

MAASTRICHTIAN AQUATIC PLANTS FROM MONGOLIA

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Abstract: The lacustrine and fluvial dinosaur-bearing Maastrichtian deposits of the Nemegt Basin, western Gobi, Mongolia, are rich in the remains of aquatic and semiaquatic plants, most of which are not known from contemporaneous deposits in other parts of the world. Notable among these are megasporophylls of isoetalean affinities (but not belonging to any of the known extant or fossil genera), pondweed-like leafy shoots, and abundant lemnaid fruits with morphological and cuticular details of the pericarp and ovule structure. These finds are of interest for both plant evolution and paleoecology.

Key words: Angiosperm evolution; aquatic flora, duckweeds; dinosaurs; Isoetales; Lemnaceae; megaspore monocots; pondweeds paleoecology.

Озерные и речные маастрихтские отложения бассейна Немегт, западная Гоби, Монголия содержат наряду с остатками динозавров и других позвоночных богатую флору водных и околоводных растений, большей частью эндемичных. Среди них наиболее примечательны мегаспорофиллы, принадлежащие вымершему роду изоетовых, побеги рдестовых и плоды рясковых, сохранность которых позволяет детально изучить морфологию и строение кутикулы перикарпа и семени. Эти находки представляют интерес для филогения растений и палеоэкологии.

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We report here some preliminary results of our ongoing study of Late Cretaceous flora from the dinosaur beds of Mongolia. The widespread Mesozoic continental deposits of this country contain fairly distinct floras of Jurassic, Early Cretaceous, and Late Cretaceous ages, most of which still await systematic treatment. The Jurassic floras are of a generalized Siberian type with abundant ginkgoalean and czekanowskialean plants, while the Early Cretaceous assemblages belong to the bennettitalean-brachyphyllous conifer realm and comprise a number of endemic genera, including aquatic lycopods (Krassilov 1982). The Late Cretaceous floras seem to represent a subtropical or ecotonal warm temperature vegetation, but are the least known of the three.

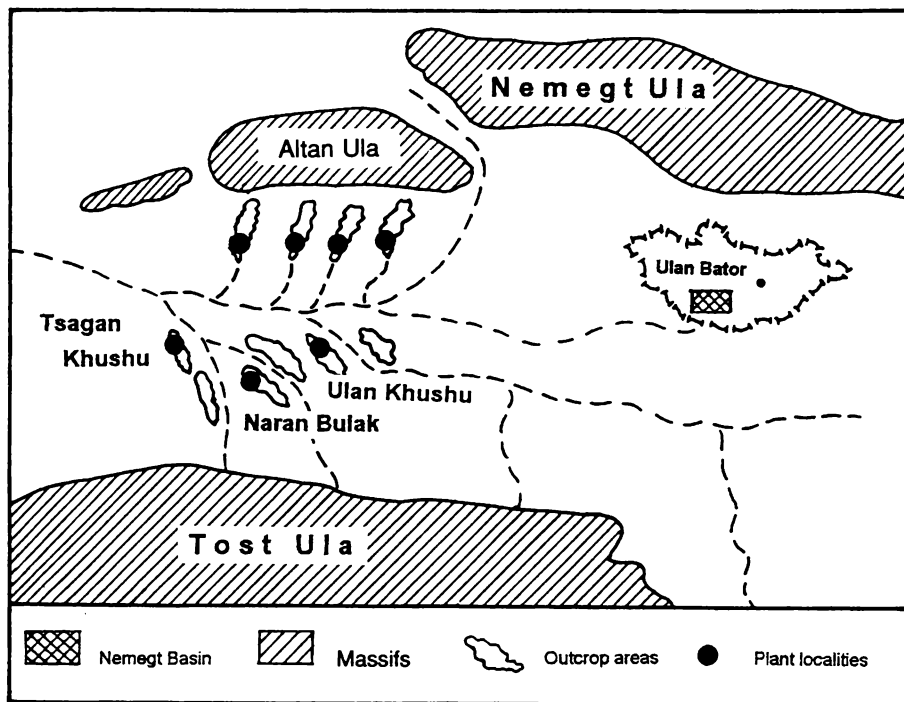


Fig. 1. Location of study area and plant localities.

Our material is from the Nemegt Formation of eastern Gobi, well known for its rich dinosaur localities. Fossil plants from the same beds have scarcely been studied, although a substantial paleobotanical collection has been made by N. M. Makulbekov and other participants of the Soviet-Mongolian Paleontological Expedition in the 1960s and 1970s. Our survey of the plant collections in the Paleontological Institute, Moscow, has revealed materials important for floristic as well as paleoecological research and, specifically, for reconstructing dinosaur habitats.

The Nemegt Basin is a large intermontane depression 35-45 km wide in the southern part of Gobi Altai filled with Mesozoic and Tertiary fluviolacustrine deposits (Gradzinski et al. 1968). Fossiliferous outcrops, shown in figure 1, occur in the western part of the basin in the area of erosional depressions and dry stream channels and their dividing ridges. The Late Cretaceous deposits outcrop along the northwestern margin of the depression south of the Altan Ula Highlands and are overlain by the Paleocene redbeds. Most dinosaur beds are confined to the upper part of the Nemegt Formation assigned to the *Tarbosaurus bataar-Saurolophys angustirostris-Dioplosaurus giganteus* zone of Maastrichtian or Campanian-Maastrichtian age (Efremov 1954; Gradzinski et al. 1968).

The Tsagan-Khushu localities occur on a ridge extending about 7 km west from the Naran Bulak Spring. The Upper Cretaceous Upper Nemegt Sequence is about 140 m thick, consisting of sands with gravel, silt and clayey interbeds in the lower 60 m, with alternating sand and silt above. Dinosaur and tortoise skeletons occur at seven successive levels along the section (Gradzinski et al. 1968). Plant remains, mostly small structureless debris and lemnioid fruits,

came from the finely laminated sandstone bed 0.6 m thick, beneath the lower dinosaur bed about 25 m above the base of the section. The Ulan Khushu locality, an erosional remnant about 10 km northeast of Naran Bulak, shows much the same Upper Cretaceous sequence; the plant-bearing horizon maintains an analogous position in respect to the dinosaur beds, but the plant remains, mostly scattered stems and parallel-veined monocot leaf impressions, *Potamogeton*-like shoots and occasional isoetalean sporophylls, occur in a light gray siltstone 1 m thick. Here the lemnoïd fruits are also abundant, but are far less conspicuous than in the Tsagan-Khushu locality. Farther up in the section are several clayey beds with nymphaeoid stem and seed remains.

