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ERETMOPHYLLOUS GINKGOALES FROM THE CENOMANIAN

INTRODUCTION

Oblanceolate leaves represent a special problematics of fossil *Ginkgoales* taxonomy. Appearing in deposits from the Permian to the Cretaceous they are known in different Mesozoic taxa (see TRALAU 1969 : 64 to 68). One of such leaf forms is associated with the genus *Eretmophyllum* THOMAS (THOMAS 1913, PONS, BOUREAU et BROUTIN 1976). This predominantly Jurassic type of Mesozoic *Ginkgoales* has been assigned to the family *Phoenicopsiaceae* TRALAU (the Division 2. sensu TRALAU, l.c., p. 66). The leaves are considered to have been originally bundled, sessile, non-petiolate, and tongue-shaped. At present time approximately eight Jurassic and one Cretaceous eretmophyllous species have been described. The latter one, *Eretmophyllum andegavense*, was described ten years ago from the Cenomanian of France (PONS, BOUREAU et BROUTIN 1976). The species shows a very strong similarity to another ginkgoalian taxon, *Nehvizdya obtusa*, coming from the Peruc Mb. (Cenomanian) in Bohemia (HLUŠTÍK 1977, 1980).

The present paper deals with several new details concerning the origin of *Nehvizdya obtusa* as well as with biometrical data worked out by simple statistics.The material treated was collected at the localities Hloubětín (eastern suburb of Prague) and Vyšehořovice village (East of Prague). In the clay pits deposits of the Peruc Mb. (Peruc-Korycany Formation) are exposed. The specimens represent hundreds of leaf individuals and some rare seeds. The results presented here supplement the previous studies on the genus *Nehvizdya* (HLUŠTÍK, 1977) and support the author's opinion that oblanceolate ginkgolian leaves from the Cenomanian cannot be simply associated with the genus *Eretmophyllum*.

DESCRIPTION OF ADDITIONAL LEAF CHARACTERISTICS AND REPRODUCTIVE ORGANS OF NEHVIZDYA OBTUSA

Nehvizdya obtusa (VELENOVSKÝ) HLUŠTÍK, 1977

1977. *Nehvizdya obtusa* (VEL.) HLUŠTÍK, pp. 173—186, Pls I—IV.
1980. *Nehvizdya obtusa* (VEL.) HLUŠTÍK, pp. 26—33, Pl. III, fig. 1.
? Secretory ducts (Pl. I, figs 4, 5, Pl. II, figs 3—6, Pl. III)

At the maceration of certain leaf compressions small, flattened, globular to spindel-shaped bodies have been observed in between adaxial and abaxial cuticles.

Rounded, originally globular to ellipsoidal bodies are formed by a cutin-like matrix. Irregularly wrinkled to network-like walls of the objects bear sometimes hyphae-like projections (see Pl. II, figs 5, 6, Pl. III, figs 3—6). The diameter of the bodies varies from 0.2 to 0.5 mm. They have been ascertained at first in naturally transparent blades (Pl. III, fig. 1). Having been regularly attached to the inner surface of the lower cuticle they are everytime in no direct connection with stomatal openings.

Spindel-shaped bodies are also irregularly wrinkled, and, perhaps, composed of the same matrix. Their total length varies from 0.5 to 1.5 mm., the maximal width represents about 1/10 of the total length (Pl. I, figs 4, 5, Pl. II, fig. 4). The objects have not been observed in situ up to now. They have been obtained by a careful outwashing of individual specimens during the maceration.

All the above described objects resemble secretory tracts as they are known in the fossil genus *Eretmophyllum* THOMAS and in the living *Ginkgo biloba* L. The hyphae-like projections have never been preserved in the outwashed and separated objects. They probably served as fibrous elements anchoring the globular ducts within hypodermal tissues of the leaves. The spindel-like bodies resemble by shape those of *G. biloba* being embeded within the mesophyll and orientated paralelly to the blade venation.

The dimensions of the objects, their composition as well as the absence of any organized morphological details allow us to have their affinity to epiphyllous fungi for excluded (comp. PONS et BOUREAU 1977, for example).

Seeds

In dark claystones overlying basal sediments of the Peruc Mb. at Hloubětín (HLUŠTÍK 1974) rounded seeds have been found (Pl. I, figs 1, 2, 6). The seeds are about 10 mm. in diameter, globular slightly tipped, with a very short petiole-like projections (Pl. I, fig. 1).Three specimens have yielded testal remains, in cell structure indentical to the leaf cuticles of *Nehvizdya obtusa* (Pl. II, figs 1, 2). The seeds were probably composed of an inner sclerotesta (a slight elevation at the central part of fossils), while the wrinkled surface resembles compressed inner tissues (sarkoteste) covered by the cutinized exotestal membrane.

The exotestal cuticle is composed of polygonal epidermal cells. Stomata are very rare, but, quite identical to those in the lower cuticle of leaves. In the seeds of G. biloba a similar situation has been stated: the shape and organization of epidermal/exotestal cells, the occurrence of stomata. Moreover, the shape, bilateral symmetry, and dimensions of the fossil seeds are also well comparable to those of *G. biloba*.

The described fossils are considered as the seeds belonging originally to the plant foliaged by leaves of the *N. obtusa*-type.

Megasporangiophores (cupulae)

In Hloubětín as well as in Vyšehořovice several cupula-like remains have been collected. They can be well compared to the similar terminations of the *G. biloba* megasporangiophores that bear ovules (seeds). The cuticle of the fossil petiolar bases (parts of broken-off sporangiophores) has shown the same epidermal structure as in the leaves and seeds of *N. obtusa* (see text-fig. 8, Pl. I, fig. 3).

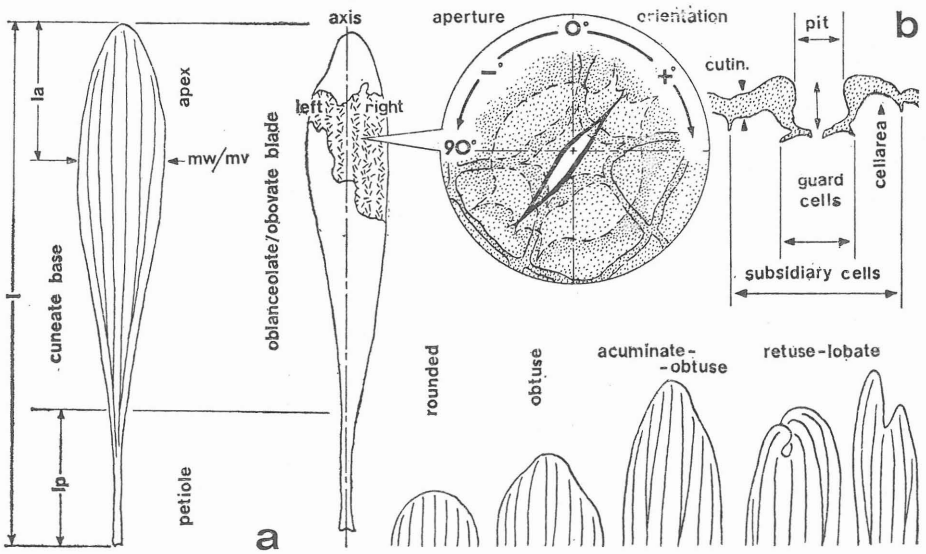

Fig. 1. Explanatory scheme showing the main morphological (a) and stomatal features (b) measured in *Nehvizdya obtusa* ssp. *obtusa*; 1 — total length of the leaf blade and petiole, 1a — the length of leaf apex, mv — maximal number of veins, mw — maximal width of the blade, lp — the length of petiole. Originally sktched by the author.

