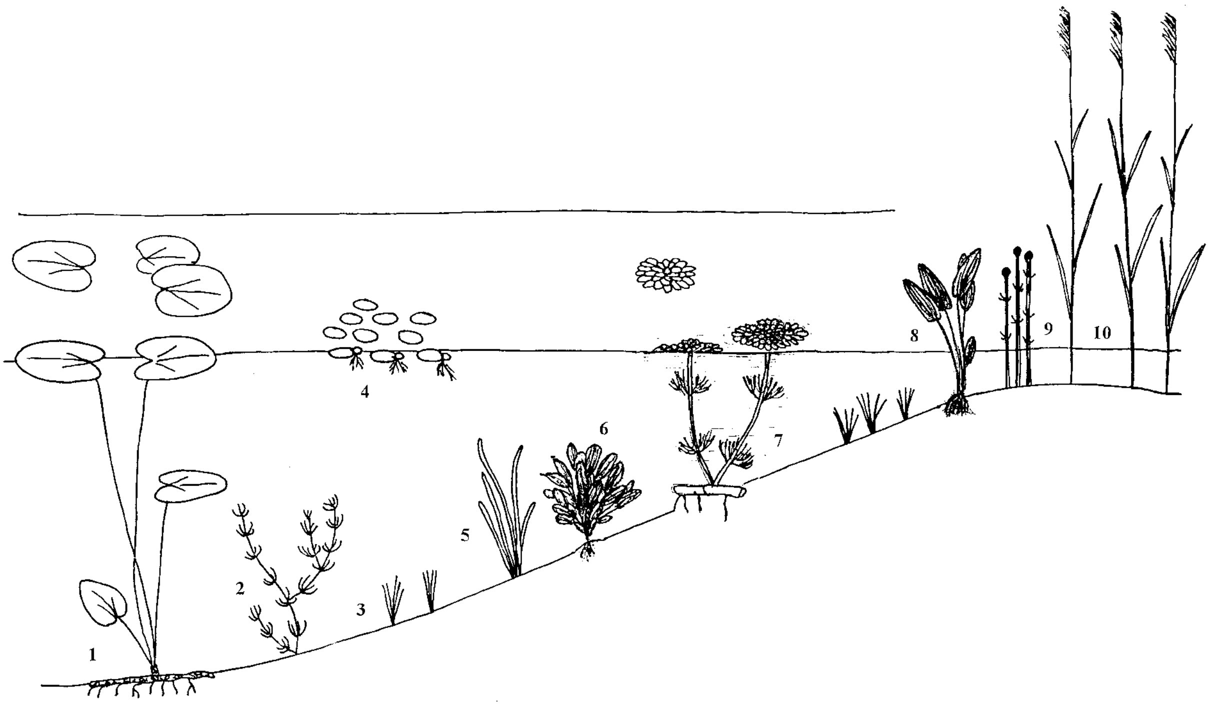

Fig. 3. The main life forms of aquatic vascular plants of the Rarytkin flora. **1** – nymphaeaceous plant, **2** – *Ceratophyllum*-like plant, **3** – *Isoëtites* sp., **4** – *Limnobiophyllum scutatum* (Dawson) Krassilov, **5** – *Sparganiophyllum multinervosum* Golovn., **6** – *Haemanthophyllum cordatum* Golovn., **7** – *Quereuxia angulata* (Newb.) Krysht., **8** – *Ottelia* – like plant, **9** – *Equisetum arcticum* Heer, **10** – tall broad-leaved "grasses"

Putative *Ceratophyllum*-like plants were another type of submerged plants with long stems and dissected leaves.

Assemblages of nymphaeaceous plants inhabited the deeper areas of lakes and quillworsts too usually preferred a rather deep environment. The presence of *Isoëtites* and other submerged plants suggests clear water.

On the whole, a considerable diversity of life forms of aquatic vascular plants is preserved in the Rarytkin flora. They had the potential to form complicated communities consisting of several belts according to the depth of the water body. However, in reality, the diversity of the individual communities was probably considerably lower. The fossil aquatic plant assemblages contain no more than 2–3 species in total, and usually only one. Such low diversity could be misleading, because some species might not have been preserved, but it probably reflects the true situation. The aquatic plans are usually represented by a large number of specimens, suggesting that they formed monospecific communities according to vegetative reproduction which prevails among aquatic macrophytes. Therefore the Rarytkin aquatic assemblages probably comprised a small number of species, which formed monodominant communities under most suitable conditions. The species composition most probably would have depended upon the depth of the water, character of the substrate and the water chemistry. *Quereuxia angulata* is the most common aquatic plant in the Rarytkin flora; it occurs in the majority of the localities and is characterized by its high abundance. Next, in both frequence and abundance, comes *Haemanthophyllum cordatum*. Other aquatic plants were found in only 1–2 localities of the Rarytkin Formation.