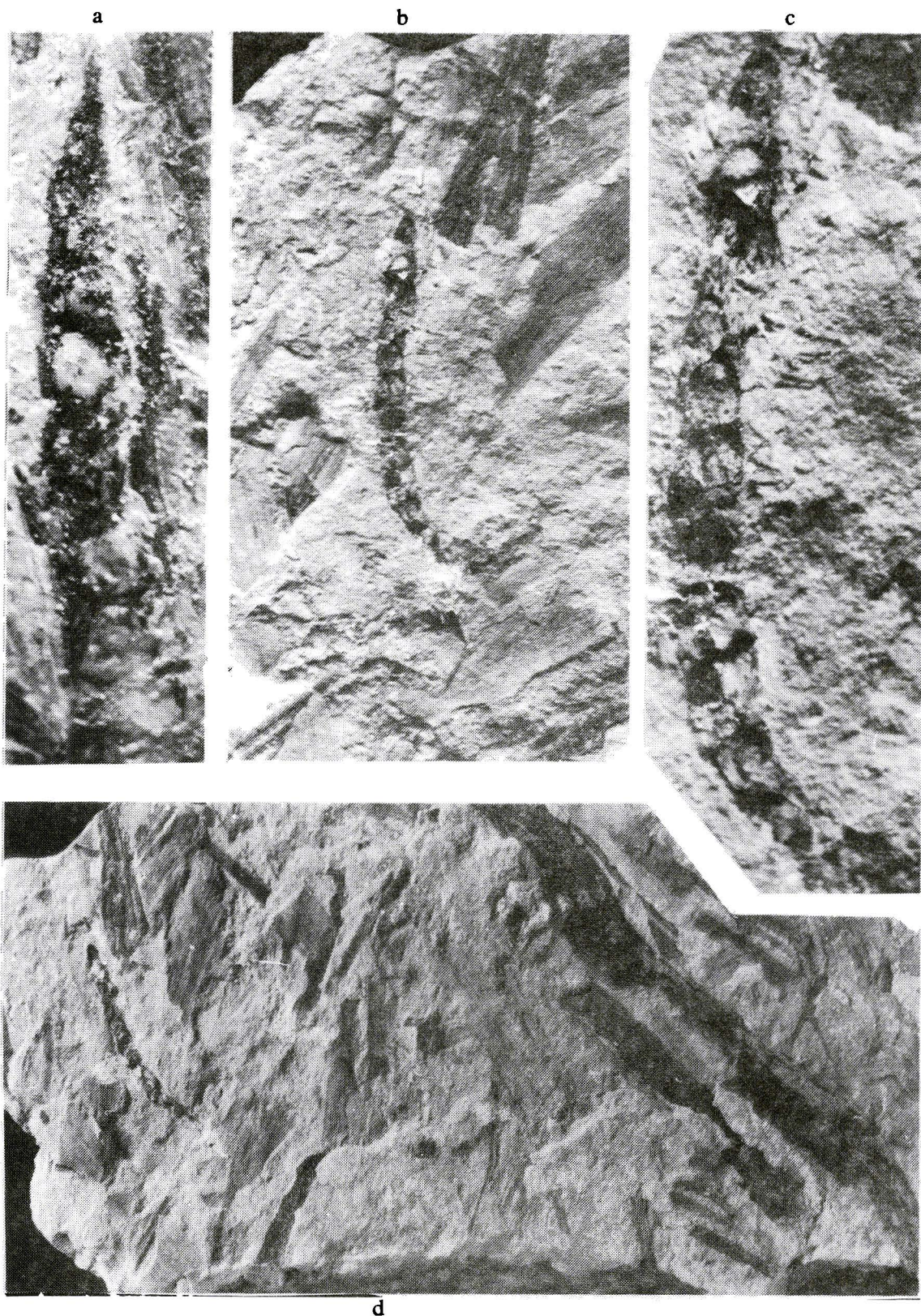
Conspicuous in these localities is the preponderance of aquatic plants and their considerable diversity—here are no less than 20 species of spore plants and angiosperms. Some of the most notable are described below.

Description of Selected Aquatic Plants

Isoetalean megasporophylls (figs. 2-4). On the surface of the light gray plant-bearing siltstone from Ulan Khushu among the parallel-veined monocot leaves we found detached remains of small linear megasporophylls about 1 mm wide, bearing a single sporangium along the entire length except on a short sterile tip. The sporangium is filled with megaspore tetrads linearly aligned in a single row. One specimen is 18 mm long, 1 mm broad, proximally curved, the base torn off, the sterile apex pointed and 1.5 mm long; the rest of the blade is entirely covered with megaspore casts of approximately ten tetrads, aligned in a single row along the sporophyll axis. Another fragment also represents a distal part of a sporophyll 9 mm long, 1.1 mm broad, with the sterile apex slightly constricted, acuminate, and 1.5 mm long. The fertile portion shows eight megaspore casts. Details of sporangial morphology are not discernible on either specimen.

An incomplete tetrad and several megaspore casts were detached and mounted for SEM. The megaspores are biconvex, their equatorial outline circular or round-ovate, diameter ranging from 850 μm to 940 μm , with conspicuous size differences within a tetrad. The laesurae are raised, gently sloping to the contact facets, about 150 μm wide, and reaching to the equator. The curvatures are distinctly marked. Two sporoderm layers are preserved in the casts—the surface reticulum and the underlying sculptured layer. The encasing solution might penetrate between these loosely coupled strata. The reticulum is fragmented and lost over much of the spore surface, but fragments occur on the both proximal and distal faces. The muri are ridged, raised at the corners, forming a perfect network with polygonal or irregular lumina, and with spine bases about 20 μm thick. The underlying layer is ornamented with conical or clavate bacula fused at the base to form a low dense reticulum with more regular rhombic lumina on the distal face, while individual bacula are relatively more prominent, with lumina appearing as irregular cavate depressions on the contact areas.

Single large sporangia proximal on linear sporophylls occur in Isoetales, and the fossil sporangia rank among the largest, although in extant *Isoetes* the upper limit is up to 30 mm long. However, our sporophylls differ from *Isoetes*, both fossil and extant, as well as *Stylites*, in being almost entirely fertile, except for a very short sterile apex. Moreover, the spore tetrads are longitudinally aligned in a single row and seem to have been dispersed with detached sporophylls, rather than being liberated from decaying sporophylls as in other genera. Whether the sporophyll shedding was regular (and, perhaps, functional) or occasional is still to be learned.



The megaspores belong to the *Erlansonisporites*-*Horstisporites* group of dispersed spores (*Infraturma Murornati*), with a perfect surface reticulum over the spore body including, or sometimes excluding, the contact facets. In *Erlansonisporites* the external reticulum is diaphanous and readily separable from the spore body, revealing the inner surface showing a trilete mark and, at least in some species, ornamented with a differently structured internal reticulum. Incidentally, a fairly distinct internal reticulum is illustrated by Taylor and Taylor (1988) in *E. sprassis* from the Lower Cretaceous of Argentina. A less regular inner reticulum of anastomosing rugae was observed through the diaphanous external layer in *E. singhii* from the Maastrichtian of Alberta (Binda and Nambudiri 1988). Specimens of *Erlansonisporites* stripped of their external reticulum might appear not unlike some species of *Horstisporites* and, in fact, an additional form-genus *Kerhartisporites* has been erected by Knobloch (1984) as intermediate between the two.

In our material and in a number of figured specimens (e.g., in the *Minerisporites*-like megaspores of the aquatic lycopsid *Limnoniobe*; see Krassilov 1982, fig. 27) the external membranous reticulum seems to have developed irrespective of the proximal trilete mark haphazardly overlapping the laesurae. This makes it developmentally different from exinal structures traversed and, to various degrees, modified by the trilete, perhaps suggesting a membrane of tapetal origin scarcely homologous to the nonseparable reticulate ornamentation of other megaspore genera.

The megaspores fall in the size range of *E. erlansonii* (Miner 1932; Kovach and Kilcher 1988) and are much larger than *E. singhii*, *E. alatus*, *E. dubius*, and other Cretaceous species having a typically coarser reticulum, with muri extended into thin lamellae, and shorter laesural relative to the spore radius (Potonie' 1956; Binda and Nambudiri 1988; Knobloch 1984; Kovach and Dilcher 1988). *E. spinosus* is similar in having spines in the external reticulum which is, however, lacking on the proximal face (Bergad 1978). *Horstisporites iridodea* is of comparable dimensions but has a much coarser reticulum. This species might have a residual perinate membrane described as an anastomosing network over the proximal reticulum (Taylor and Taylor 1988). In the much smaller *H. reticuliferus* and *H. cenomanicensis*, the surface ornamentation resembles the interior reticulum of the *Mongolian* megaspores. However, these European species lack any evidence of a membranous external layer (Knobloch 1984).

The dispersed *Erlansonisporites*-type megaspores have been thought of as representing plants with sellaginelloid affinities (previously assigned to *Selaginellites*), although Binda and Nambudiri (1988) have extended the comparison to *Isoetes*. Our *in situ* material, though not assignable to any of the species for dispersed megaspores, nonetheless gives a definite evidence in favor of the Isoetalean affinities of the group.

