

# USHIA, A PALAEOCENE ANGIOSPERM OF NOTHOFAGUS AFFINITIES FROM THE LOWER VOLGA AND WESTERN KAZAKHSTAN

BY

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With 4 plates and 3 text-figures

## Abstract

Leaf architecture and cuticular characters observed on mineral films impregnated under the cuticle (subcrustations) confirm a fagaceous affinity for the fossil genus *Ushia* dominant in the Palaeocene floras of the Lower Volga and western Kazakhstan. It is more similar to the Tertiary and extant *Nothofagus* than to the northern hemisphere fagaceous genera. At the same time *Ushia* shares some supposedly archaic features with lower hamamelids. The associated fruiting organs, *Oxycarpia*, are interpreted as casts of bivalved cupules with the basal and apical lamellae. Phylogenetically *Ushia* is conceived of as a plesiomorphic descendant of ancestral stock giving rise to the northern and southern Fagaceae.

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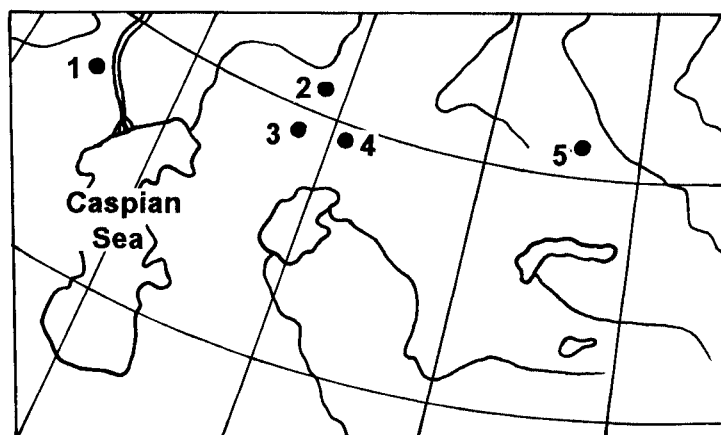
## 1. Introduction

Fagaceae, a dominant family of extant woody angiosperms, first appears, on palynological evidence, in the Late Cretaceous (e. g., *Nothofagidites* pollen in the Campanian and subsequent stages in South America and New Zealand (see ROMERO 1986). However, the first reliable megafossil records appear not earlier than Late Maastrichtian or even Early Palaeocene (reviewed in JONES 1986, CREPET 1989). Until recently they have been traditionally assigned to extant genera. *Ushia* was one of the early exceptions to this taxonomic practice. It was first described by GOEPPERT in MURCHISON's collections from the Ushi Hill locality near Kamyshin Town in the lower reaches of the Volga River as *Phyllites kamyshinensis*

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(MURCHISON 1845). The type locality is an outcrop of the Kamyshin Formation consisting of basal conglomerates with shark teeth and, above them, coarse crossbedded quartzitic sandstones with marine shells and plant fossils indicating a Late Palaeocene age (MAKULBEKOV 1977). They represent delta channel or point bar facies. Local silification of the Kamyshin sandstones is thought to be due to hydrothermal activity responsible for quartzitic dykes traversing the Palaeocene sedimentary strata. The leaves make beautiful impressions on the hard sandstone and, since the 1860's they have been widely known as Kamyshin oaks (EICHWALD 1865–1868, PALIBIN 1903, KRASNOV 1910, and references in KOLAKOVSKY 1965 and MAKULBEKOV 1977) though some authors have suggested a closer affinity with *Castanopsis* than *Quercus* (e. g. JÄHNICHEN 1956).

KOLAKOVSKY (1965) has rejected both these assignments (as well as *Castanea* and *Dryophyllum*) on the basis of the basiscopically branched basal secondary veins with regularly looping branches and forking superjacent secondaries – “betuloid” features typically lacking (though occasionally and irregularly developed) in the Fagaceae. He erected a new genus *Ushia* diagnosed as having ovate or elongate-ovate leaves with rounded, cuneate or cordate base, proximally entire or occasionally serrate. The marginal teeth are typically of a single order, some of them bearing a secondary serration. The venation is prominent, with 8–14 pairs of secondary veins of which the basal ones have looping branches which occasionally enter the marginal teeth. In his opinion, all the records of “Kamyshin oaks” from western Europe (e. g. UNGER 1867) might be incorrectly assigned to *Ushia*.



Text-fig. 1. Localities of *Ushia* in the Lower Volga and western Kazakhstan: 1 – Ushi Hill, 2 – Romankol, 3 – Tykbutak, 4 – Karakol, 5 – Ekibastuz.