Discussion

The first records of seeds produced by *Podozamites obtusus* (= *Nehvizdya obtusa*) were published about 60 years ago by VELENOVSKÝ et VINIKLÁŘ (1926, 1927). They described the objects as follows:

„... Bei Kralupy (NE of Prague, Peruc Mb. — noted by A. H.) sind nicht selten runde, etwa 1 cm breite, glatte Samen zu finden, welcher von einer fleischigen Aussensicht umhüllt waren, was die lockere Grube, in welcher sie eingebettet sind, bezeugt.

Auch ein kurzer Stiel ist stellenweise deutlich. Am Scheitel sind sie mit einem Spitzchen versehen und auf der Oberfläche netzartig gerunzelt. Es ist nicht ausgeschlossen, dass diese Samen mit beschreibenen Blättern (i.e. *Podozamites obtusus* — noted by A. H.) in Zusammenhang gebracht werden könnten in infolgedessen auf die Verwandschaft der Ginkgoaceen hinweisen dürften..." (VELENOVSKÝ et VINIKLÁŘ 1926 : 34).

The affinity suggested by both authors is fully supported by the present study. It appears that intuitive considerations of VELENOVSKÝ, a well experienced plant morphologist, were quite correct.

Leaf biometrics

The following data have been obtained by simple biometric measurement of the leaves of *N. obtusa*. The features measured have been experimentally selected to show a possible range of the leaf size, venation, and epidermal structure variables. Although limited by mostly fragmentary material the measurement has proved the leaves belonged to a uniform, homogenous species.

In text-figs 1a, 2, 3, and 4 all measured parameters are graphically explained. The table 1 shows the main features of variability of the leaf blades and venation patterns. Generally, it is evident that the species produced oblanceolate leaves with distinctive petioles. The blade apices vary from rounded to obtuse (or acuminate-obtuse) in shape, sometimes irregularly wave-margined to deeply lobed (text-figs 1a, 3a). Deeply divided leaf apices (text-fig. 3a) are rare and in this respect resemble other ginkgoalian leaves, as in *G. biloba* can also be seen; no pathological causes of such irregularities has been ascertained up to now (see also HLUŠTÍK 1977). The leaf blades as such vary in shape from straight-oblanceolate over S-shaped-oblanceolate to a very rare form of sickle-shaped-oblanceolate (text-fig. 3b). All kinds of symmetry of the blade might also be influenced by the development of the venation.

Table 1. *A* survey of variability of the leaf blade in *Nehvizdya obtusa* (116 specimens)

feature	degree of variability
l:mw ratio	8:1 — (3)4:1
la:mw ratio	<4:1 — >1:2
mv:mw ratio	<5:3 — >3:5
lp:l ratio	1:4 — 1:3
mw variability coeficient	v = 24,16
average mw in mm. (10—12 mm.)	11,25 (in 44,8 %)
la variability coeficient	v = 28,65
average la in mm. (12—18 mm.)	14,65 (in 60,0 %)
la:mw ratio variab. coeficient	v = 26,80
average la:mw ratio (0,9—1,6)	1,302 (83,5 %)

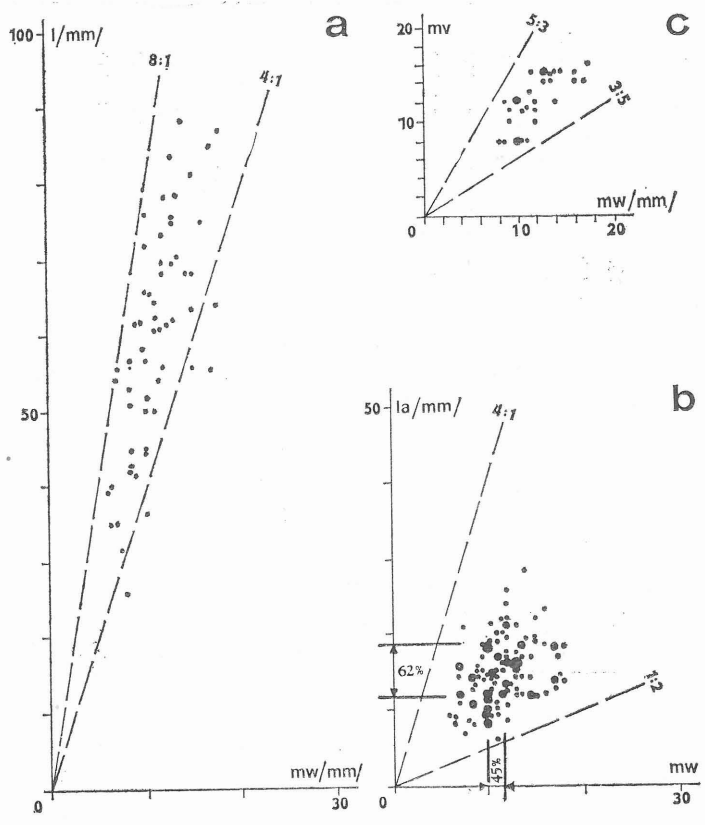

Fig. 2. Bi-dimensional diagramms reflecting relations between principal features of leaves in *N. obtusa ssp. obtusa*; a — total legnth/maximal width ratio (52 specimens), b — the length of apex/maximal width ratio (116 spec.), c — maximal number of veins/ /maximal width of blade ratio (29 spec.). The leaves show distinctive homogenity of morphological variations. After original material from the Peruc Mb. deposits (Hloubětín, Prague, Bohemia).

It is everytime parallel, dichotomous, the number of veins is in direct relation to the maximal width of the lamina; the petiolar two veins bifurcate 2—4 times forming regular pattern, mostly of bilateral symmetry.

Besides normal statistics of epidermal topography (HLUŠTÍK, 1977) the following phenomena have been pursued: stomatal pits and their share in the blade area (Tab. 2, text-fig. 7b), and stomatal aperture orientation (Tab. 2, text-figs 1b, 5—7a). Taking the measurements into account the leaves can be characterized as hypostomatal, coriaceous, and strongly cutinized (Pl. IV). Stomata are sunken, obliquely orientated; at marginal areas of blades stomatal apertures preferably incline to the nearest margin (text-fig. 5). In the petiole stomata are aligned more or less longitudinally having apertures orientated sub-parallelly to

Table 2.
A survey of some epidermal features measured in cuticles of *N. obtusa* (Peruc Mb.)

