#### ACTA PALAEOBOTANICA XVI (1): 3-70, 1975

#### JANINA JENTYS-SZAFEROWA

# STUDIES ON THE EPIDERMIS OF RECENT AND FOSSIL FRUITS OF CARPINUS AND OSTRYA AND ITS SIGNIFICANCE IN THE SYSTEMATICS AND HISTORY OF THESE GENERA

Badania na skórką dzisiejszych i kopalnych owoców *Carpinus* i *Ostrya* oraz ich znaczenie dla systematyki i historii tych rodzajów

#### ABSTRACT

Part I of these studies on the epidermis of the fruits of Carpinus and Ostrya deals with recent fruits from the point of view of the structure of the perigone, i.e. the foliaceous covering of the hard nutlets, as the outer parts of this, the epidermis and the first layer of parenchyma, have cells with markedly cutinized walls, and show more features characteristic of the genera mentioned than were found when studying the stone-hard pericarp. Since this epidermis is preserved in fossil fruits, a method was devised for stripping it in order to make a detailed investigation of its characters both in transverse sections and in the picture as seen from above. A key for the determination of the genera and species was then prepared. In Part II the results of applying the epidermal method to the determination of fossil fruits are given, and some conclusions drawn from these studies in relation to the history and evolution of the species included in the genera Carpinus and Ostrya.

# PART I FRUITS OF RECENT SPECIES

#### CONTENTS

Introduction		•	• 1									4
Anatomical studies of perigones .					•							5
A. Transverse sections of perigones												6
verse sections of the perigones .												11
Perigones seen from above						•						12
	Anatomical studies of perigones  A. Transverse sections of perigones  B. Key to the determination of the ger verse sections of the perigones.	Anatomical studies of perigones A. Transverse sections of perigones . B. Key to the determination of the genera verse sections of the perigones	Anatomical studies of perigones A. Transverse sections of perigones B. Key to the determination of the genera Carverse sections of the perigones	Anatomical studies of perigones A. Transverse sections of perigones	Anatomical studies of perigones	Introduction Anatomical studies of perigones A. Transverse sections of perigones B. Key to the determination of the genera Carpinus and Ostrya from transverse sections of the perigones Perigones seen from above						

	A. General characterization and method of work	12
	B. Detailed studies	15
4.	Description	16
	I. Differences between the genera Carpinus and Ostrya	16
	A. Genus Carpinus	17
	B. Genus Ostrya	21
	II. Dimensions and shape of the cells of the epidermis and first parenchy-	
	mal layer	22
	III Mensural results	30

#### 1. INTRODUCTION

In palaeobotany, the systematic determination of fossil plants on the basis of their epidermal structure has hitherto been used almost solely for studies of the shoots and leaves. The markedly cutinized epidermal cellwall, or the cuticle itself, is preserved in the remains of even very old fossil plants. The author has not found any information in palaeobotanical literature on the application of the epidermal method for determining the systematic appurtenance of fossil fruits. She was also surprised to discover that in carbonized and flattened hornbeam nutlets from the Tertiary, which are sometimes only a few millimetres in lenght, the epidermis of the external non-lignified part, i.e. the perigone, is often preserved. Studies on the epidermis of the perigone and the layer of parenchyma lying immediately below it in recent species of Carpinus and Ostrya brought a still greater surprise, as it proved that more characters for the differentiation of these genera and the species composing them could be found in their structure than by studying the morphology and anatomy of the lignified part of the fruits, i.e. the pericarp.

In 1953 the author, jointly with dr M. Białobrzeska, published a paper, "Owoce rodzajów Carpinus i Ostrya. Cz. I. Analiza cech i klucze do oznaczania" (Fruits of the genera Carpinus and Ostrya. Part I, Analysis of characters and classification keys). The purpose of this study was to discover the morphological and anatomical characters differentiating these genera and the species composing them, so that it would be possible to determine the fossil fruits on this basis. It was the reason that this treatise was included in the publications of the Institute of Geology in the series: "Research on the Tertiary flores". The studies on the fossil fruits of the genera Carpinus and Ostrya were to be published as Part II of this treatise, but it so happened that the results of the morphological and anatomical studies on the fossil fruits of the genus Carpinus in Poland appeared not in the publications of the Institute of Geology but in "Acta Palaeobotanica" in 1960 and 1961.