MAKULBEKOV (1977) has assessed morphological variation of *Ushia* using material from several new localities representing the same floristic horizon (Text-fig. 1) and compared it not only to the genera of Fagaceae, but also to *Alnus*, *Alnaster* and *Viburnum* having superficially similar leaf morphologies, but differing in details of marginal characters and venation. Recently BOULTER & KVAČEK (1989) and KVAČEK et al. (1994) have erected a new combination *Ushia olafsenii* (for *Quercus olafsenii* HEER) synonymizing with it a number of species previously assigned to *Quercus*, *Alnus*, *Betula*, *Hamamelis*, *Platanus*, *Grewiopsis*, etc. Thus, *Ushia*, a locally abundant midlatitude angiosperm genus, was raised to the status of a major dominant plant of the high latitude Palaeocene floras. Because of this, if not for other reasons, a revision of the type material is of some international interest. In the course of revision we revealed certain features in common with both lower hamamelids and *Nothofagus*, henceforth giving *Ushia* a special place in the phylogeny of Fagaceae.

Our descriptive terminology is traditional with the exception of, first, “submarginal vein” – a continuous or interminuent vein running along the margin but not entering the teeth (thus different from the fimbrial or intramarginal vein) and, second, “intrabasal vein” – a vein confined to the area proximal to the basal vein (“suprabasal” is avoided as ambiguous).

## 2. Leaf morphology

In the type species, *Ushia kamyschinensis* (GOEPPERT) KOLAKOVSKY the leaves are petiolate, with petioles about 15 mm long (about one seventh of the blade length), slightly thickened and curved at the point of attachment. The leaf blade is lanceolate to ovate, with the maximum breadth in the lower third or, less frequently, near the middle and with long or, less typically (in about 25 % of the type locality sample) short attenuate apex (Plate 1, Figs. 1-3; see additional illustrations in MAKULBEKOV 1977). Contrary to the original diagnosis (KOLAKOVSKY 1965), the leaf base is never rounded or cordate, but is broadly cuneate, asymmetrical, one half of the blade decurrent, the opposite one abruptly ending or even truncated up to 5 mm higher on the midrib (Plate 2, Fig. 5). The leaf dimensions are highly variable, from 3.7 mm long, 1.7 mm broad to 15 mm long, 7 mm broad, typically about 12.5×6.5 mm.

The leaf margin is entire in the proximal quarter of the blade, biserrate in the next quarter with two to one additional serrations per first rank tooth, simply serrate in the distal half. Deviations from this typical pattern include occasional leaves with the second rank serrations extending above the midlength of the blade or developed on a few proximal teeth alone. In the latter case the serration approaches a conventional fagaceous pattern. The teeth are nonglandular, acute, upcurved, acroscopically concave, basiscopically convex, of a variable prominence but never rounded or crenate (some retouched photographs, e. g. in KOLAKOVSKY 1965, Plate 12, Figs. 1-3 give a wrong impression of highly irregular, partly crenate teeth). The sinuses are sigmoid, neatly curved.

The venation is pinnate, prominent, typically brochidodromous to semicraspedodromous in the basal vein area, craspedodromous above. The midrib is stout, straight or slightly bent, basally as thick as the petiole, gradually attenuating to the apex but still thicker than secondary veins. The latter, 12 pairs, alternate, occasionally subopposite, arising at a uniform angle of about 45°, straight or slightly arched towards the apex, parallel or slightly divergent, regularly spaced, entering marginal teeth medially, abruptly upcurved at the tooth point. Intersecondary veins are lacking. The proximal secondaries have basiscopic branches while the distal secondaries appear unbranched. There is a more or less distinct gradient of distalward decreasing branching.

The secondary veins and their branches terminate in the marginal serrations except in the basal area. The basal secondaries produce five to six branches starting from the base. Their basal branch diverges at a very acute angle nearly parallel to the margin. In a few leaves this branch is given off directly from the midrib appearing as a weak intrabasal vein (Plate 1, Fig. 1, right side of the leaf). This feature, when present, is asymmetrically developed on one side of the midrib alone. The rest of the basal vein branches arise at a more open angle, arch along the margin and loop with superjacent branches or, the one or two distal ones, enter marginal teeth after forking or directly. In the rest of the proximal secondaries the basiscopic branches are normally produced in the distal part and are craspedodromous. Typically they decrease from three in the second pair of secondaries to one in the fourth or fifth pair, but the number of branches is variable as well as the number of branched secondaries. The latter can be different in the opposite halves of the same lamina adding to the leaf asymmetry otherwise evident in the basal shape alone.

A major deviation from the above pattern occurs with the second proximal pair of secondary veins rising high in the blade, diverging at a more acute angle, supplying a larger area and even having more basiscopic branches than the basal pair (Plate 2, Fig. 5). They fork at various distance from the margin and occasionally produce looping branches. The excessive development of the second pair of secondary branches, resulting from disruption of the branching gradient, may or may not correlate with the branching frequency in superjacent veins. In the latter a basiscopic branch may loop with the opposite tertiary vein forming an angular connection with the antecedent secondary vein. Such joints are regularly produced near the margin resulting in a stepwise ascending submarginal vein bordering the sinuses while avoiding the teeth (Text-fig. 2). The fimbrial vein was observed in a few better preserved specimens. The tertiary veins are distinct, percurrent, arched between the midrib and secondaries, straight or slightly arched and subparallel between secondaries, opposite to subopposite on both sides of the latter, mostly unbranched, but about 10 to 25 % forking at acute angle. The frequencies of forking tertiaries seem to correlate with the branching frequencies in the secondary venation. We recognized five orders of venation

but the quaternary one is not uniformly developed. When distinct, it consists of irregular areoles, about four to five per intertertiary area (Plate 2, Fig. 8). The quinternary venation is more uniform, mostly orthogonal, with rectanguloid or polygonal areoles about 0.5 mm wide. The freely ending veinlets are lacking.