feature measured		lower cuticle
stomatal cells participating in 1 mm² of non-venous epidermal surface (in μ²)	minimal	130 000 (about 13 %)
	maximal	630 000 (about 63 %)
number of stomata per 1 mm² of non-venous area		38—65 (average about 50)
stomatal pit perforations participating in 1 mm² of non-venous epidermal surface (in μ²)	minimal	10 580 (about 1,1 %
	maximal	18 100 (about 1,8 %)
	average	14 404 (about 1,5 %)
stomatal pit contour (volume in μ²)	minimal	79
	maximal	907
	average	278,5
stomatal index per 1 mm (across a blade): $i_s = \frac{\text{number of stomata}}{\text{number of stom + number of epid. cells}}$	minimal (2 stomata)	0,0288
	maximal (7 stomata)	0,0944
	average (5 stomata)	0,0738
depth of stomatal pit (in μ)	maximal	15,0 (1,5 %)
	minimal	2,0 (1,5 %)
	average	6,0—8,0 (ca. 47 %)
number of subsidiary cells (in average leaf blade)		4 (4 %) 5 (54 %) 6 (42 %) 7 (rare)
a share of non-stomatal areas participating in maximal width of blade		about 20 %

the axis of the blade (text-fig. 6). The number of stomata per 1 mm^2 of the stomatal band surface is clearly comparable to that of the living *G. biloba* (Tab. 2). On the other hand, the thickness of cutization is enormous; this feature indicates that the plant probably grew under specific conditions, alike those of certain xerophillous (or halopillous?) plants. This assumption is also supported by the presence of frenelopsid *Conifers* in the Peruc Flora taphocoenosis. The presented data validate only the conclusions previously published (HLUŠTÍK 1977, 1980).

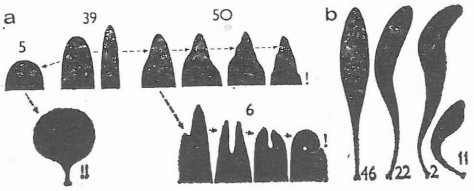

Fig. 3. Percentual representation of the main variables of both apical contour (a) and the blade symmetry (b) in leaves of N. obtusa ssp. obtusa (cca. x 0,3); a — an artificial seriation of leaf apices from rounded to divided ones, the only example of a reniform leaf see left below, b — four principal symmetries of leaf blades (sickle-shaped ones are relatively not abundant). After 350 measured specimens from the Peruc Mb. deposits (Hloubětín, Prague, Bohemia).

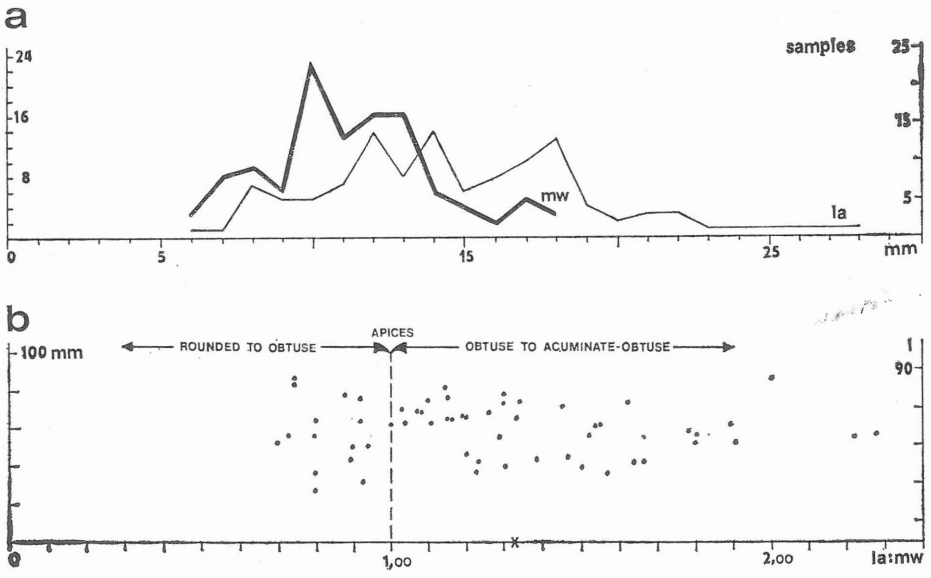

Fig. 4. The variability of leaf apices in *N .obtusa* ssp. *obtusa*; a — a histogrammatic demonstration of the numerability of maximal widths and apical lengths (116 spec.), b — a point diagramm showing a possible way of terminological differentation of leaf apices: after the measurement of 57 well preserved specimens from the Peruc Mb. deposits (Hloubětín, Pragpe, Bohemia). See also text-fig. 1 a, below right.

NEHVIZDYA OBTUSA VERSUS ERETMOPHYLLUM ANDEGAVENSE?

In the Middle Cenomanian of France a leaf form similar to Bohemain species *Nehvizdya obtusa* was described by PONS, BOUREAU et BROUTIN (1976). The leaves, named as *Eretmophyllum andegavense*, closely resemble those from the Peruc Mb. not only in the leaf shape, but also in epidermal structures (see HLUŠTÍK 1980). Nevertheless, several differences are to be marked out. As far as we can judge from the information published, the French species differs in the presence of clear secretory cells within epidermides, in the appearance of stomata, and in the number of petiolar veins (see Tab. 3, 4).

Table 3. Comparative survey on leaf morphology (after Pons, Boureau et Broutin 1976 and original measurements compiled by the author)

feature/species	*E. andegavense*	*N. obtusa*
total length variability in mm. (l)	40—70	25—100
maximal width variability in mm. (mw)	7—12	5—30
mw position: total length (l)	2:3	4:5—2:3
number of veins in petiole	1 (l)	2
number of veins per 10 mm. (mw)	7—8	8—12

Rather less important differences can be seen in the number of veins per 1 mm. of the blade width, and in some details of the cutinization. The presented tables bring comparative surveys on both species.

Regardless fragmentary data on *E. andegavense* the above mentioned three main differences are of indubitable importance, which makes any direct integration of both Bohemian and French species incorrect.

In the Bohemian species the leaves are evidently narrowed into the petiole. Moreover, no indication of a bundled position of leaves at shoots (or dwarfshoots) has been observed up to now in a very abundant material from the Peruc Mb. In this connection it would be useful to quote again some observations of VELENOVSKÝ et VINIKLÁŘ:

„... Auf den Schieferplatten von Kralupy, wo die Blätter massenhaft allein ohne Begleitung anderer Abdrücke erscheinen, die runde Samen ausgenommen (see p. 101 here — noted by A. H.), liegen hin und weider blattlose Zweige... Sie zeigen längliche, sehr stark hervortretende Blattpolstern, die mit einer rhombischen Blattnarbe abgeschlossen sind. Nun finden wir auf den gut erhaltenen Blattstielen dieselbe, ähnlich geformte und gleich grosse Abfallnarbe. Es ist demzufolge sichergestellt, das diese Blätter von den Blattpolstern durch die beschreibene Narbe abfielen... Es ist bestimmt eine Conifere oder Ginkgoacee..."

„... Wir haben wiederholt den Standort bei Kralupy besucht und sorgfältig untersucht. Alles bestätigt sich so, wie es ... auseinande gesetzt wurde. Die polstertragenden Äste sind unter den Unmasse von Blättern recht häufig und ebenso die rundlichen, glatten Früchte, so dass ihre Zusammengehörigkeit bestimmt festgestellt wird..." (VELENOVSKÝ et VINIKLÁŘ 1926 : 34—35, 1927 : 33).