The author has now returned to the task which she set herself in

1953: a search for bases for the determination of fossil fruits belonging to the genera *Carpinus* and *Ostrya*. At that time the perigones of these fruits were rather neglected, reporting some characters of their structure more in order to supplement the information on the genera *Carpinus* and *Ostrya* than in the hope that they might be of use in palaeobotanical research. From a superficial observation of fossil fruits of these genera it was assumed that the only remains of the perigone, i.e. the foliaceous covering of the nutlet, are the adherent longitudinal ribs containing the vascular bundles. It was also assumed that only the number of these ribs can to a certain extent give evidence of the species.

When studying the anatomy of fossil nutlets immeresed in 8 per cent celloidin, it was found that in transversal sections the celloidin became detached from the hardened perigone of the nutlets, but there were almost always crushed layers of thin-walled cells on the inner side of these loosened rings. In some places these small layers broadened out and surrounded formations which on careful examination turned out to be transversal sections through vascular bundles. They were the remains of horn-beam fruit perigones becoming detached from the hard pericarp. This phenomenon was so common that it induced more careful investigation. First of all the anatomical structure of perigones of representatives of the recent species of *Carpinus* and *Ostrya* was repeatedly examined in order to discover what differences there are between them

#### 2. ANATOMICAL STUDIES OF PERIGONES

As already reported in 1953, it is extremely difficult to make a transverse section of a mature fruit in such a way that the thin-walled perigone and the stone-hard pericarp are both cut at the same time. This was successfully done only on young nutlets with a weakly lignified pericarp. These studies were now repeated, taking even more pains, in the hope that indications helping to elucidate some of the problems of the history and evolution of the hornbeam in Europe would be obtained by investigating the structure of its perigone. These questions had not been fully answered by investigations on the pericarp.

The present treatise is in two parts. Part I follows on the publication of 1953 and includes a study, more careful than the former, of the structure of the perigone in species of *Carpinus* and *Ostrya* now existent. Special attention has been given to the epidermis as seen from above. Part II includes an elaboration of the fossil fruits of these genera from the point of view of the structure of the epidermis of their perigones and the first layer of parenchymal cells lying immediately under the epidermis. The materials previously examined from the point of view of

the anatomy and morphology of the pericarp were analysed again and new materials were added, this time concentrating on the extant remains of the perigone. This has led to the elucidation of a number of questions to which no answer could be found previously.

#### A. TRANSVERSE SECTIONS OF PERIGONES

The results of studies of transverse sections of perigones of recent species of Carpinus and Ostrya confirmed the descriptions of their structure given in the treatise published in 1953 and supplemented them in certain details. Better sections were obtained, on the basis of which the author's co-workers dr M. Białobrzeska and dr J. Truchanowiczówna were able to draw more detailed illustrations than in 1953. Dr Białobrzeska's drawings, shown in Text-figs. 1 and 2, were made by means of an Abbe's drawing apparatus, and give a good impression of the differences between the perigones of the species studied. They supplement the drawings of the hornbeam pericarps in Text-fig. 11 and 12 of the 1953 treatise and Text-figs. 1 and 2 of the 1961 treatise. Truchanowiczówna experienced great difficulty in making the photographs, since the cross-sections prepared by the author were not always suitable for the purpose. None the less they confirm the pictures presented in the figures, and so these fragments have also been included in Plate I. Cordial thanks are due to both my co-workers for the help they have given me and for the trouble they have taken.

The descriptions of the perigones of *Carpinus* and *Ostrya* published in 1953 were confined to short characterizations in the general descriptions of the fruits of the eight main recent species of hornbeam and of three species of the genus *Ostrya*, and to the key by which it was possible to determine the species to which the recent fruits belonged on the basis of anatomical cross-sections of their perigones. A more accurate description of the structure of the perigone in the species studied is now given. These descriptions are important in the determination of fossil materials, since — as will be shown further — they facilitate the understanding of the structure of the epidermis and the layers beneath it. Since it was not possible to perceive characters which might serve as a basis for the differentiation of the genera *Carpinus* and *Ostrya*, only descriptions of cross-sections of species within the two genera have been given, with a common artificial key to their determination at the end.

All the transverse sections of the perigones were made at the broadest part of the nutlet, and were drawn under the same magnification (Text-figs. 1 and 2). In the descriptions of the perigones the resin glands have been omitted, since they appear mainly in the upper part of the nutlets and were not found in any of the cross-sections. These glands are not preserved in fossil material.