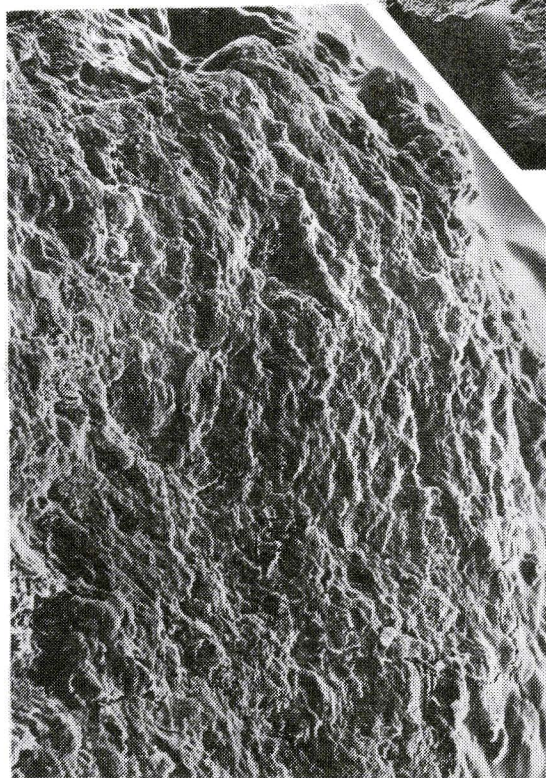
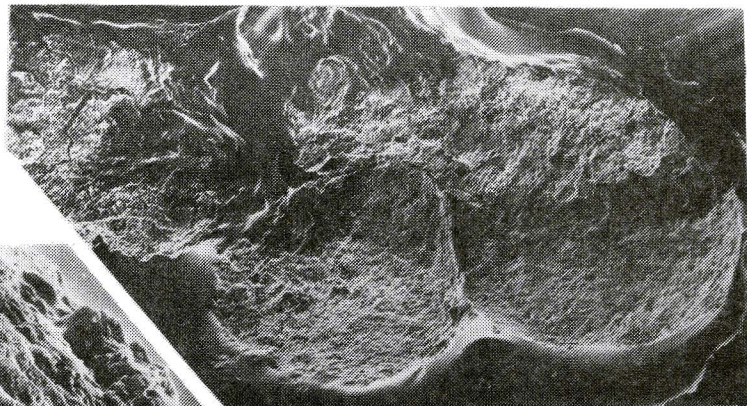
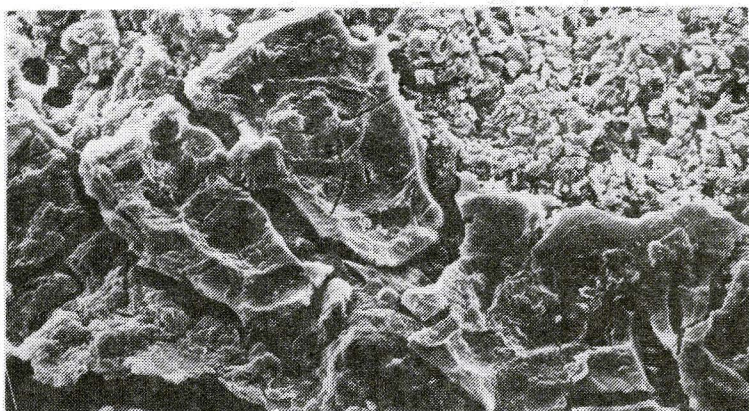
Pondweed-like shoots (fig. 5.). In the Ulan Khushu siltstones there are numerous fragments of branched shoots bearing laminar and filiform leaves. The shoot axes are about 1 mm thick, ribbed, flattened, perhaps, originally tubular. The branching appears dichopodial, forking about 10 mm above the attachment to a more massive structure, and each branch then forking distal-

Fig. 2. Isoetalean megasporophylls from Ulan Khushu: *a* - megasporophyll, No. 4135/2-148 showing sterile tip, ($\times 81$); *b*, *c* - nearly complete megasporophyll, No. 4135/2-147a, ($\times 3$) and ($\times 10$); *d* - megasporophyll (arrow) on a siltstone slap among monocot leaf debris, ($\times 1.5$).

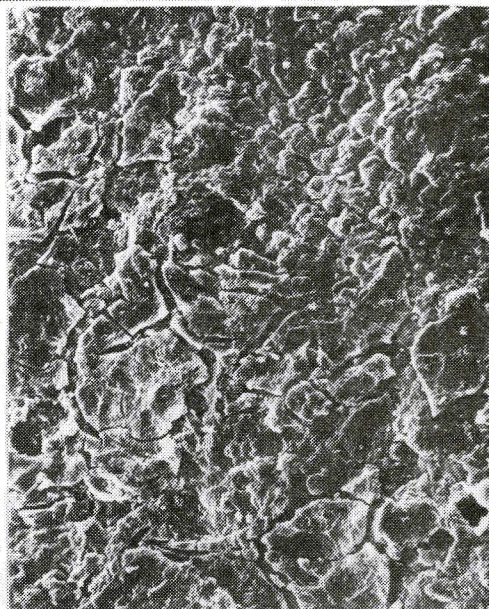
a



b



d



e

ward at decreasing intervals. The laminar leaves tend to appear at the angle of proximal forking. Distally, they are crowded making the attachment obscure. They seem spirally arranged at an acute angle to the axis, alternate or subopposite, shortly petiolate to almost sessile. In a few cases a swelling is discernible at the point of attachment, indicating a short basal sheath. The leaves are narrowly elliptical with entire margins bluntly pointed or acuminate. Occasional detached leaves have a short petiole no more than 1.5 mm long. In each shoot the leaves are uniform, but there is considerable variation in the leaf form and in dimensions between shoots. The leaf blades are 7 to 14 mm long, 2 to 0.5 mm wide, with average dimensions 10×3 mm. They appear fleshy with immersed veins. The venation is acrodromous with a distinct or indistinct midrib and typically three lateral veins at both sides of it emerging from the base and converging to the apex. The tertiary venation was observed in a few leaves only, and consists of thin marginally decurrent crossveins. In a number of specimens there are delicate setaceous leaves, apparently attached at the same nodes as the laminar leaves. A single specimen shows a poorly preserved lateral spike.

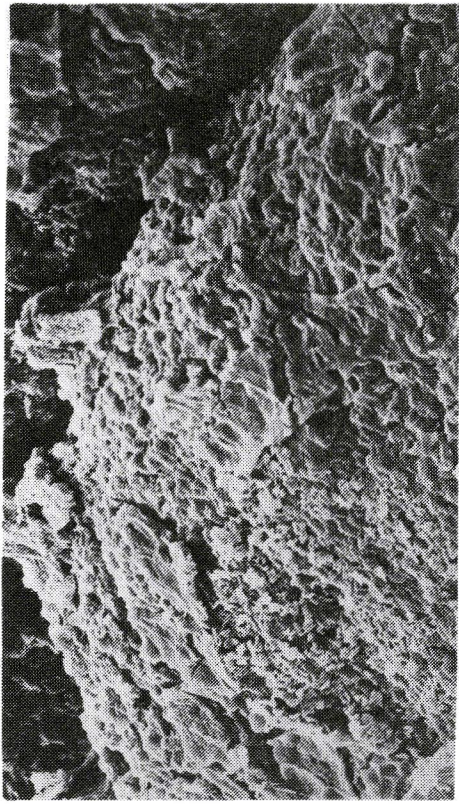
Given the variation of the blade shape, the dimensions and prominence of the midrib, more than one species might be detected. However, the leaf characters might vary with environmental parameters. The midrib is typically less distinct and the lateral veins are more numerous than in the slightly broader leaves of *Potamogetophyllum parvum* from the transitional terminal Maastrichtian-lowermost Paleocene deposits of Sakhalin (Krassilov 1979). The slightly younger Paleocene species assigned to *Potamogeton nordenskioldii* Heer or *Alisma macrophylla* Heer have far larger leaves with more distinct tertiary veins (Krassilov 1976).

Although the pondweed affinities of the Mongolian Maastrichtian shoots seem fairly plausible, they are hardly referable to any extant genus. They resemble the *Potamogeton maakianus* group of extant species in their short sheaths, but differ in their branching pattern and angular leaf attachment. Furthermore, the sheath characters and the inflorescence are insufficiently studied.

Lemnoid fruits (figs. 6-12). Notable in both the Tsagan Khushu and Ulan Khusu localities are abundant fruit remains assignable to the duckweed family, the Lemnaceae. They are amphoriform utricles about 1.27×0.62 mm, with short pedicel and persistent funnel-shaped stigma. The fruit wall is membranous, with large lime-secreting glands. The ovules are solitary, orthotropous to slightly hemianatropous, basal, operculate with sclerified caruncle, with their funicle directly continuing the fruit peduncle.