Table 4. A comparative survey of epidermal features in *E. andegavense* and *N. obtusa* (after PONS, Boureau et Broutin 1976 and original measurements compiled by the author)

feature/species			*E. andegavense*		*N. obtusa*	
			upper cut.	lower cut.	upper cut.	lower cut.
non-stomatal area width in mm.				?		0,3—0,8
epidermal cell dimensions	non-stomatal areas		?	10—60	40—70	10—80
	stomatal areas			30—44		30—50
punctuation of cell walls			?	visible	uncertain	uncertain
radial striae upon periclinal walls			?	visible	absent	absent
number of stomata per 1 mm²			0,5—2,5	56	0	(38)—50(—65)
epidermal secretory cells			rare	present	absent	absent
orientation of stomatal apertures			perpend.	perpend.	perpend.	perpend.
guard cell dimensions in μ			(10—15) X (35—70)			10 X 50
number of subsidiary cells at stomata				(3)4—6(8)		(4)5—6(7)
cell walls cutinization in μ	epidermal cells	anticlinals	?	2,5—3,0	2,0—4,0 (average 2,5)	
		periclinals	?	?	9,0—12,0	5,0—9,0
	subsidiary cell periclinals		?	3,0—8,0	15,0—17,0 (average 15,5)	
non-epidermal secretory elements			?	?	supposed	
stomatal pit dimensions in μ (contour)			(3—10) X (22—32)		(15—20) X (20—35)	

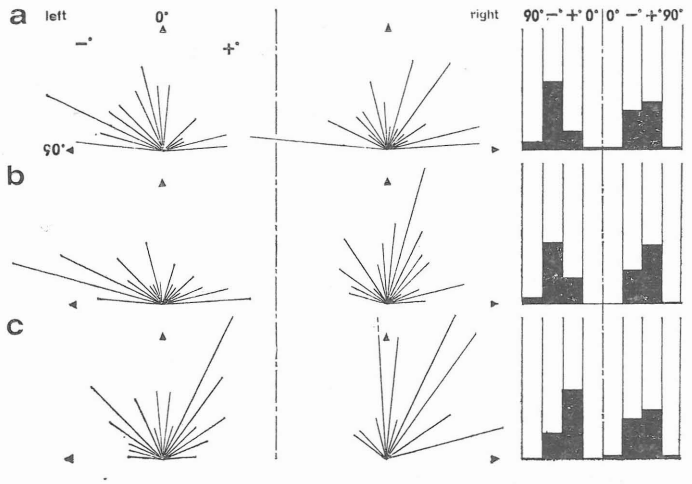

Fig. 5. Diagramm reflecting general orientations of stomatal apertures in lower epidermides of *N. obtusa* ssp. *obtusa*; a, b, c — three leaves measured across the lamina (in the mw direction). The length of abscissae expresses a numerability of individual angles (grouped by 10°), block diagramms summarize it percentually (right). Stomata at the right half of blade are orientated more in positive sense, while those at the left half of blade seem to prefer negative orientation (a, b); this possible affinity is rather suppressed in the third leaf (c), most probably due to its asymmetry (slightly S-shaped leaf). After original material from the Peruc Mb. deposits (Hloubětín, Prague, Bohemia).

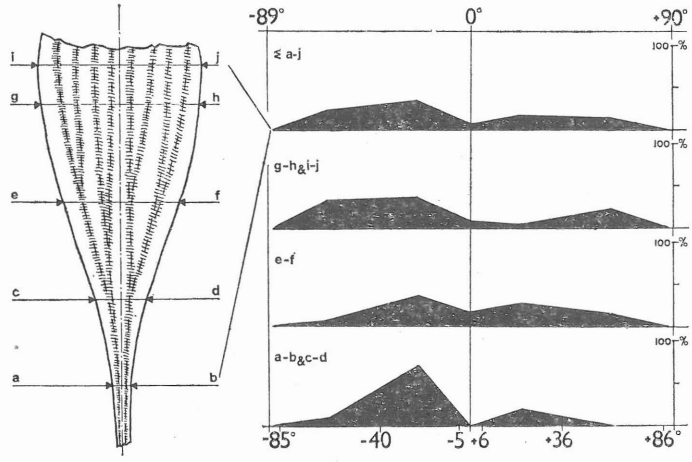

Fig. 6. Percentual representation of both negative and positive angles of stomatal apertures in a leaf of *N. obtusa* ssp. *obtusa* (see left, profiles a—j); a tendency from closed angles to open ones towards maximal width of the blade is well visible (see apices of curves, right). The orientation of stomatal apertures is also well expressed by the uppermost, summarizing diagramm (Σ a—j). After original material from the Peruc Mb. deposits (Hloubětín, Prague, Bohemia).

At the localities of Hloubětín and Vyšehořovice, where the leaves are also found in a mass, no similar shoots have yet been recognized among other plant axes, neither any rests of another type of foliaged ones that would belong to the species *N. obtusa*. After a careful examination of original specimens from Kralupy we can state that the defoliated shoots are hardly to be interpreted as belonging to a *Conifer*[1], but, the leaf scars upon their surface quite fit with the dehiscence facets at petioles of *N. obtusa*.

As shown above, the seeds have been found together with the leaves at the Hloubětín locality. In this way, the same situation repeats as at Kralupy (VELENOVSKÝ et VINIKLÁŘ, the text quoted). Moreover, other places in Bohemia can be added where abundant occurrence of the *N. obtusa* leaves is apparent (e.g. Libušín near Kladno, Podlešín near Slaný, etc.). As in the living *G. biloba* can also be observed, the bundled leaves fall off not only as individuals, but they can often be broken off together with dwarfshoots, too. According to the abundance of fossil leaves in some layers of the Peruc Mb. it is highly probable that bundles or dwarfshoots should have been found somewhere. Regarding these facts *N. obtusa* is considered as deciduous ginkgolian plant with spirally arranged leaves, probably not bundled. In the author opinion, the same type of foliage can be supposed in the French *E. andegavense*; there is no evidence of bundled leaves in the species (see PONS, BOREAU et BROUTIN 1976).

Considering the mentioned close relation between the species *N. obtusa* and *E. andegavense* the phyllotaxy of similar leaf forms of fossil *Ginkgoales* must be examined in detail, especially in the connection with the genus *Eretmophyllum* Thomas. As recorded in the inintroductory remarks here, oblanceolate eretmophyllous leaves have been characterized as non-petiolate, bundled ones (TRALAU 1968). This feature was not proved in the species *E. andegavense*, although, the leaf form has been related to the genus *Eretmophyllum* THOMAS (PONS, BOUREAU et BROUTIN, l.c.), e.g. to the family *Phoenicopsiaceae* Tralau[2] (TRALAU 1968). This interpretation cannot be accepted. According to original descriptions, published by THOMAS (1913), both English species (incl. generotypic one!) *did bear distincively petiolate leaves*. Similarly, up to now we have obtained only a very unclear and disputable information as to the apperance of bundled leaves in eretmophylla as such.