The morphotypes previously described as separate species (see MAKULBEKOV 1977) are within the range of variation of the type species except *Ushia alnophylla* (KRASNOV) MAKULBEKOV. This differs not only in the broad elliptical leaf blade and smaller falcate serrations but also in that the submarginal veins at least partially consist of distal acroscopic branches ascending from secondary veins before their entering the teeth (Plate 2, Fig. 9).

### 3. Cuticular structures

All the leaves are preserved as impressions lacking any compressed material. However some cuticular structures are preserved on silicate film which forms the impression. Insofar as the film reflects the interior cuticular relief, it is thought to have been impregnated beneath the cuticle along the decaying leaf tissue. We described this mode of preservation as “subcrustation” (KRASSILOV & MAKULBEKOV, in press). In SEM the subcrustation appears as a thin coat of amorphous material 5 µm thick overlying coarse sand grains about 0.1 mm wide. The smaller venation is reflected by several files of elongate rectanguloid costal cells with occasional stomata, bordering areoles with less distinctly marked intercostal cells and crowded stomata (Plate 3, Fig. 11; Plate 4, Fig. 19). The stomatal frequency varies from 640 to 720 per sq. mm. The stomata are cyclocytic with six to seven subsidiary cells irregularly oriented, often contiguous. The guard cells appear sunken in a rounded elliptical stomatal pit about 16–20 µm long. The stomatal pit borders are raised as a prominent ridge. The aperture is filled with silica. The guard cells are transversely striated, lacking T-shaped polar thickenings. The subsidiary cells show more or less prominent papillae (Plate 3, Figs. 13, 16).

In addition to the regular stomata there are sparse giant stomata occurring within the areoles adjacent to stomatal pits or even overlapping the latter (Plate 3, Figs. 11–14). Such arrangements suggest that the two types of stomata might have been under different spatial control. The giant stomata are elongate, about 45–50 µm long, not sunken, surrounded by two incomplete rings of radially aligned cells.

The trichomes are solitary, of three types: (1) small conical trichomes lacking modified surrounding cells (Plate 3, Fig. 12), (2) small trichomes with a thick knob-like foot cell surrounded by radially aligned cells (Plate 3, Fig. 12) and (3) large capitate, supposedly deciduous but occasionally intact, glandular trichomes, leaving scars of a central canal and concentrically arranged small cells (Plate 3, Fig. 15; Plate 4, Fig. 19). Of these the type (1) trichomes are the most frequent occurring both in the costal zones and areoles. The type (2) trichomes were found adjacent to stomata while the larger glands (type 3) are confined to stomata-free areas.

On the basis of the above morphological and cuticular observations we propose the following extended diagnosis of the genus:

#### Genus *Ushia* KOLAKOVSKY 1965

Type species: *Phyllites kamyschinensis* GOEPPERT in MURCHISON 1845, p. 502, Plate G, Fig. 1. *Ushia kamyschinensis* (GOEPPERT) KOLAKOVSKY 1965, p. 128, Plates 12, 13, and synonymy herein.

Emended diagnosis: Leaves medium-sized, petiolate with short petioles. Blade lanceolate or ovate, average length 12.5 cm, breadth 6.5 cm, base broadly cuneate, asymmetrical, apex pointed or attenuate. Margin entire in the proximal quarter of the blade, biserrate in the next quarter with two to one additional serrations per first rank tooth, simply serrate in the distal half, occasionally with the second rank serrations extending above the midlength of the blade or developed on a few proximal teeth alone. Teeth nonglandular, acute, upcurved, acroscopically concave, basiscopically convex, of variable prominence.

Venation pinnate, prominent, typically brochidodromous to semicraspedodromous in the basal vein area, craspedodromous above. Midrib stout, straight or slightly bent, basally as thick as the petiole, gradually attenuating to the apex but still thicker than secondary veins. The latter, 12 pairs, occasionally with a weak intrabasal vein on one side of the midrib, alternate, rarely subopposite, arising at a uniform angle of about 45°, straight or slightly arched towards the apex, parallel or slightly divergent, regularly spaced, entering marginal teeth medially, abruptly upcurved at the tooth point. Intersecondary veins lacking. Proximal secondaries with basiscopic branches decreasing distalwards from five-six in the basal pair of secondaries to one in the fourth or fifth pair, the distal ones unbranched. Branches of the basal veins and occasionally of the second pair arch along the margin and loop with superjacent branches or, the one or two distal ones, enter marginal teeth. In the rest of the secondaries angular submarginal joints are produced by the distal reflexed branchlets arising before the teeth and looping with the opposite tertiary vein. Tertiary veins distinct, percurrent, arched between the midrib and secondaries, straight or slightly arched and subparallel between secondaries, opposite to subopposite on both sides of the latter, mostly unbranched, some forking at an acute angle. Quaternary veins not uniformly developed, forming irregular areoles, about four to five per intertertiary area. Quinary venation more uniform, mostly orthogonal, with rectanguloid or polygonal areoles. Freely ending veinlets lacking.