### Genus Carpinus (Text fig 1; Pl. I)

### Section Eucarpinus Sargent

#### 1. Carpinus betulus L.

Roundish epidermal cells with evenly thickened walls, markedly smaller than the thin-walled parenchymal cells. Thin cuticle, scarcely visible. Hairs on the epidermis considerably shorter than the diameter of the vascular bundle, few or densely distributed. Up to 7 rows of parenchymal cells between the bundles and 14 in the vicinity of the bundles. Rather round, rarely elliptical bundles, 5—12 (8) in number, lying in the centre of the perigone. Numerous small vessels, with more or less the same dimensions as the epidermal cells; 2—5 rows of thin-walled cells between the epidermis and the bundle.

#### 2. Carpinus caroliniana Walt.

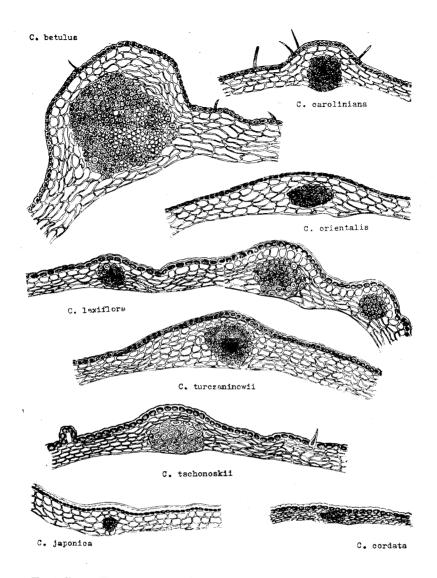
Epidermal cells small, round, with a distinct cuticle. Numerous single-cell hairs, more or less corresponding in length to the diameter of the bundles. Perigone narrow between bundles, composed of 4, seldom 6, rows of large thin-walled cells. Bundles 6—11 (8) in number, round, rarely elliptical, situated near the inner part of the perigone. Cross-sections of the vessels correspond to the dimensions of the epidermal cells. Between the bundle and the epidermis, 2—4 rows of parenchymal cells.

# 3. Carpinus orientalis Mill.

Small oval epidermal cells, with weakly formed cuticles, seldom developing hairs. Thin-walled parenchymal cells located in 4—6 rows between the bundles. Perigone slightly enlarged at the site of the bundle. Bundles, 6—11 (8) in number, elongated elliptically in cross-section, situated nearer the inner margin of the perigone than the epidermis; in cross-section, bundles more or less the same size as the epidermal cells. Between the bundle and the epidermis, 2—3 rows of parenchymal cells.

# 4. Carpinus laxiflora (Sieb. et Zucc.) Blume

Perigone very characteristic in cross-section. Epidermal cells small, roundish or oval with a semicircular thickened wall with a protruding apex having a distinct cuticle. Under the epidermis, one row of



Text-fig. 1. Transverse section through perigone; genus *Carpinus* Ryc. 1. Przekroje poprzeczne przez perigony rodzaju *Carpinus* 

considerably larger parenchymal cells, round or sligthly oval; under these, 5—6 rows of thin-walled cells, usually flattened. Round bundles, 7—11 (9) in number, occupying almost the whole width of the perigone. Between the epidermis and the bundle, 1 row of cells. Vessels in cross-section correspond in size to the epidermal cells. The perigone usually becomes detached when cutting through the 2—3 layers of parenchymal cells, showing the delicacy of the walls of these cells.

#### 5. Carpinus turczaninowii Hance

Perigone composed of about 6 rows of cells more or less the same in size and slightly smaller epidermal cells with markedly thickened outer walls having a cuticle and thin transversal walls. Round or slightly elliptical bundles, 7—12 (9—10) in number, with numerous vessels mainly accumulated in the inner part of the bundle and more or less the same size as the epidermal cells. The bundle is separated from the epidermis by only one or two layers of parenchymal cells.

#### 6. Carpinus tschonoskii Maxim.

Large epidermal cells, the largest that appear in the species of horn-beam studied, are a characteristic feature of transverse sections of the perigone. These cells have a thickened wall, with a distinct cuticle. Hairs sprout from them, few in the broadest part of the nutlet, more abundant approaching the apex. Columnar appendages, usually ending in a narrow stoma, are also found on the surface of the perigone. Next to the bundles the perigone is composed of 6—8 rows of thin-walled cells of uniform dimensions. Between the bundles the rows of cells diminish in number. Bundles 8—13 (10) in number, roundish, elliptical or spherical. Few but comparatively large vessels, more or less the same size as the epidermal cells. Between the epidermis and the bundle, 2—3 rows of parenchymal cells.