In the Ulan Khushu locality the fruits are preserved as light brown impressions with regular rows of white spots on the surface. They are concealed by the larger leaf impressions of aquatic monocots. In contrast, the Tsagan Khushu locality contains numerous compressions of these fruits among small plant debris, often several on a slab, with a black or dark brown shiny coat against which the white patches are even more conspicuous. The compressions are easily detachable with a needle. When placed in a Petri dish they float persistently due to air bubbles

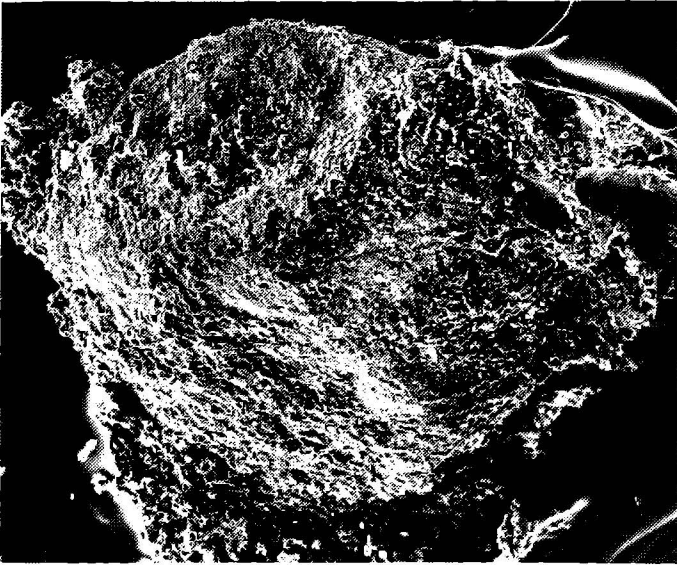
Fig. 3. Megaspores from the isoetalean megasporophyll shown in fig. 2b: *a* - *in situ* megaspores, ($\times 20$); *b* - fragmented external reticulum, SEM, ($\times 500$); *c* - incomplete megaspore tetrad detached from the megasporophyll, SEM, ($\times 50$); *d* - megaspore distal face interior reticulum, SEM, ($\times 300$); *e* - megaspore contact area with remains of exterior reticulum and interior bacula, SEM, ($\times 300$).



b



p



a



s

caught in the apical funnel. The fruits might have been good floaters when alive. Both the treated (with HCl and HNO₃) and untreated fruits have been mounted for SEM, some of them opened to show ovules, with a number of the latter mounted separately.

The fruit body is ovate to elliptical with a very short, stout, straight or slightly curved pedicle. Apically the body is constricted to a short, thick style and then expands to a funnel-shaped, or occasionally flabellate, stigma. The 25 measured fruits range from 1.00 to 1.35 mm long, 0.60 to 0.65 mm maximum width, average 1.27×0.63 mm, with an apical extension 0.36×0.46 mm wide.

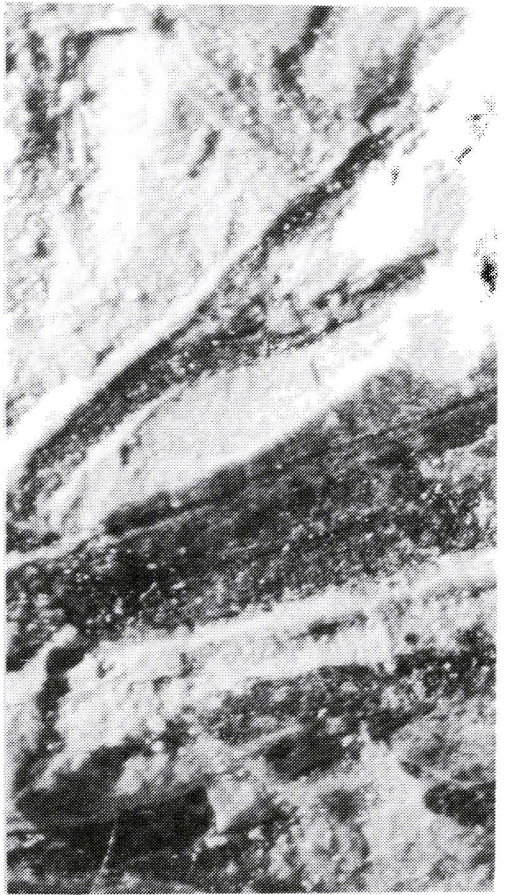
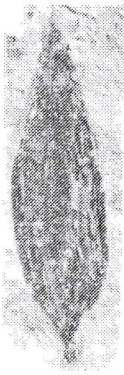
The fruit wall is soft, utricular, and heavily cutinized. The white patches occur on the body as well as on the funnel. They are irregularly elliptical or elongate, about 80 μm long, typically longitudinal, but occasionally oblique to the long axis of the fruit, evenly spaced, rarely contiguous, readily dissolvable in either HCl or HNO₃, leaving elliptical gland scars about 30-35 μm long, which are surrounded by radially disposed cells. On the inner side of the wall membrane the glands appear as deep pits surrounded by several circles of relatively small bulging cells. The epidermal cells are irregular-polygonal, about 20 μm long, longitudinally arranged except near the glands, with straight distinctly marked anticlinal walls and smooth periclinal walls. Occasional round cells in a ring of radially aligned cells might represent hair bases. A transverse groove on the inner side of the wall corresponds to the rim of the ovular operculum. The fruits opened with a needle reveal a single ovule filling the locule, except for a narrow space beneath the style. The ovules are typically elliptical, but occasionally ovate, rounded at both the chalazal and micropylar ends, 0.78-1.16 μm long 0.60-0.83 μm wide, average dimensions 0.83×0.60 μm , and apparently flat, which may be due to compression. The funicle, about 100 μm long, appears to be a direct continuation of the fruit pedicel. At the micropylar end is an operculum in the form of a shallow cap about 130 μm high, marked off from the rest of the ovule by a circular groove. A small sclerified knob, 30 μm high, in the center of the operculum represents the caruncle.

The funicle and caruncle typically occur on the median line of the ovule, thus maintaining a strictly orthotropous position; however, in a few specimens the funicle is somewhat displaced on one side, as if approaching a hemianatropous state.

The ovules show a single layer of cuticle with poorly marked polygonal cells in a bricklike pattern. The funicle is longitudinally striated. The operculum shows radial rows of table-shaped cells with ridged anticlinal walls, far more distinct than on the rest of the ovule. The caruncle is a tuft of radially aligned, thick-walled, straight or folded macrosclereids showing annular wall thickenings and small pits.

Our fossil fruits and fruitlike structures show a certain similarity to some microfossils assigned to the form-genus *Costatheca* Hall emend. Knobloch, notably *C. dijkstrae* Knobloch from

Fig. 4. Megaspores from the isoetalean megasporophyll shown in fig. 2b: *a* - megaspore, proximal face, SEM, ($\times 100$); *b* - megaspore, distal face showing partly preserved surface reticulum overlaying the interior reticulum of fused bacula, SEM, ($\times 700$); *c* - *in situ* megaspores, ($\times 30$); *d* - megaspore showing curvature, SEM, ($\times 300$).



the Paleocene of The Netherlands (Knobloch 1986), which has a funnel-shaped apical extension said to cover a small apical knob or caruncle of the inner body (Knobloch 1986). Details of the inner body are unknown. At the base is a disk or shallow cup—a feature absent in our material. Moreover, *C. dijkstrae* differs from the Mongolian fruits in showing weak external ribs. *C. hurgadensis* Knobloch from the Egyptian Late Cretaceous (Knobloch 1986) lacks distinct ribs, is apically expanded (though with a less perfect funnel than the previous species) and shows outlines of an inner body not unlike the Mongolian utricles. However, a detailed comparison is precluded by the less complete preservation of the Egyptian fossils. Although some *Costatheca* species might have been related to our fruits, the latter are hardly assignable to the form-genus intended for problematic fruitlike and seedlike bodies as well as bryophyte capsules.

The utricular fruit wall, persistent funnel-shaped stigma on a thick short style, single basal orthotropous ovule with persistent operculum, perhaps partly formed of pericarp tissue, and small caruncle make a combination of fruit and ovule characters found in the Lemnaceae, a small family of aquatic monocots characterized by flask-shaped unilocular carpels with a funnel-shaped stigma on a thin (Lemnoideae) or short and stout (Wolffioideae) persistent style. The style appears as a mere extension of the ovary expanding upward into the stigma, usually falling off in the ripening fruits. The fruits are utricular, indehiscent, about 1.4×0.9 mm in *Lemna gibba*, somewhat smaller in other species, and contain one to several (in Wolffioideae, always solitary) seeds. During maturation the pericarp is reduced to a cutinized membrane. The ovules are ellipsoid, somewhat flattened, orthotropous, and in *Lemna* typically turning hemianatropous at maturity. Cuticles develop at the same time on both the outer and inner surfaces of disintegrating inner integument (Maheshwari and Kapil 1964). The seeds are ribbed or smooth (*Wolffia*), the operculum includes sclerified remnants of the nucellar beak while a prominent hypostasis develops at the chalazal end.

In the larger and allegedly progenitorial family Araceae, orthotropous operculate ovules are known in the Pistioideae, which have also one-seeded fruits, but the fruits are capsular rather than utricular, and the seeds are elongate and cavate, with a large hilum.