In the lower cuticle, the last order areoles marked by costal cells, contain crowded stomata which are cyclocytic with six to seven subsidiary cells, irregularly oriented, often contiguous. Guard cells transversely striated, lacking T-shaped polar thickenings. Subsidiary cells with more or less prominent papillae. Sparse giant stomata occur adjacent to or even overlapping the smaller stomatal pits. Trichomes solitary, of three types: (1) small conical lacking modified surrounding cells, (2) small with a thick knob-like foot cell surrounded by radially aligned cells and (3) large capitate, supposedly glandular, leaving scars of a central canal and concentrically arranged small cells.

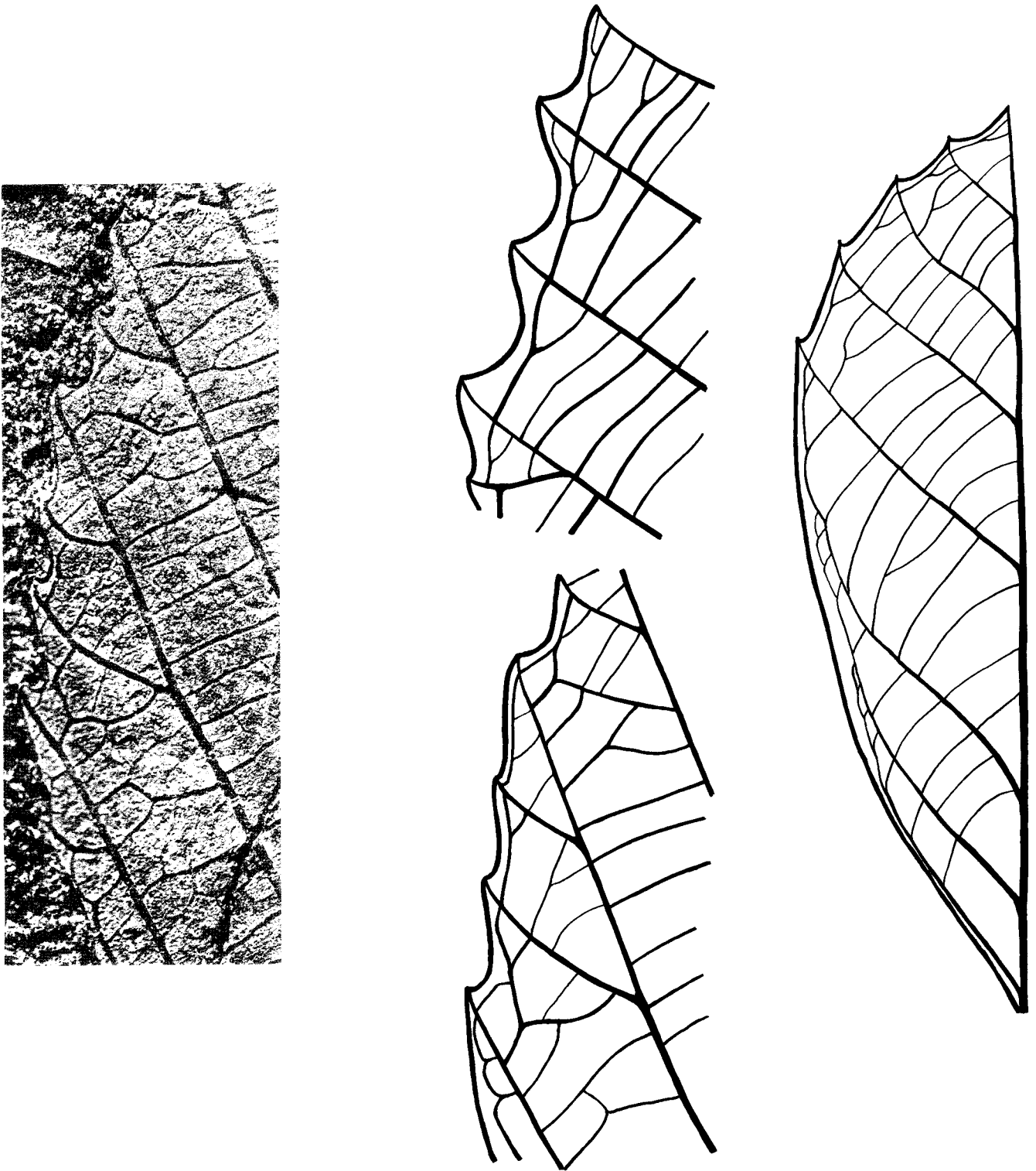
#### 4. Comparison

Comparisons with the extant northern hemisphere fagaceous genera were given in KOLAKOVSKY (1965) and MAKULBEKOV (1977). *Ushia* differs from all these as well as extinct genera, such as *Castaneophyllum* and *Berryophyllum* (JONES & DILCHER 1988) primarily in the regularly branched secondaries, looping basiscopic branches of the basal veins and partly biserrate margin. A submarginal vein avoiding the teeth is characteristic of *Castanea* and *Berryophyllum*, but in these genera it is thought to have been formed by the ascending acroscopic (apical) branches of secondary veins (JONES & DILCHER 1988). Our observations suggest a chimerical nature of the submarginal vein formed of the secondary vein distal branches looping with their opposite tertiary veins. In *Ushia* the basiscopic branch seems to have been a major contributor to the submarginal vein. There is no particular similarity in epidermal characters except that *Berryophyllum* has similar types of heteromorphic solitary trichomes.