On the whole, the structure of the aquatic vegetation of small lakes and ponds at the beginning of the Palaeogene was similar to that which exists today. But the Rarytkin aquatic ecosystems obviously differ from modern ones in the weaker development of such groups like inshore aquatic "grasses" and submerged plants with long stems and dissected or entire leaves. The latter group is widely represented in modern aquatic ecosystems by numerous species of the genera *Potamogeton*, *Myriophyllum*, *Najas*, *Elodea*, *Hydrophyllum* and many others.

The development of the aquatic ecosystems of north-eastern Asia during the Mesozoic was studied by Kalugina (1980) on the basis of the evolution of the aquatic insect fauna. According to her data, the lakes of the alluvial lowlands in the Jurassic were nutrient poor with a rich insect fauna of well oxygenated water and a prevalence of detrital food chains. The nutrient deficiency in these lakes was consequence of peculiarities in the decay of leaves of the Mesozoic trees and shrubs, a process which was accompanied by a suppresion in microbial activity. In the Cretaceous the appearance of angiosperms initiated considerable changes in the soil and water chemistry. In comparison to gymnosperms, most angiosperm leaves decay more quickly and do not suppress microbial activity. The expansion of angiosperms led to the eutrophication of water bodies, especially in the small lakes of the alluvial plains. Eutrophication apparently induced periodical mass propagation of algae, followed by a drop in the oxygen level and hydrogen sulphide poisoning of the bottom layers of water. This resulted in a remarkable extinction of the lacustrine fauna depending on well oxygenated water and an impoverishment of the benthos during the Cretaceous.

On the other hand eutrophication was probably favourable for the development of aquatic macrophytes, because the majority of them are nutrient demanding plants. Aquatic macrophytes can absorb nutrients more effectively than algae (Hutchison 1975) and store the nutrients in their tissues. Moreover, they can obtain additional nutrients from the bottom sediments. In modern lakes aquatic macrophytes may prevent excessive eutrophication and the mass propagation of algae. From a human perspective, regulation of the nutrient content was one of the most important consequences in the development of aquatic plant communities. In addition, rich and dense aquatic vegetation increased the primary productivity of aquatic ecosystems and created a food source and many new biotopes for insects, fish and other animals (herbivorous, carnivorous and scavengers).

In other regions of north-eastern Asia and North America diverse associations of freshwater macrophytes also appeared in the Maastrichtian or Palaeocene. The assemblage of aquatic plants from the Tsagajan Formation of the Amur region (Krassilov 1976) is closest to the Rarytkin flora. It also contains such plants as *Quereuxia, Limnobiophyllum, Haemanthophyllum,* several nymphaeaceous plants and broad-leaved “grasses”. Additionally, one of the earliest sets of remains of *Carex* is known from this locality. The flora from the Maastrichtian deposits of Mongolia represents another type of aquatic vegetation (Krassilov & Makulbekov 1995). This assemblage contains *Potamogeton*-like shoots, quillworts (*Isoëtites*), nymphaeaceous remains, parallel-veined monocot leaves and numerous fruits of Lemnaceae and their allies fruits. *Quereuxia*, *Limnobiophyllum* and, to a lesser degree, *Haemanthophyllum*, were widely distributed in the Maastrichtian and Palaeocene floras of North America (Berry 1935, Bell 1949, Brown 1962, McIver & Basinger 1993). Moreover, the amphibious heterosporous fern *Hydropteris pinnata* Rothwell & Stockey and the angiosperm *Fortuna marsilioides* McIver & Basinger have been reported from Maastrichtian deposits of Canada (Stockey & Rothwell 1996). The Palaeocene associations of aquatic plants from North America are more diverse and have, as additional representatives, *Azolla, Salvinia, Isoëtites, Nelumbo, Paranymphaea, Sparganium* and *Harmsia* (Brown 1962, Hickey 1977, McIver & Basinger 1993).