On the other hand, we find much more resemblance of eretmophylla with the leaves concluded by TRALAU within the family *Glossophyllaceae* (the Division 3. after TRALAU 1968). This monotypic family is characterized by the only species *Glossophyllum florini* (KRÄUSEL 1943). The leaves of the species, Upper Triassic in age, show general morphology as well as epidermal pattern comparable to eretmophylla first of all. The leaf shape, venation, petiolate bases of leaves, epidermal

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[1] The specimens are deposited in the collection of the Department of Palaeontology, Charles University, Prague.

[2] The term was used incorrectly: it should be written as Phoenicopsi-d-aceae!

composition, and the type of foliage indicate that *G. florini* might be an early Mesozoic praecursor of the genera *Eretmophyllum* THOMAS (Jurassic) and *Nehvizdya* HLUŠTÍK (Cenomanian). This presumption was also suggested by the author in previous studies (HLUŠTÍK 1977, 1980). Thus, considering the mentioned incorrectness of the Tralau phylogenetical assumptions, we can better suppose that the mentioned genera represented some ancient lineage of ginkgoalian plants with petiolate, *non-bundled leaves*, surviving up to the latest Mesozoic.

In view of these facts new taxonomical characteristics of both Cenomanian taxa has been suggested:

Ordo: *Ginkgoales*, Mesozoic Group (Division 3. sensu TRALAU 1968)
Family: *Glossophyllaceae* TRALAU, 1968 : 67
Genus: *Nehvizdya* HLUŠTÍK, 1977 : 174—175
Generotype: *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK, 1977 : 174
Basionym: *Podzamites obtusus* VELENOVSKÝ, 1885 : 9—10

The generotypic species is subdivided into two subspecies:

1. *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK ssp. *obtusa*
   1977. *Nehvizdya obtusa* sensu HLUŠTÍK, p. 174—186, text-figs 1—6, Pls I—III, IV, figs 1—4.
   1980. *Nehvizdya obtusa* sensu HLUŠTÍK, p. 26—28, Pl. III, fig. 1.
   Locus typicus: Nehvizdy village, E of Prague, Bohemia.
   Stratigraphical range: (? Lover —) Middle Cenomanian, Upper Cretaceous of the Bohemian Massif.
   Occurrence: claystones and sandstones of the Peruc Mb. (Peruc-Korycany Formation).

2. *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK ssp. *andegavensis* (PONS, BOUREAU et BROUTIN) stat. nov.
   1976. *Eretmophyllum andegavense* PONS, BOUREAU et BROUTIN, pp. 358—366, text-figs 1—4, Pls I—III (*basionym*).
   Locus typicus: ville d'Angers, quarry of Brouillard, Departement Maine-et-Loire, France.
   Stratigraphical range: Middle Cenomanian.

Remarks: The presented subdivision reflects very slight differences in the morphology and epidermal structure of the two closely related leaf forms of Cenomanian *Ginkgoales*; they were originally described as *Podozamites obtusus* and *Eretmophyllum angavense*. Both the species represent two intraspecific entities of a deciduous plant with non-bundled patiolate leaves in spiral arrangement (see text-fig. 9). The name of the generotypic species is chosen according to the priority principle (HLUŠTÍK 1977). The above recorded characteristics show that *N. obtusa* ssp. *andegavensis* could be a geographical subspecies of a glossophyllous ginkgoalian plant inhabiting Late Cretaceous maritime biotopes of circumtethyd areas. The subspecies *N. obtusa* ssp. *obtusa* is considered as another geographical deviation of the same species, inhabiting coastal areas of the Bohemian Massif archipelage in the Cenomanian.

Assemblege: Both subspecies are commonly found in a typical association with Cenomanian species of the genus Frenelopsis SCHENK (BROUTIN et PONS 1975, BOUREAU et BROUTIN 1976, HLUŠTÍK 1977, 1980).

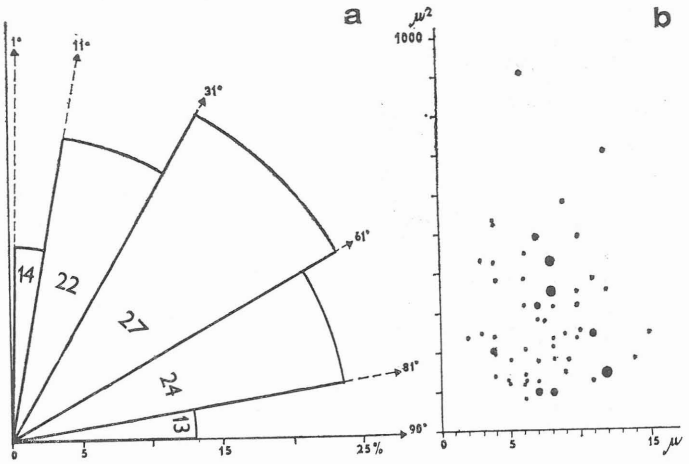

Fig. 7. Stomatal characteristics in leaves of *N. obtusa* ssp. *obutsa*; a — a percentual diagramm showing predominant orientations of stomatal apertures (after 5 measured specimens), b — a correlation between the depth of stomatal pits (in μm^2, after 66 measured specimens, Peruc Mb., Hloubětín).

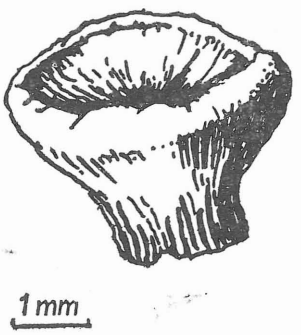

Fig. 8. A cupule from the Peruc Mb. claystones (Vyšehořovice village, E of Prague) representing an apical part of the megasporangiophore of *N. obtusa* ssp. *obtusa* (specimen A, National Museum, Prague); from the stalk-like base of the object a ctuicle was obtained (see Pl. I, fig. 3 here). After original state sketched by the author.

CONCLUSIONS

The Cenomanian species *Nehvizdya obtusa* (VEL.) HLUŠTÍK represents a typical ginkgoalian plant with deciduous, single situated leaves in spiral phyllotaxy, producing globular seeds (tex-figs 8, 9). The plant was probably a woody element of coastal vegetation surrounding the former Tethyd Ocean in the Upper Cretaceous. There are strong indi-

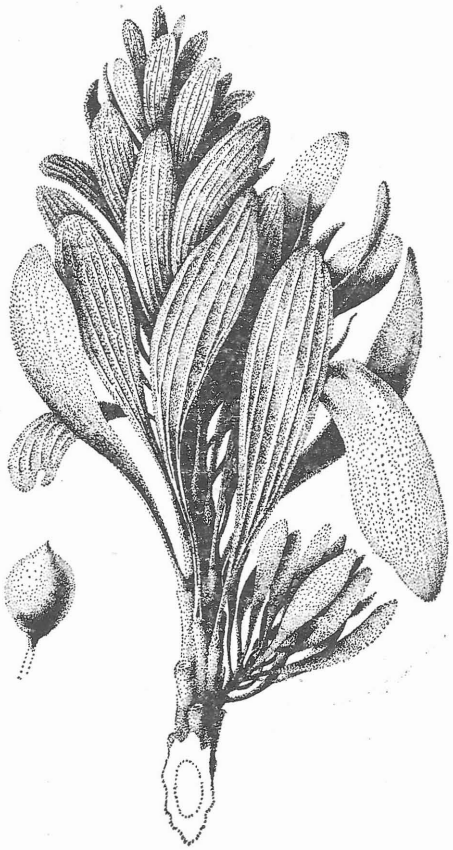

Fig. 9. The most probable restoration of the *N. obtusa* ssp. *obtusa* phyllotaxy. After original material from the Peruc Mb. deposits (Hloubětín, Kralupy, Vyšehořovice), cca. x 1. Sketched by the author.