At the same time, the large-leaved species of extant *Nothofagus*, such as *N. alessandri*, resemble *Ushia* in the leaf shapes, secondary venation and marginal characters (HILL & READ 1991). In this species secondary veins terminate in prominent serrations while their basiscopic branches enter smaller teeth, thus giving rise to two orders of serration. This marginal feature is associated with an incomplete fimbrial vein. The asymmetry of the leaf base is more pronounced in *N. obliqua* and *N. moorei* (Plate 1, Fig. 4) occasionally showing also a weak intramarginal vein beneath the basal secondaries. Characteristically, some species with crenate leaves have serrate juvenile leaves. The submarginal vein is fairly distinct in, e. g., *N. cunninghamii* (HILL & READ 1991: Fig. 61). The cuticular similarities include giant stomata, trichome types (JONES 1986, HILL & READ 1991) and papillate subsidiary cells (in *N. obliqua*).

However, *Ushia* differs from any group of *Nothofagus* in the combination of diagnostic characters. Moreover, it resembles some lower hamamelids, notably *Parrotia*, *Fothergilla* and several species of *Hamamelis* not only in the general pattern of venation, but also in characteristic association of craspedodromous secondaries with looping basiscopic branches of the basal veins. In herbarium specimens of *Hamamelis virginiana* we observed an asymmetrically developed intrabasal vein which extends parallel to

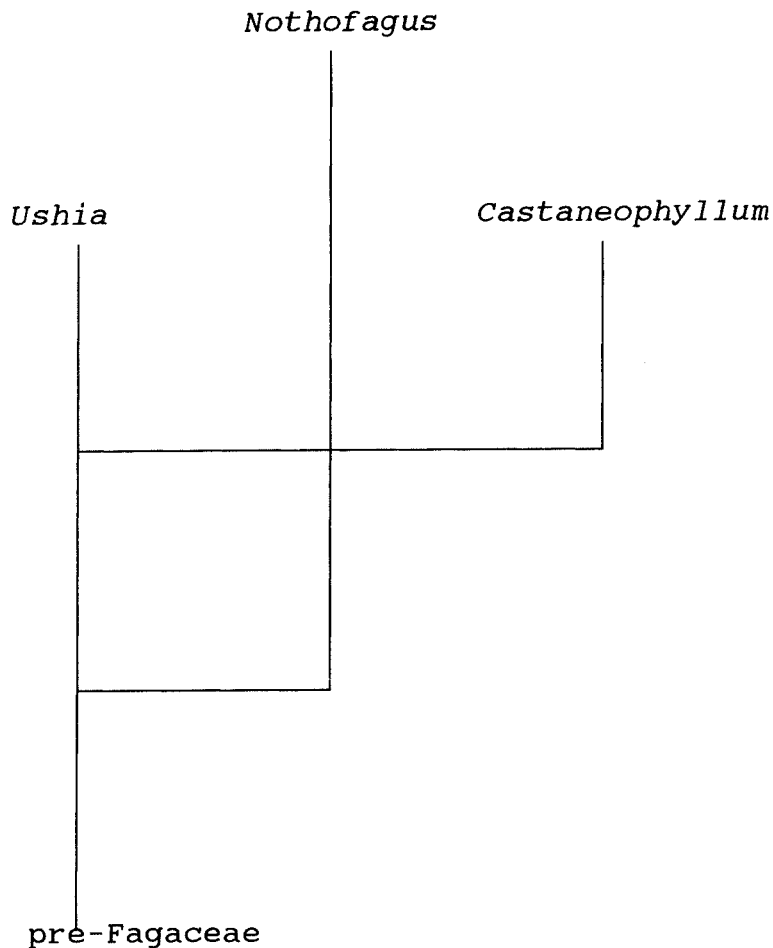
the leaf base and loops with the proximal branch of the basal vein. A submarginal vein similar to that of *Ushia* occurs in *Eustigma* (Text-fig. 2) while in *Sycopsis* and *Distylium* there are even stronger submarginal loops approaching a semicraspedodromous pattern.



Text-fig. 2. Marginal venation in *Ushia kamyschinensis*, middle part of a middle-sized leaf (left and middle) and extant *Eustigma* (right, drawn from a herbarium specimen).