# Section Distegocarpus (Sieb. et Zucc.) Sargent

# 7. Carpinus cordata Blume

Epidermal cells oval with a distinct cuticle and markedly thickened outer cell-wall. Under epidermis, 5—7 rows of similar thin-walled cells, more or less rectangular, markedly elongated. Bundles 8—13 (10) in number, flat, elongated. Vessels in cross-section smaller than epidermal cells. Between epidermis and bundle, 2—3 rows of parenchymal cells. Perigone only very slightly enlarged at site of bundle.

# 8. Carpinus japonica Blume

A typical character of nutlets of this species is a perigone as broad as and sometimes broader than the pericarp. As for the anatomical characters of the perigone itself, striking are the roundish thick-walled epidermal cells in the upper part with a distinct cuticle, a comparatively

narrow (4—5 rows) parenchymal layer, and very small round bundles, so that the perigone is only very slightly enlarged at the site of these. Bundles usually about 11 in number, situated in the central part of the perigone.

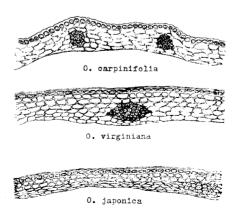
# Genus Ostrya Scop. (Text-fig. 2; Pl. I)

### 1. Ostrya carpinofolia Scop.

Small roundish epidermal cells with walls markedly thickened, especially in the inner part, without any distinct cuticle. Under epidermis, 6—7 rows of much larger elongated thin-walled parenchymal cells. Bundles, 6—10 (8) in number, small, round, about half as broad as the perigone, lying in the centre. Between bundle and epidermis, 2—3 rows of cells. Vessels in cross-section smaller than the epidermal cells.

### 2. Ostrya virginiana (Mill.) K. Koch

Perigone composed of thick-walled epidermis with a distinct cuticle and of 6—7 (8—9) rows of somewhat larger rectangular cells with gradually attenuated walls. The epidermal cells do not clearly differ in dimensions from the cells of the underlying parenchyma. Between epidermis and bundle, 2—3 rows of cells. Bundle elliptical or fusiform, markedly elongated. The perigone is not enlarged at the site of the bundle. Vessels smaller than the epidermal cells.



Text-fig. 2. Transverse section through perigone; genus Ostrya Ryc. 2. Przekroje poprzeczne przez perigony rodzaju Ostrya

# 3. Ostrya japonica Sargent

Perigone composed of epidermis and 6—7 rows of cells, of which the 2—3 rows underlying the epidermis resemble it in size and the thickness of their walls. Distinct cuticle on epidermis. Bundles markedly elongated. Between epidermis and bundle, 2 rows of thick-walled cells. Cells under bundle are thin-walled, much flattened, and so give the impression that the bundle lies not in the centre but in the lower part of the perigone. Vessels differ little in size from the peridermal and parenchymal cells, so that the bundle is not clearly distinguished from the rest of the perigone.

In 1953 two keys were prepared, one to the determination of species of the genus *Carpinus* on the basis of transverse sections of the perigone and a second analogous key to the determination of species of the genus *Ostrya*. As has already been said, it was difficult to find specific characters differentiating the perigones of these two genera. A common key was therefore prepared, on the basis of which the species both of the genus *Carpinus* and the genus *Ostrya* might be determined.

# B. KEY TO THE DETERMINATION OF THE GENERA CARPINUS AND OSTRYA FROM TRANSVERSE SECTIONS OF THE PERIGONES

1.	Epidermal cells show no distinct difference from the underlying parenchymal cells. Bundles elliptical, markedly elongated.
	Perigone not enlarged at site of bundle
1.	
	wall from the underlying parenchymal cells
2.	Vessels smaller in cross-section than epidermal cells
	Ostrya virginiana
2.	Vessels not smaller in cross-section than epidermal cells
	Ostrya japonica
3.	Bundles always elliptical in cross-section
3.	Bundles round, seldom elliptical in cross-section 5
4.	Epidermal cells oval, differing both in size and in the thickening
	of the external part of the wall from the rectangular, often flat-
	tened parenchymal cells. Distinct cuticle
	Carpinus cordata
4.	Epidermal cells much smaller than the parenchymal cells but do
	not differ from these in shape or thickness of wall. Delicate
	cuticle, scarcely evident
5.	the period of th
	diameter 6
5.	Bundles markedly larger in diameter than half the breadth of the
	perigone