cations that the species was variable in certain morphological and epidermal features. Therefore, it is subdivided here into two various subspecies. The western subspecies *N. obtusa ssp. andegavensis* is known from the Middle Cenomanian deposits in France and represents a type of rather more delicate leaves with secretory cells in epidermides; the leaves are amphistomatal, with one petiolar vein. The eastern subspecies *N. obtusa* ssp. *obtusa* is recorded from deposits of the Peruc Mb. in Bohemia (Middle Cenomanian). It produced leaves penetrated by numerous secretory ducts within mesophyllous tissues; the blades of leaves were hypostomatal, with two petiolar veins. The seeds were of a common ginkgoalian type. The subspecies as such probably represents a more coriaceous, xerophillous form of the plant.

The genus *Nehvizdya* is considered to be a homogenous, independent and well determinable taxon of extinct *Ginkgoales*. It is not related to the group of Jurassic eretmophylla s. s. It could be interpreted as a younger type of the evolutionary lineage of glossophyllous ginkgoalian plants (*Glossophyllaceae* TRALAU, 1968). The lineage included the species

Glossophyllum florini KRÄUSEL (Upper Triassic), different species of the genus *Eretmophyllum* THOMAS (Jurassic), and the species *Nehvizdya obtusa* (VEL.) HLUŠTÍK.

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ANTONÍN HLUŠTÍK

ERETMOFYLNÍ JINANOVITÉ ROSTLINY Z CENOMANU

Na základě podrobného studia morfologie a epidermální stvby listů, semen a pohárkovitých sporangioforů byly potvrzeny původní úvahy o příslušnosti české cenomanské *Nehvizdya obtusa* (VEL.) HLUŠTÍK k vymřelým jinanovitým rostlinám s opakvejčitými listy. (HLUŠTÍK 1977, 1980). Jakkoli se nepodařilo prokázat způsob olistění in situ, zdá se, že nejpravděpodobnějším bylo husté spirální uspořádání asimilačních orgánů na větévkách (srov. VELENOVSKÝ et VINIKLÁŘ 1926, 1927, text-fig. 9 zde). Během macerace četných izolovaných listů se podařilo získat drobná, okrouhlá nebo vřetenovitá tělíska (Tab. I—III). Jednalo se s největší pravděpodobností o původní sekreční orgány (kanálky, dutinky) uložené v mezofylu listů. Podobné útvary jsou běžně známy u řady fosilních jinanovitých i u dnešního druhu *Ginkgo biloba* L.

Hojnost původního materiálu z nalezišť v Praze-Hloubětíně a ve Vyšehořovicích dovolila pokusit se o jednoduché statistické zpracování tvarové variability listů a o vyhodnocení některých základních znaků epidermis (text-figs 1—7, tabulky 1, 2). Výsledky ukázaly, že *N. obtusa* tvoří dobře definovatelný fosilní druh s mírně zvýšenou variabilitou tvaru listových čepelí; tento znak nijak nevybočuje z rámce variability u jinanovitých.

Zjištěné údaje rovněž posloužily ke srovnání s velmi podobným druhem *Eretmophyllum andegavense* PONS, BOUREAU et BROUTIN (197ú) ze středního cenomanu Francie (Anjou) a k vyčlenění dvou samostatných poddruhů: *Nehvizdya obtusa* (VEL.) HLUŠTÍK ssp. *obtusa* a *N. obtusa* (VEL.) HLUŠTÍK ssp. *andegavensis* (UONS, BOUREAU et BROUTIN) stat. nov. Oba poddruhy představují listové typy, dosti odlišné od typicky jurských ginkgovitých z okruhu rodu *Eretmophyllum* THOMAS (THOMAS 1913, PONS, BOUREAU BROUTIN 1976, HLUŠTÍK 1977, 1980). Je velmi pravděpodobné, že eretmofylní ginkgovité mají fylogeneticky velmi blízko k rodu *Glossophyllum* KRÄUSEL (KRÄUSEL 1943) a že představují spolu s druhem *Glossophyllum florini* KRÄUSEL vývojovou řadu vedoucí k cenomanskému rodu *Nehvizdya* HLUŠTÍK (srov. TRALAU 1968, tabulka 3, 4 zde).

EXPLANATION OF PLATES

The specimens figured are deposited in the paleobotanical collections of the Department of Palaeontology, National Museum, Prague, under inv. cat. nos F 189—191. Cuticular preparations are registered in a separate collection in the same institution SEM photographs were made at the Institute of Geology and Geotechnics, Czechoslovak Academy of Sciences, Prague.

PLATE I.

1. *Nehvizdya obtusa* ssp. *obtusa,* seed compression in claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 1,5 (specimen F 189). Photo M. Páralová.
2. Dtto, another specimen (F 190) with pyritized inner matrix and poorly preserved exotestal cuticle, claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian cca. x 1,5. Photo M. Páralová.
3. Dtto, a cuticle of stalk-like base of the cupula A with stomata, sandy claystone Peruc Mb., Vyšehořovice (East of Prague), Middle Cenomanian, cca x 200. Photo A. Hluštík.
4. Dtto, spindel-like secretory ducts outwashed from macerated leaves, claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 100. Photo A. Hluštík.
5. Dtto, a single secretory element, claystone, Peruc Mb.. Hloubětín (Prague), Middle Cenomanian, cca. x 100. Photo A. Hluštík.
6. Dtto, a seed compression (F 191), claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 1,5. Photo A. Hluštík.

PLATE II.

1. *Nehvizdya obtusa* ssp. *obtusa,* a leaf cuticle (lower) with stomata, claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 60. Photo A. Hluštík.
2. Dtto, an exotestal cuticle of the seed (F 189), claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 60. Photo A. Hluštík.

3.—6. Dtto globular secretory sacs with hyphae-like projections, outwashed (3, 4) and attached to inner surface of lower cuticle of a leaf (5, 6), claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 100. Photo A. Hluštík.

PLATE III.

1. *Nehvizdya obtusa* ssp. *obtusa,* a central part of leaf, naturally translucent, showing the detachement of globular secretory ducts between cuticles, claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 6. Photo A. Hluštík.

2.—6. Different kinds of globular secretory ducts (2 — separated) as visible between cuticles of leaf, claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, cca. x 100. Photo A . Hluštík.

PLATE IV.

1. *Nehvizdya obtusa* ssp. *obtusa,* an inside view of lower cuticle; stomatal area pattern (left) is well differenciated from that of venous band (right). Claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, SEM photo no. 0417 (A, Hluštík), cca x 200.
2. Dtto, an inside view of stomatal aparatus cutinization, lower cuticle. Claystone, Peruc Mb., Hloubětín (Prague), Middle Cenomanian, SEM photo no. 0408 (A. Hluštík), cca x 1000.