## 5. Associated fruiting structures

In the type locality as well as in Romancol *Ushia* is associated with peculiar fruit-like structures described by TRAUTSCHOLD (1875) as *Oxycarpia bifaria*, a monotypic fossil genus initially compared to fagaceous cupules but subsequently considered as a seed or fruit *incertae sedis* (KRYSHTOFOVICH 1934, MAKULBEKOV 1977). *Oxycarpia* is a common fossil in both localities containing no other types of reproductive material. It is preserved as solid casts which can be easily detached from the rock matrix. The casts are rhomboid to ovate or obovate, 24–41 mm long, 23–34 mm broad, with a shallow cup-like structure at the base (Plate 2, Fig. 7; Plate 4, Figs. 17, 18). The distal part of the body is wedge-shaped in side view, attenuating to a bluntly pointed or notched apex. The cup-like structure shows a prominent median keel interrupted by the elliptical scar of a stout peduncle which is partly preserved in a few specimens. At the brim of the cup-like structure there are prominent scars of glandular trichomes. The wedge-shaped part shows longitudinal striation converging to the apex. The striae are punctuated by deep pits evidently representing trichome bases (Plate 4, Fig. 18).



Text-fig. 3. Hypothetical relationships of the Palaeocene genus to the northern and southern Fagaceae showing *Ushia* as a termination of a conservative line close to hypothetical ancestral forms of which a slightly divergent *Nothofagus* lineage and then a more divergent *Castaneophyllum* lineage branch off at successive chronological levels.

In our interpretation *Oxycarpia* is a cast of a massive bivalved cupule with the valves appressed to one another, perhaps woody in the basal part, membraneous at the apex, densely pubescent and bearing glandular lamellae at the base. The apical notch might have been left by a deciduous distal lamella. Comparable cupular structures are known in the extant *Nothofagus* species from New Caledonia and New Guinea and the closely related fossil species from Tasmania (HILL & READ 1991, HILL 1991). They have comparatively large bivalved cupules with woody non-gaping valves which can be sessile but in the fossil species are mostly pedunculate. In these species, however, the lamellae are persistent and non-glandular and the cupules are glabrous at maturity. Large trichomes and glandular lamellae are more characteristic of the species with four-valved cupules.

## 6. Conclusion

Our revision of leaf architecture in *Ushia*, a Palaeocene leaf genus from the Lower Volga and western Kazakhstan, has supported its assignment to the Fagaceae. However, in such characters as the regular, distalward diminishing branching of the secondaries giving rise to at least two orders of serration, *Ushia* is closer to *Nothofagus* than to any of the northern genera. The similarity extends to details of venation and cuticular structures preserved on subcrustations – mineral films impregnated beneath the cuticle of decaying leaves during fossilization. The associated fruit-like fossils, *Oxycarpia bifaria*, are interpreted as bivalved cupules resembling those of some extant and fossil *Nothofagus* species. The Kamyshin leaves combine diagnostic features of several deciduous and evergreen species groups of extant *Nothofagus*. A wide range of leaf sizes in the type locality suggests deciduous habit. This, however, is yet to be confirmed by special taphonomic studies.

At the same time *Ushia* shares certain morphological characters, notably the leaf blade asymmetry including a one-sided intrabasal vein, looping branches of the basal veins and their excessively developed superjacent pair of secondaries off-setting the branching gradient, with several genera of Hamamelidaceae. This latter family includes the examples of mixed brochidodromous – craspedodromous venation and transition from a weakly defined submarginal vein joining craspedodromous secondaries to a fully developed semicraspedodromous pattern. Similarly, *Ushia* illustrates an intermediate state from which both the simple craspedodromous venation of the northern Fagaceae and the branched semicraspedodromous pattern characteristic of *Nothofagus* might have been derived. It is considered to have been a little modified plesiomorphic descendant of the ancestral stock giving rise to the both northern and southern Fagaceae. Its putative phylogenetic position is schematically depicted in Text-fig. 3.

*Ushia* might have survived in the ecotone between the broad-leaved deciduous and evergreen laurophyllous forests achieving a dominant status at least in some local delta plain woody plant communities. It is not recommended to assign to this genus superficially similar leaves from Arctic localities unless the details of leaf architecture and cuticular structures match those of the type species. On cuticular evidence, certain *Ushia*-like morphotypes belong in Hamamelidaceae or Platanaceae rather than Fagaceae (KRASSILOV 1979). This morphological group needs a thorough taxonomic revision.

## 7. Acknowledgements

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## 9. Explanation of plates

### Plate 1

- Figs. 1–3. *Ushia kamyschinensis*, leaf shapes, that in Fig. 1 showing a one-sided intrabasal vein to the right of the midrib, 1×.
- Fig. 4. *Nothofagus moorei*, extant, 3× (courtesy ROBERT S. HILL).