6.	Wall of epidermal cells markedly thickened on external aspect, with a hemispherical protrusion, often broader than the lumen of	
0	the cell, distinct cuticle	
ь.	Wall of epidermal cells evenly thickened, narrower than cell-	
	-lumen, delicate scarcely visible cuticle Ostrya carpinifolia	
7.	Under epidermis, a row of large round thin-walled cells, easily	
	distinguished from the other cells of the perigone	
	Carpinus laxiflora	
7.	Under epidermis, no row of large round cells distinctly differing	
	from the other parenchymal cells	8
8.	Large epidermal cells with markedly thickened walls and	
	distinct cuticle, protruding from the surface so that the edge of	
	the cross-section is indentated	
8.		9
9.	· · · · · · · · · · · · · · · · · · ·	9
θ.	per en pe	
	often longer than the diameter of the bundles	
_		
9.	Bundle situated in central part of perigone, hairs (if any) very	
	short	10
10.	Epidermal cells many times smaller than parenchymal cells.	
	Perigone markedly swollen at site of bundle, where rows of	
	parenchymal cells may reach 14 in number Carpinus betulus	
10.		
	chymal cells do not exceed 7 in number	

#### 3. PERIGONES SEEN FROM ABOVE

#### A. GENERAL CHARACTERIZATION AND METHOD OF WORK

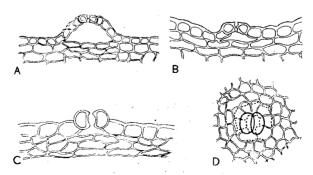
Next, after learning the anatomical structure of the perigone from transverse sections, came the preparation of specimens on which the epidermis and the underlying parenchymal layer could be observed from above.

Various methods of investigation were tried. An attempt to detach the cuticle itself by the acetolysis method, however, proved to be particularly futile. Although it was possible to observe the outlines of the epidermal cells on the cuticles and gain an idea of their size, the structure of their walls could not be detected, and still less that of the underlying parenchymal layer, of which the characters are of diagnostic importance for species within the genera *Carpinus* and *Ostrya*. Two lines of procedure were

therefore followed. One method was to boil the nutlets in water with soda in order to soften the perigone. The outer layer was then stripped off in such a way as to separate the thinnest possible shreds. It was then possible to observe the unchanged surface of the perigone, and so also both the hairs often covering its surface and the margins of its leaflets as well as the resin glands and crystals of calcium oxalate contained in the epidermal cells. It was, however, difficult to observe the structure of the walls of the perigone cells, especially since the cells are not translucent unless emptied of their contents.

A better idea of the structure of the epidermis and parenchyma of the pericarp was given by the method used by M. Was when preparing specimens of some Pliocene materials from Mizerna for Prof. W. Szafer (1954). This method, adapted to hornbeam fruits, gave excellent results. It consisted in boiling the nutlet in a test-tube for about 5 min in a small amount of water in which a crystal of soda (Na<sub>2</sub>Co<sub>3</sub>) had been dissolved. After quickly pouring off the water (but leaving a little liquid at the bottom), a few drops of perhydrol (H<sub>2</sub>O<sub>2</sub>) were introduced into the test-tube and heated for some time. This induced an initial slight effervescence, followed by a violent reaction shown in the energetic expulsion of gas bubbles. After some time the perigone began to crack and its external portion, usually composed of epidermis and the first layer of parenchyma, peeled off the fruit like a glove. At this moment the liquid together with the external pant of the perigone floating in it was quickly poured out of the test-tube into a vessel of cold water, as if prolonged the action of H<sub>0</sub>O<sub>9</sub> damaged the epidermis. The further procedure merely consisted in dextrously transferring the detached portion of the perigone on to a slide on which it could be stained and fixed with glycerogelatin or Canadian balsam. Sometimes the bundles were detached together with the external portion of the perigone, especially in fruits in which the walls of the parenchymal cells lying between the epidermis and the bundle were more resistant to the action of H<sub>2</sub>O<sub>2</sub>.