The Lemnaceae is a highly specialized, neotenous, and, according to the currently prevailing view, fairly advanced family of monocotyledonous angiosperms derivable from the Araceae, with *Pistia* and *Spirodela* as morphological links (see Maheshwari 1958, for a comprehensive discussion of the phylogenetic relationships). Fossil leaves resembling *Spirodela* have been described from the Maastrichtian and Paleocene deposits as *Lemna* (*Spirodela*) *scutata* (Dawson 1875; Ward 1887; Bell 1965), *Numphaeites brownii* (Dorf 1942), and *Hydromystria scutata* (Brown 1962). They were subsequently assigned to the form-genus *Limnobiophyllum*, which has cuticular structures, confirming the aroid affinities (Krassilov 1973, 1976). Unambiguous aroid fructifications appear not earlier than the Middle Eocene (Crepet 1978; Cervillos-Ferriz and Stockey 1988). The fact that aquatic lemnooid forms preceded the terrestrial aroids in the fossil record can be accounted for by preservational bias. Alternatively, it may point to the independent origin of lemnooids and aroids from a diversified Late Cretaceous-Paleocene protoaroid stock. The operculum is a specialized structure perhaps related to fast germination and tending to occur in the monocot orders of predominantly tropical distribution and putative tropical origin.

Fig. 5. Pondweed-like shoots from the Ulan Khushu locality: *a* - leaf with sheathing base, ($\times 8$); *b* - detached leaf, ($\times 4$); *c*, *d* - shoots with floating laminar and submersed filiform leaves, ($\times 4$); shoot with a fruiting spike (?), ($\times 8$).

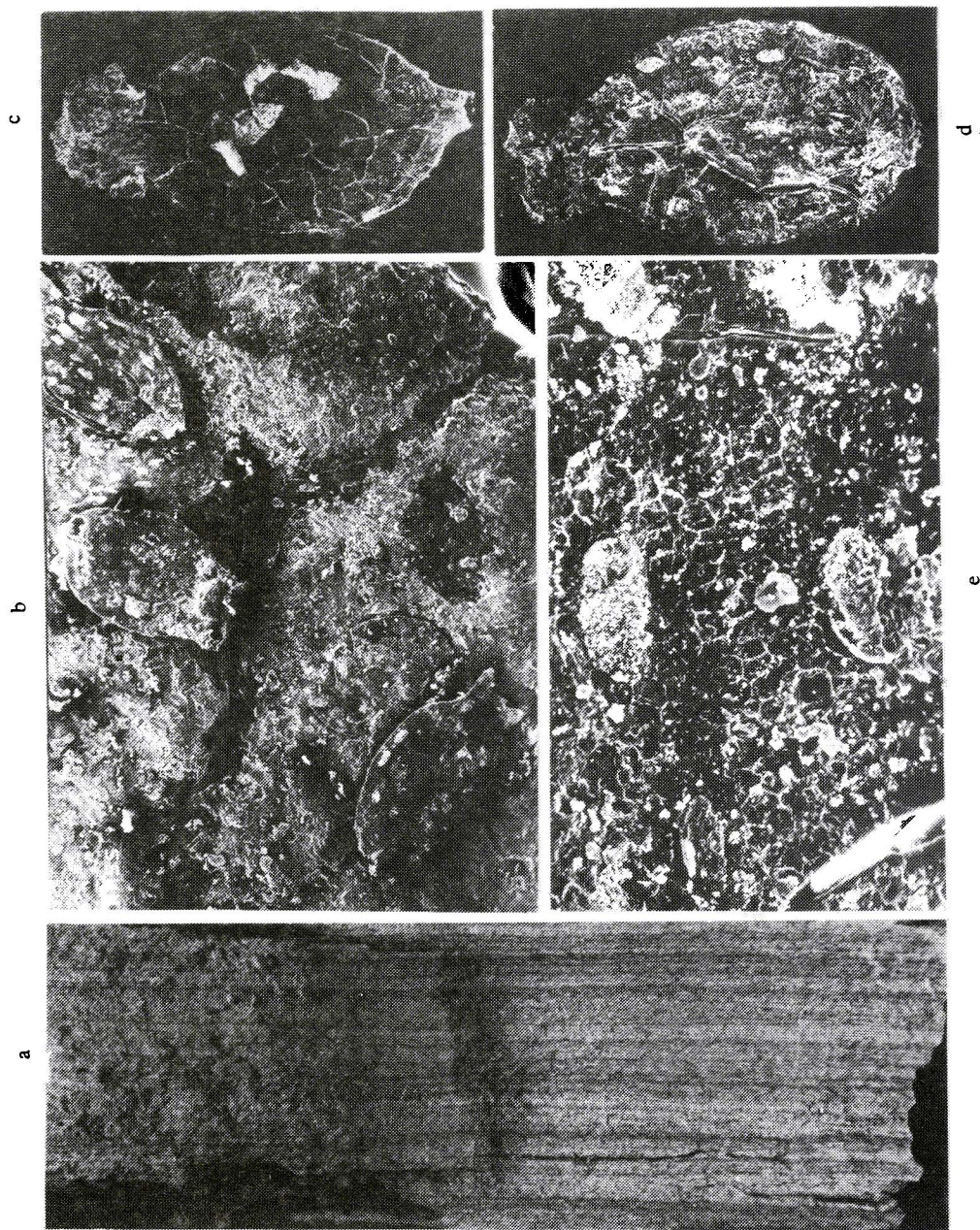


Fig. 6. Lemnoid fruits from Tsagan Khushu locality: *a* - sandstone slab showing lamination, ($\times 1$); *b* - several fruits on the sandstone slab surface, SEM ($\times 30$); *c*, *d* - utricles with differently shaped apical funnels, SEM, ($\times 53$ and 70); *e* - lime spots on fruit surface, SEM, ($\times 300$).