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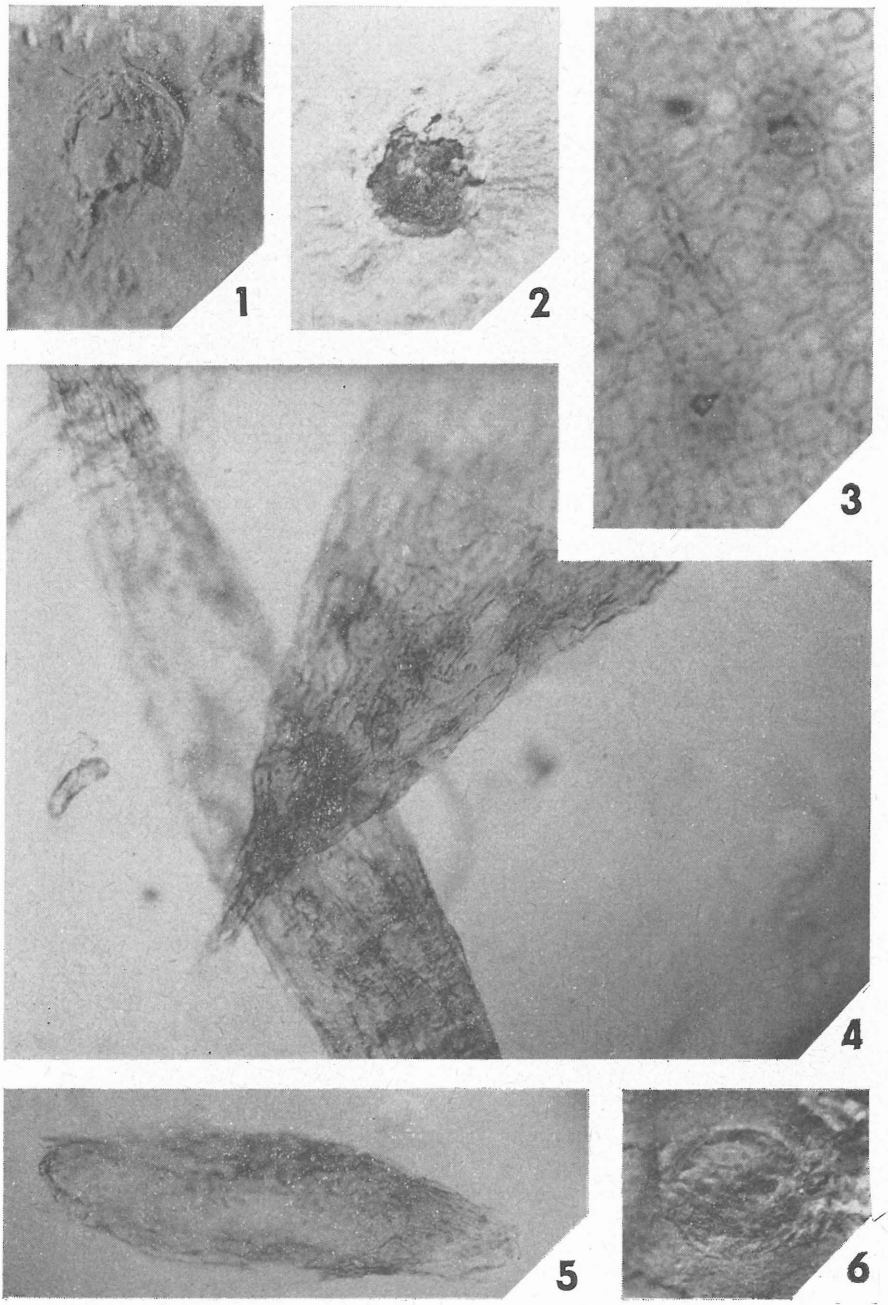
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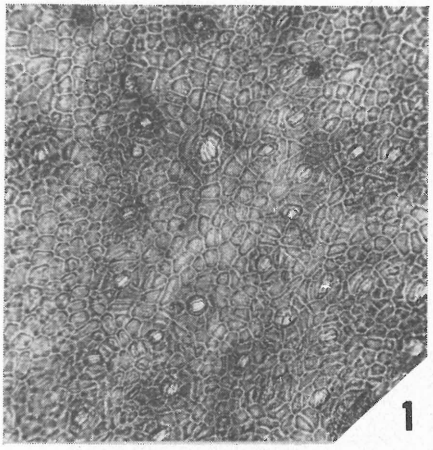
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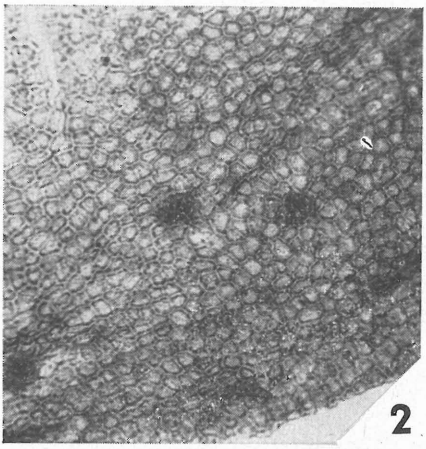
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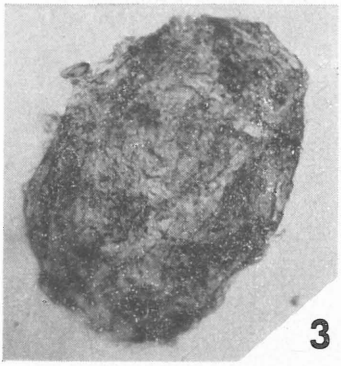
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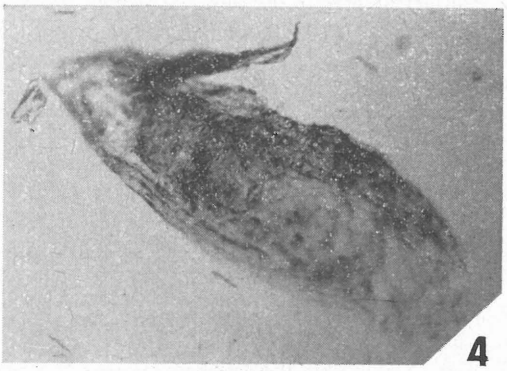
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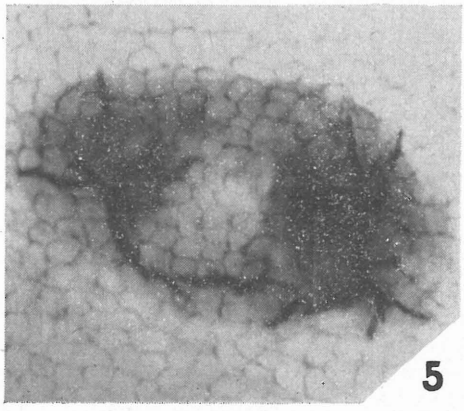
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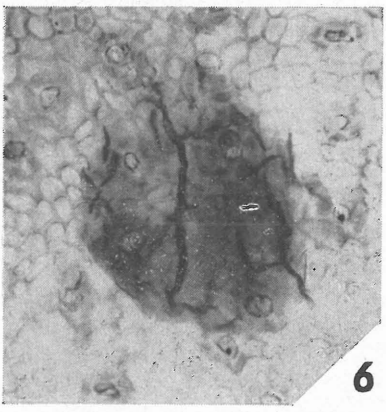
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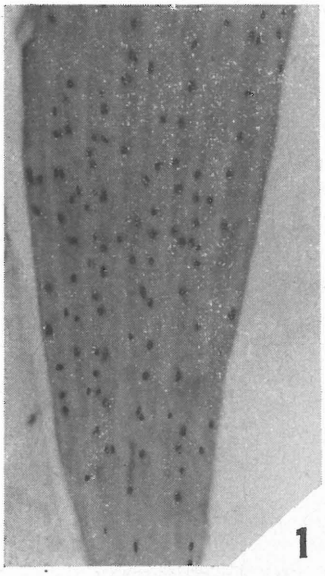