### Plate 2

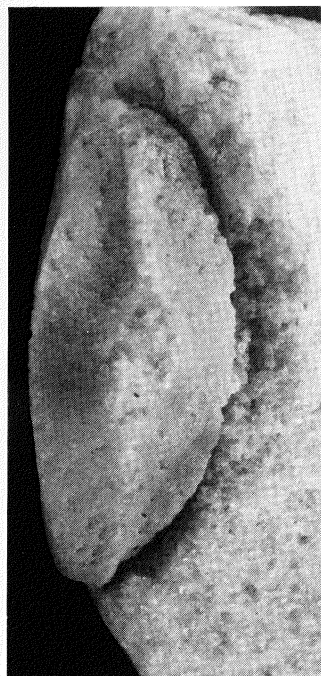
- Fig. 5. *Ushia kamyschinensis*, a strongly asymmetrical leaf base with the basal veins weaker than their superjacent veins, 1×.
- Fig. 6. *Ushia alnophylla*, 1×.
- Fig. 7. *Oxycarpia bifaria*, a reproductive structure associated with *Ushia* leaves, 1×.
- Fig. 8. *Ushia kamyschinensis*, leaf margin and venation, 5×.
- Figs. 9, 10. *Ushia alnophylla*, leaf margin and venation, 5×.

### Plate 3

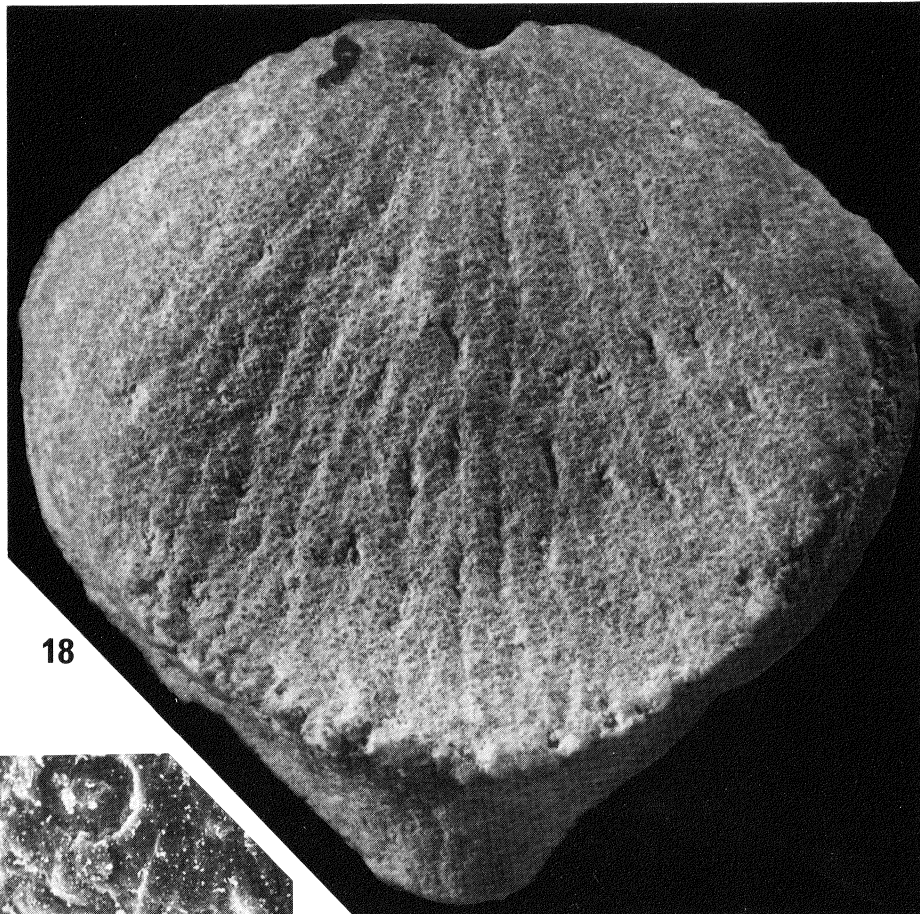
- Figs. 11–16. *Ushia kamyschinensis*, subcrustation showing cuticular structures, SEM.
- Fig. 11. Costal zone with few stomata bordering areole with closely packed stomata and a single giant stoma, 530×.
- Fig. 12. Close up of the areole showing a giant stoma, a trichome base with radially disposed surrounding cells (centre) and conical trichomes to the right, 1000×.
- Figs. 13, 14. Giant stomata onlapping the normal stomata, 2000×.
- Fig. 15. Base of a glandular trichome, 700×.
- Fig. 16. Stoma showing papillae on subsidiary cells, 2000×.

### Plate 4

- Fig. 17. *Oxycarpia bifaria*, basal view showing scar of peduncle, 2×.
- Fig. 18. *Oxycarpia bifaria*, side view, showing gland stumps and striation with pits of trichome bases, 4×.
- Figs. 19–20. *Ushia kamyschinensis*, cuticular topography showing costal zones and areoles with stomata, 400×.