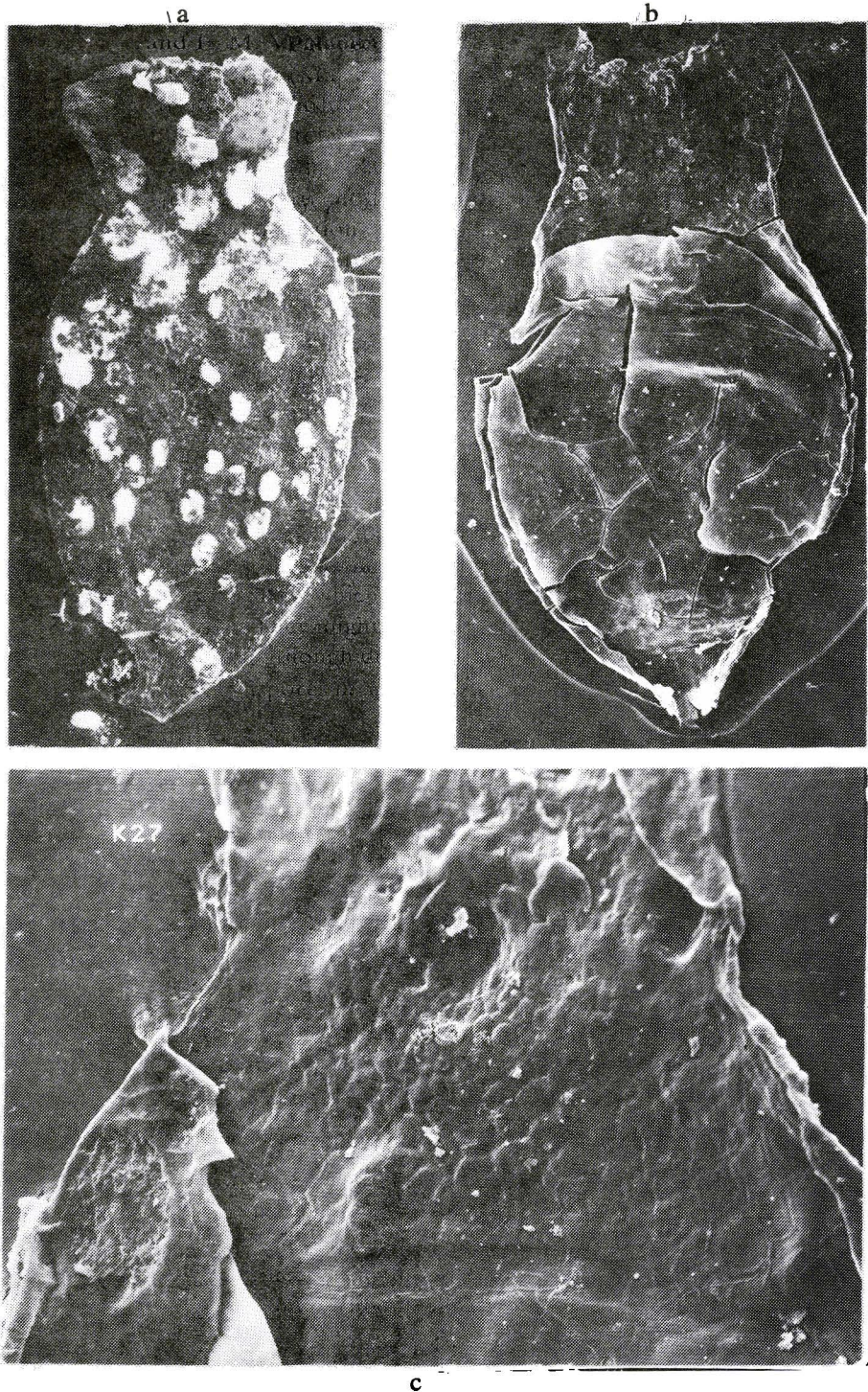


Fig. 7. Lemnoid fruits from Tsagan Khushu locality, SEM: *a* - utricle with white spots marking lime-secreting glands ($\times 70$); *b* - opened utricle showing ovule, ($\times 70$); *c* - distal part of fruit walls membrane showing gland scars from outside (left) and inside, also transverse groove marking base of ovular operculum, ($\times 280$).

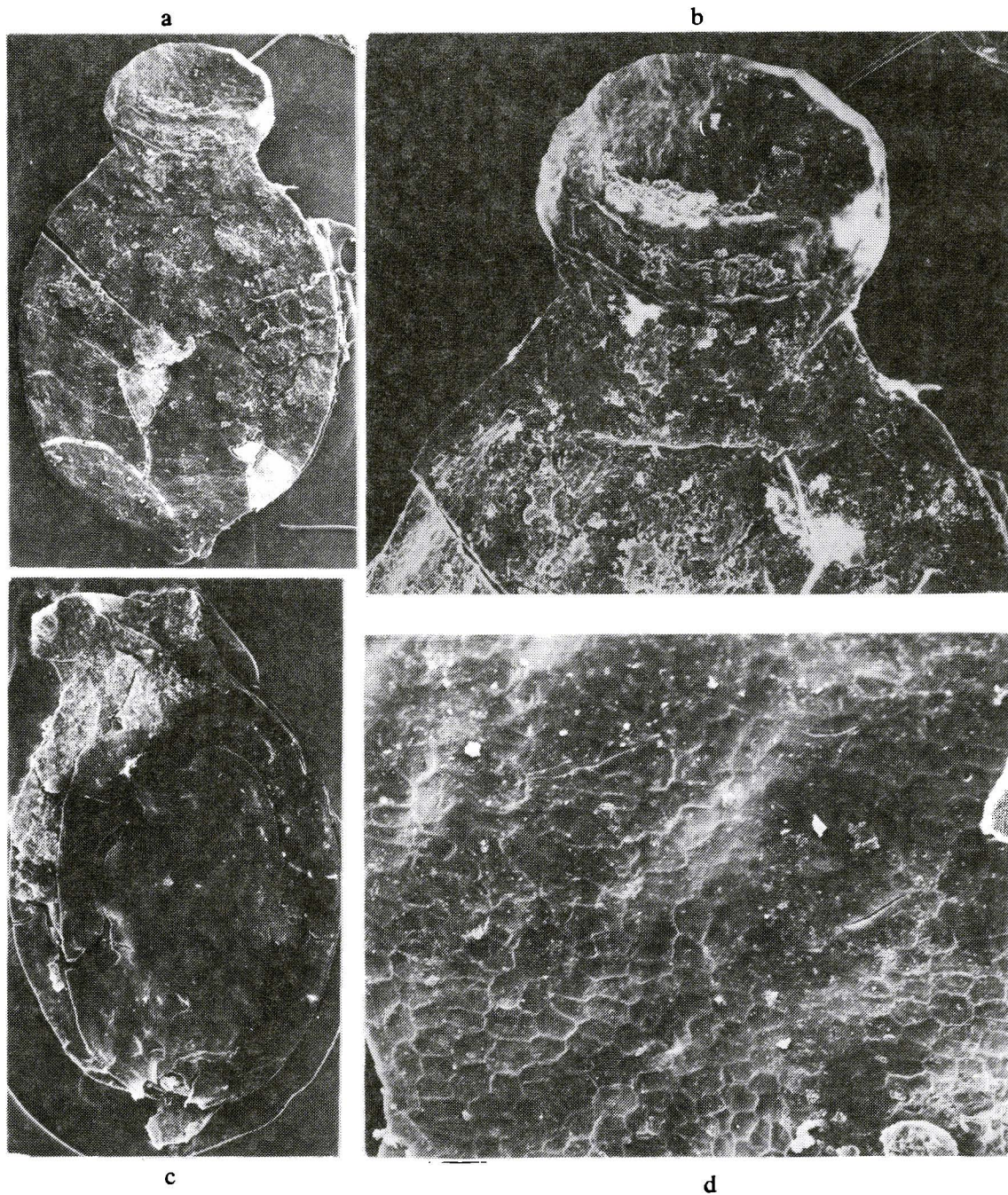


Fig. 8. Lemnoid fruits from Tsagan Khushu locality, SEM: *a, b* - utricles with perfect apical funnel, SEM, ($\times 70$) and ($\times 150$); *c* - opened utricles showing ovule, ($\times 70$); *d* - bases, ($\times 300$).

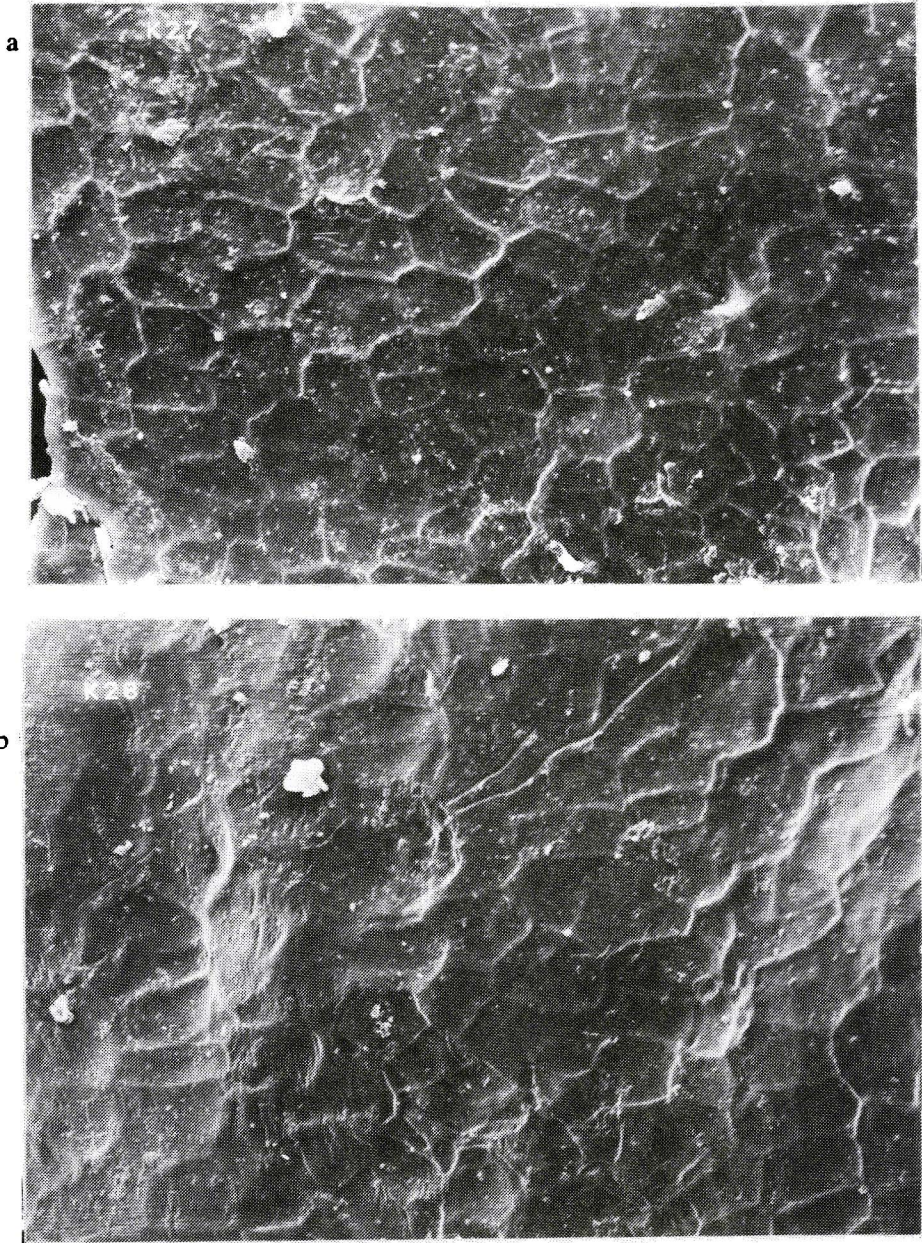
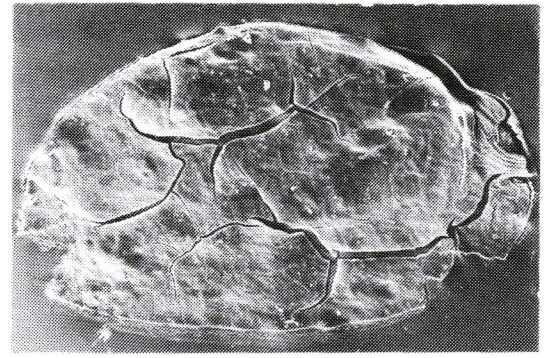
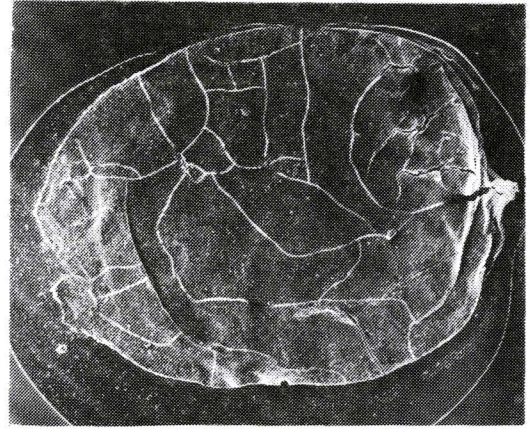