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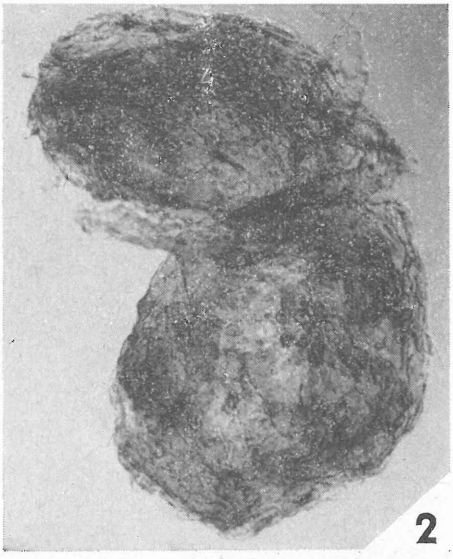
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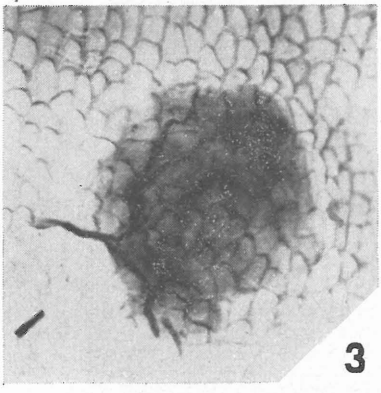
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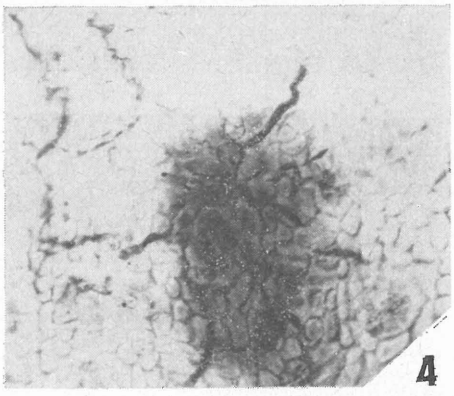
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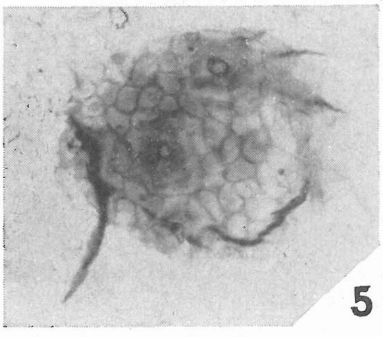
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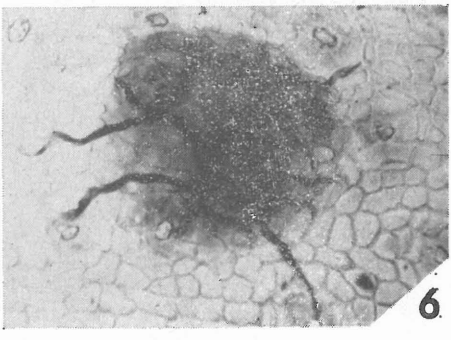
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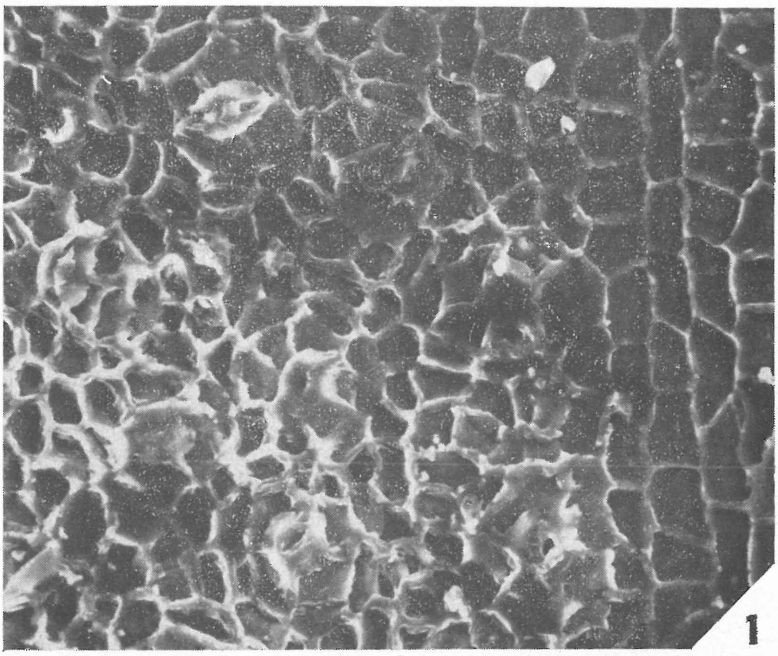
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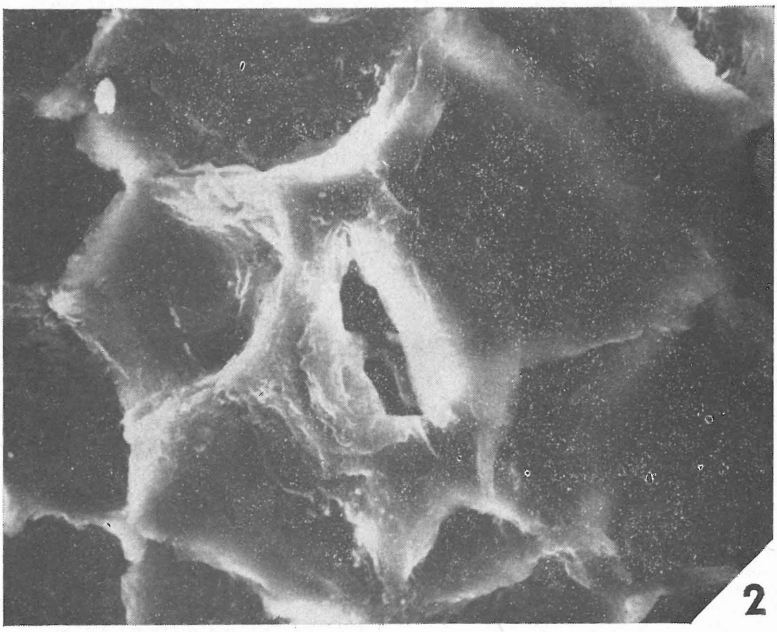
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