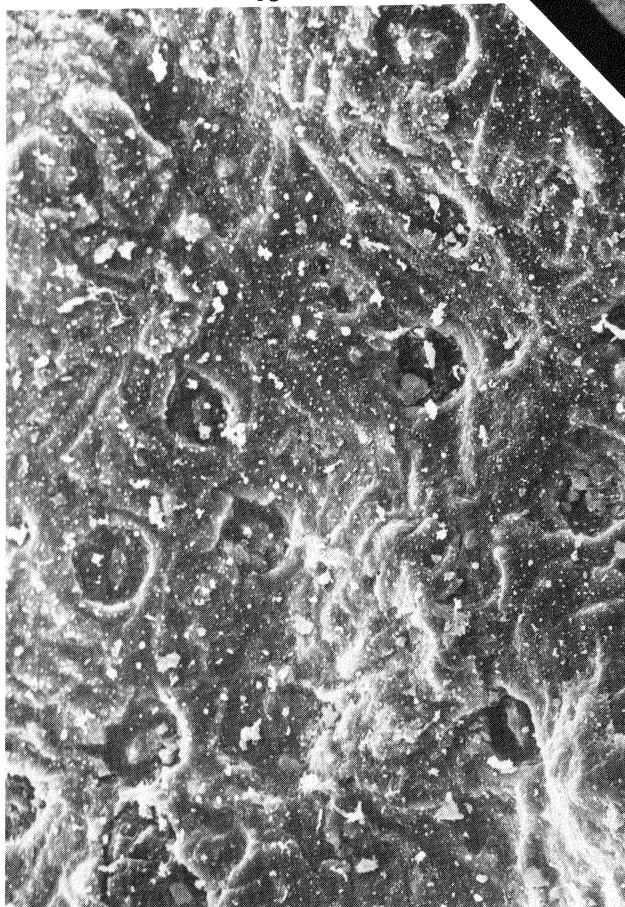


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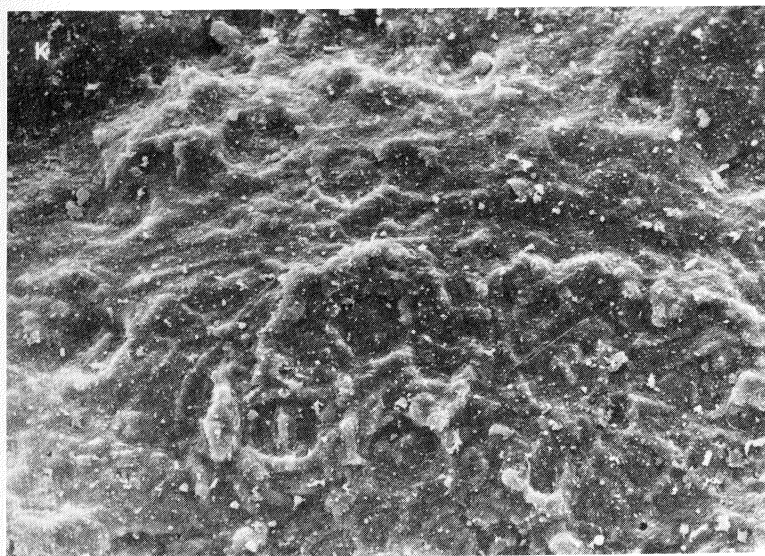


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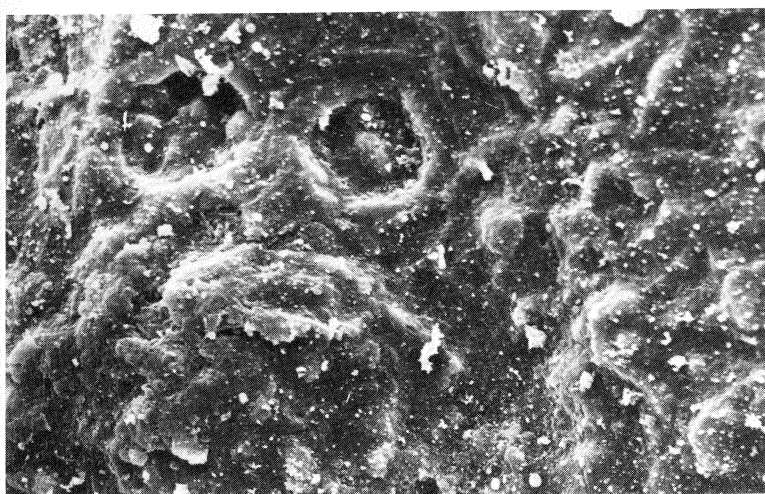
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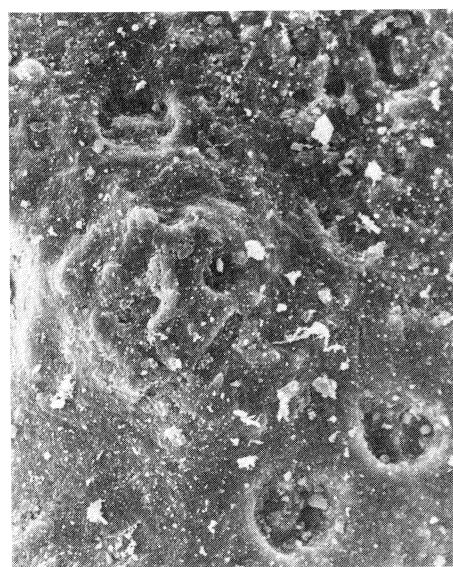
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