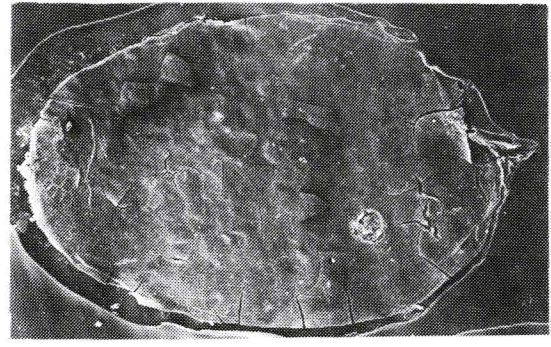
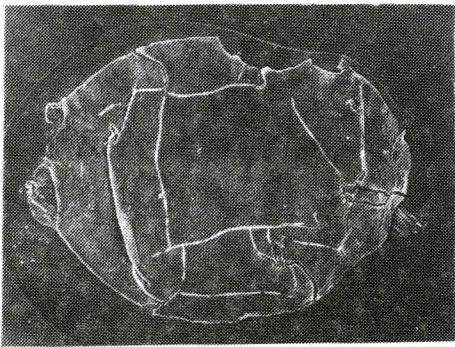
Fig. 9. Lemnoid fruits from Tsagan Khushu locality, SEM: *a*, *b* - fruit wall cuticle with gland scars and hair bases ($\times 700$).

The Cretaceous lemnoid fruits show a mosaic of the supposedly primitive and advanced characters that are mostly retained by the extant representatives of the group. They seem closer to *Wolffia* than *Lemna*, thereby defying the linear phylogenetic relationships of, in descending order, *Pistia*, *Lemna*, and *Wolffia*, postulated on the evidence of the comparative morphology of their extant representatives.

a



b



Paleoecological Implications

When compared with the Early Cretaceous assemblages (Krassilov 1972, 1982; Collinson 1988), the Late Cretaceous flora reflects a major change in aquatic ecosystems related to the appearance and expansion of floating macrophytes. These developments presumably led to the profound change in water chemistry, producing the eutrophication process that altered both the successional stages and the composition of lacustrine biota.

We can distinguish two facial types of plant-bearing strata (there certainly will be more with the progress of our studies): (1) the levee facies of finely laminated sandstones with abundant small plant debris on the bedding planes; and (2) the oxbow facies of clayey siltstone lenses with the better preserved plants, both large and small, scattered on the bedding planes as well as embedded in the rock matrix. They contain the following types of aquatic plant assemblages:

(1) Pondweed assemblage. This type occurs in the Ulan Khushu oxbow facies and is dominated by the *Potamogeton*-like shoots bearing both floating and submersed leaves. They are mostly preserved on the bedding planes and seem to have been autochthonous or nearly so, while the parallel-veined monocot leaves, which are also common, are fragmented and are frequently embedded in the rock matrix. They might have been transported from the nearby reed marshes. The isoetalean megasporophylls, though detached, could hardly be transported for a considerable distance with their bulky megaspores *in situ* while the leaf detachment could naturally occur in these submersed plants.

While pondweeds inhabit a wide range of fluviatile and lacustrine environments, the production of both floating and submersed leaves is more common in permanent open, still, or sluggishly flowing water bodies, and the associated quillworts might suggest clear water oligotrophic conditions.

(2) Nymphaealean assemblage. Plants from this assemblage have not yet been systematically studied, which precludes any paleoecological inferences. Our first impression is that this assemblage might reflect a further successional stage of the type 1 ecosystem on the way to eutrophication and expansion of aquatic macrophytes.

(3) Duckweed assemblage. The lemnioid fruits, although fairly abundant, seem allochthonous in both the levee and pondweed oxbow facies. In the Tsagan Khushu locality, abundant fruit compressions occur in the clayey organic films with small structureless plant debris covering mm-thick sand lamellae. This high-energy sedimentary environment was scarcely suitable for a dense growth of floating plants. Since the fruits are almost undistorted in contrast to the rest of the plant material, they might have been well adapted to dispersal by water currents, perhaps using the air-filled apical funnels as floats. The Ulan Khushu locality represents a low-energy sedimentary environment, abounding in diverse aquatic macrophytes. However, the

Fig. 10. Lemnioid fruits from Tsagan Khushu locality, SEM: *a* - caruncle scar of ovule ($\times 800$); *b-e* - ovules removed from utricles; note strict tendency to hemianatropous position of funicle relative to micropyle in (*b*) ($\times 70$).