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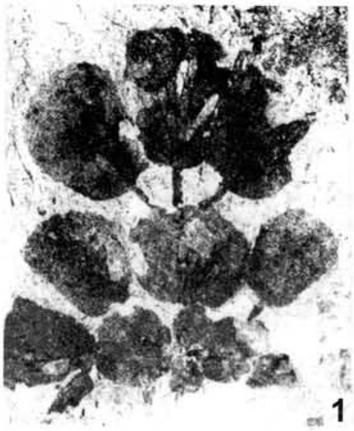
PLATE

Plate 1

1, 3. *Quereuxia angulata* (Newb.) Krysht.
1. part of a floating rosette with simple and compound leaves, × 1, N 642
3. dissected submerged leaves, × 1, N 641
2. *Palaeotrapa aculeata* (Krysht.) Golovn., fruits associated with *Quereuxia* leaves, × 1, N 635
4. *Sparganiophyllum multinervosum* Golovn., upper part of leaf, × 1, N 1263
5, 9, 10. Tall broad grass-like leaves, × 1, NN 1506, 1550, 1507
6. *Isoëtites* sp., × 1, N 1412
7, 8. *Carpolithes aculeatus* Vassilevsk. & Golovn., fruits, × 1, N 1401, 1402
11. Nymphaeaceous rhizomes; *Rhizomites* sp., × 2, N 675b
12. *Limnobiophyllum scutatum* (Dawson) Krassilov, floating leaf, × 5, N 649
13. *Haemanthophyllum cordatum* Golovn., leaf, × 1, N 101
14. Nymphaeaceous rhizomes; *Nuphar* sp., rhizome with roots and leaf scars, × 1, N 646

Plate 1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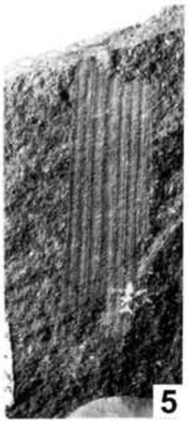
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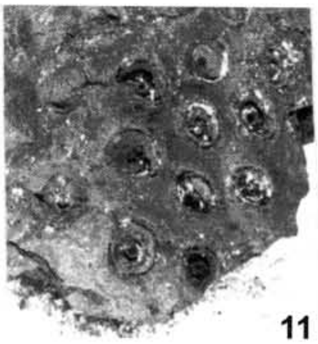
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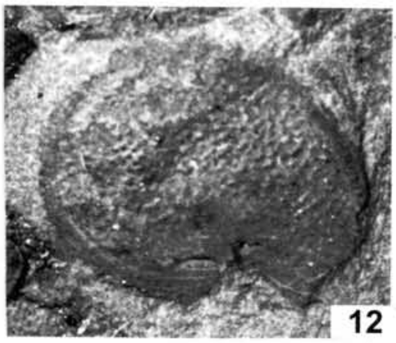
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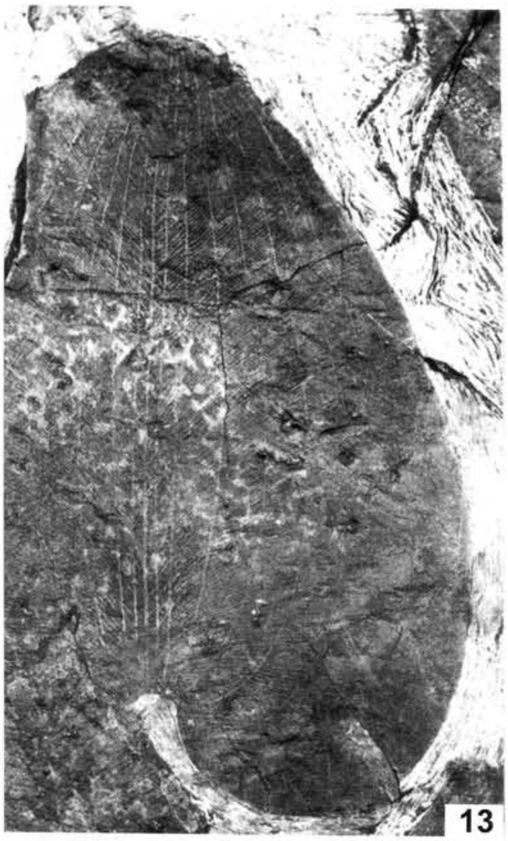
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