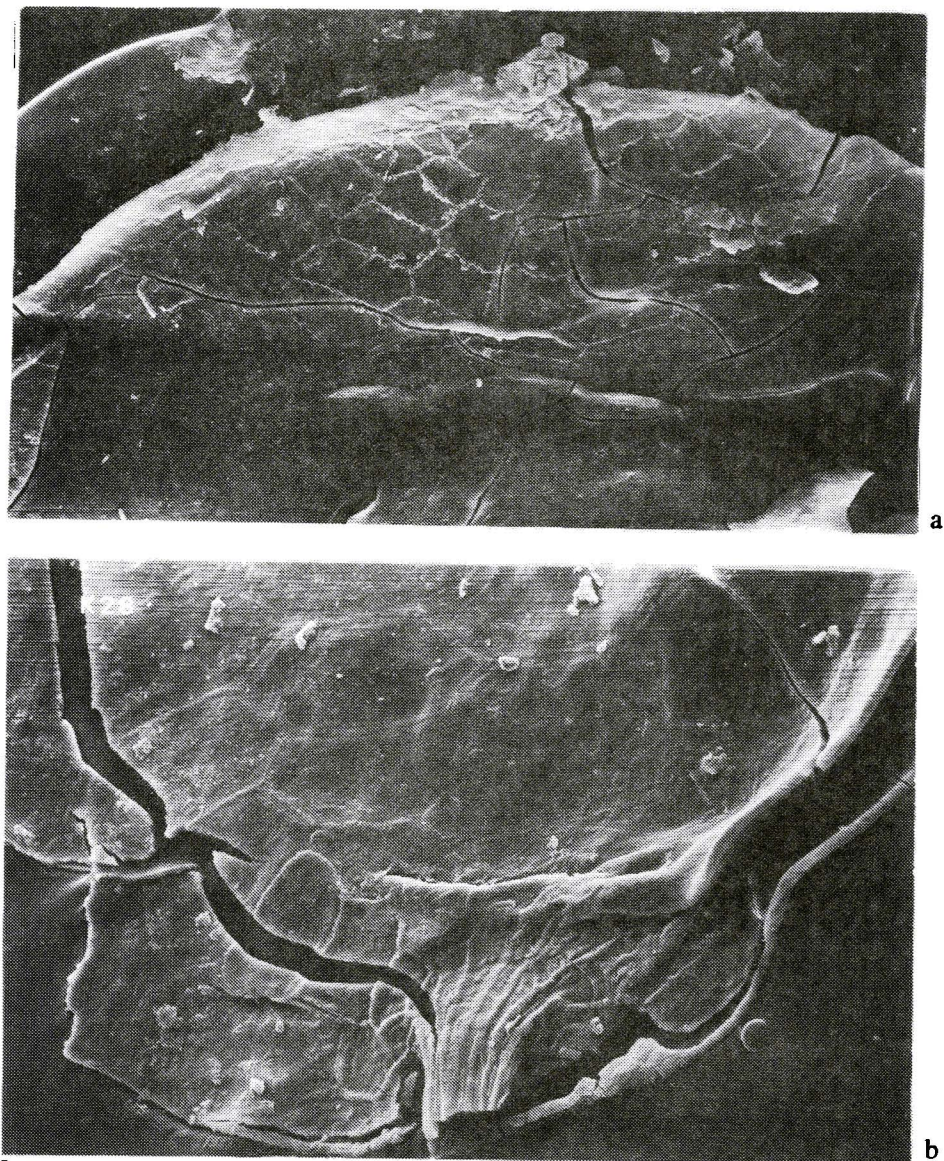


Fig. 11. Lemnioid fruits from Tsagan Khushu locality, SEM: *a* - operculum with caruncle of ovule shown in fig. 10*c* $\times 300$; *b* - funicle of ovule shown in fig. 10*d*, $\times 300$.

presence of *Isoetes*-like plants suggests a clear-water, low CO_2 content, oligotrophic regime hardly compatible with a dense duckweed cover. The latter tends to reduce oxygen content and light intensity thus suppressing photosynthesis of submersed plants. The lack of any lemnioid vegetative remains seems accounted for by a wide dispersal of fruits produced elsewhere in eutrophic environment.

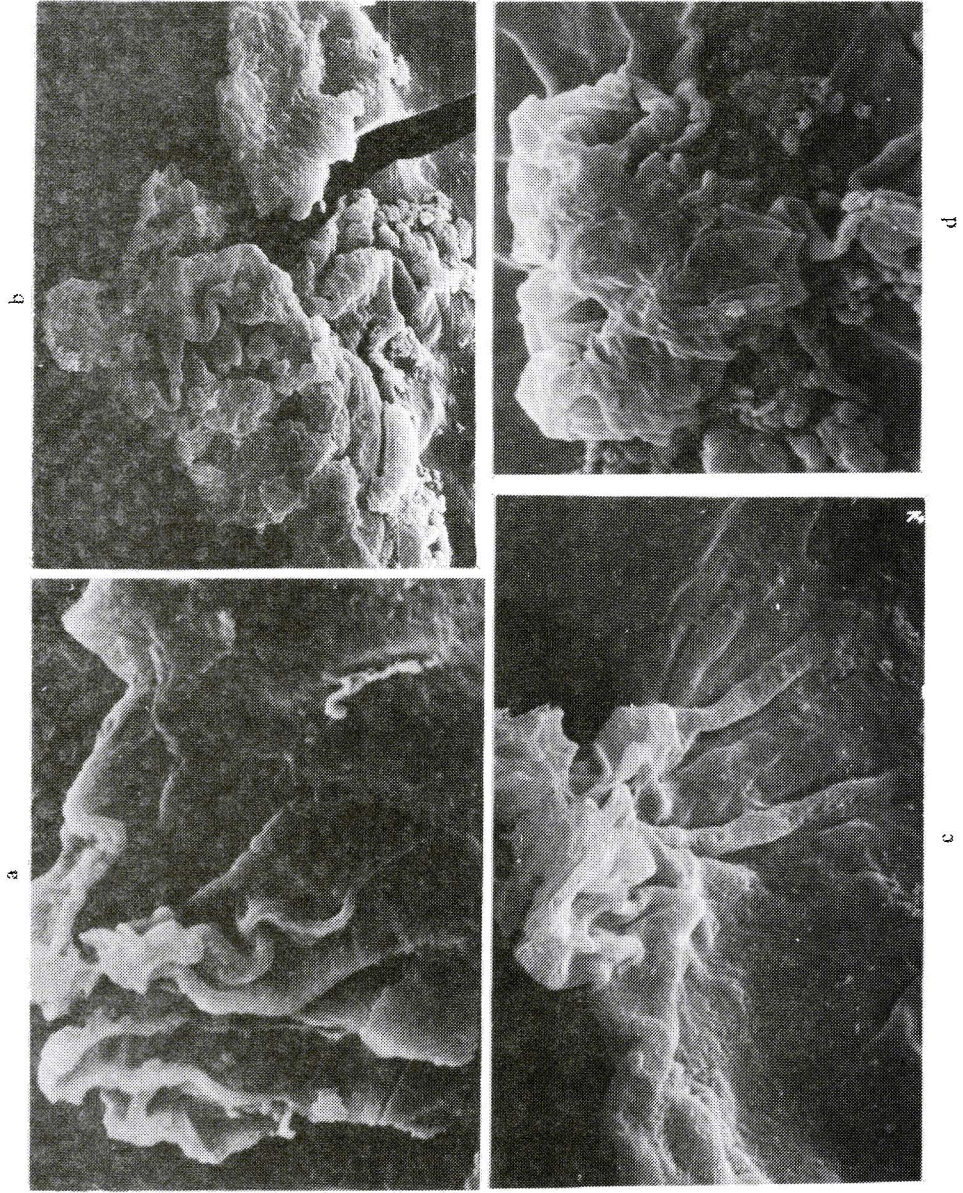


Fig. 12. Lemnoid fruits from Tsagan Khushu locality, SEM: *a* - caruncle showing sclereids with pits and annular thickenings, ($\times 2000$); *b* - *d* - caruncle shapes ($\times 1500$) (*b*) and ($\times 2000$).

The present-day Lemnaceae flourish in still or slightly moving water covering the entire surface of shallow ponds with several layers of their thalloid bodies, or "fronds." Optimal for them are fresh waters with pH ranges of 4.5-7.5, and surface temperatures between 20 and 30°C, although they tolerate brackish water and pH extremes of 3.5 to 8.5 (see Hillman 1961, for a review). Both tropical and cosmopolitan species can survive adverse periods of drought or low temperature with the help of dormant seeds or vegetative resting bodies (turions) buried in mud. In monsoonal climates duckweeds are said to appear with the onset of monsoons in July and persist till November (Maheshwari and Kapil 1963). Their flowering and fruit production seem to be induced by crowding, drought, or high temperatures. These factors might have operated in the Cretaceous.

Insofar as the prevailing mode of reproduction in duckweeds is vegetative, we are led to assume by the fruit abundance in the Nemegt deposits either a very high overall reproductive effort or a relatively higher fruit production than in the extant examples or both. In the extant duckweeds more fruit/seeds are produced in seasonal climates, the diaspores wintering in bottom sediments. Our material might, thus, suggest a considerable seasonality, the thickly cutinized fruits with lime-excreting glands conceivably capable of surviving adverse environmental conditions in carbonate mud. Even allowing for a higher fruit production in the Cretaceous lemnoids, we have to postulate vast expanses of water covered with thick duckweed mats.

The latter suggestions seem pertinent to reconstruction of feeding habits of vegetarian dinosaurs or, at least, some of them. Insofar as duckweeds are eaten by various animals and even humans, there seem to be no reasons whatsoever for them being neglected by dinosaurs.

Presently, duckweeds are regularly used for food by fish, waterfowl, muskrats and other vertebrates, and are considered as a food source of high nutritional value (comparable to that of alfalfa) for farm animals. It is, thus, surmisable that extensive duckweed mats provided an excellent feeding ground for the hadrosaurian duckbills.

Occasional remains of land plants in the gut contents of hadrosaurs seem to suggest that these animals might have fed on land (Krausel 1922). Alternatively, such remains might come from gyttja (Krassilov 1981). Whatever the feeding habits, hadrosaurs came to dominance simultaneously with the appearance of diverse modern-looking aquatic angiosperms in the latter half of the Late Cretaceous. Also, the hadrosaurian general *Saurolphus* and *Barsboldia* constituted a dominant element in the Nemegt dinosaur fauna.

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