Sometimes the perigone broke into two or more pieces. When these



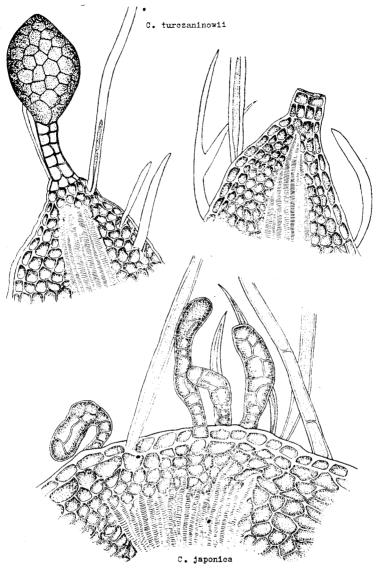
Text-fig. 3. Stomata of perigones; genus Carpinus Ryc. 3. Aparaty szparkowe perigonów rodzaju Carpinus

were placed on the slide one lying face up and the other face down, a good view could be obtained of the structure of the epidermis, the stomata, and the parenchymal cells underlying the epidermis. Usually only the resin glands often found on the surface of the fruit and the calcium oxalate crystals in the parenchymal cells were destroyed. These two elements, however, are not preserved in the fossil state. The pictures seen under the microscope on the external portion of the perigone removed from recent fruits were completely similar to those given by perigones removed from fossil fruits. The difference between them is that the stomata can be seen very easily on the epidermis of perigones stripped from recent fruits while they are seldom preserved in fossil fruits. The stomatal apparatuses of hornbeam perigones are raised above the surface, sometimes very slightly, but sometimes so high that the epidermis rises dome-like over the air-chamber found under the stoma (Text-fig. 3). Seen from above, this gives the impression that the stomatal cells lie on top of the epidermis. Since both the stomatal cells and often the subsidiary cells are thin-walled and their walls are neither lignified nor cutinized and do not stain with iodine green (they appear as white spots in stained specimens), it is not surprising that they undergo destruction during fossilization. The epidermal cells are grouped around the hairs in so characteristic a manner, however, that it is not difficult to determine where the hairs grew (Text-fig. 5, 16).

The epidermal cells are not uniform over the whole perigone. At the base of the nutlet they are narrow and considerably elongated, running in rows towards the bottom. On the surface of the leaflets surrounding the hard paricarp at the apex of the nutlet, they are as broad as they are long, often undulating, and usually thin-walled. Above the bundles, they sometimes become elongated. They vary little over the rest of the perigone, and so it was here that specific characters were sought for. The perigones of the genus *Ostrya* are similarly constructed.

The resin glands appear on the surface of the perigone, mainly on the upper part of the fruit. They are piriform and multicellular, sometimes markedly enlarged, so that when seen from above they appear peltate. In some species, e.g. C. japonica, clavate glands only slightly broadened at the ends are found on the edges of the leaflets. The glands in the species C. turczaninowii are very characteristically situated, as they lie at the apex of the leaflets of the perigone at the places where the bundles end (Text-fig. 4).

As the studies on the epidermis of perigones of the genera were to provide bases for the determination of their species in fossil material, the author observed those characters of the epidermis which could be seen both in living and in fossil fruits, and so attention was not paid to the greater or lesser tendency of particular species to form druses in the cells of the perigone or to the shape of the resin glands. On the other hand,



Text-fig. 4. Resin glands on perigone margins; genus Carpinus Ryc. 4. Gruczoły żywiczne na listkach perigonów rodzaju Carpinus

the shape and size of the epidermis and the first layer of parenchyma, the structure of their walls, the mode of distribution and the shape of the cells surrounding the hairs were carefully studied, taking the perigone of the medial portion of the nutlet as the principal basis.

#### B. DETAILED STUDIES

The detailed studies of the perigones seen from above form three parts which supplement one another: I. Descriptions of the external appearance and details of the structure of the cell-walls, with drawings and photographs; II. Measurements of the length and breadth of the cells of the epidermis and the first layer of parenchyma; III. The mutual relationship of these elements. In addition, the length of the stomatal cells was measured. All together this forms a sort of key to the determinations of fossil fruits.

The drawings of the perigones seen from above were made by dr M. Bialobrzeska from photographs supplementing her observations of microscopic specimens (Text-figs. 5, 6). The pictures seen on the photograph were each time divided into two in the drawings, i.e. the epidermis and the parenchymal cells lying immediately beneath it were drawn separately in each specimen. The photographs of the perigones were made by dr J. Tr u chanowiczówna.

#### 4. DESCRIPTIONS

#### I. DIFFERENCES BETWEEN THE GENERA CARPINUS AND OSTRYA

Although when characterizing the genera Carpinus and Ostrya on the basis of transverse sections through the perigones of their fruits no distinguishing features were found, when looking from above on the external portion of the perigones the genus can be determined without difficulty. In the genus Ostrya, the epidermal cell walls are evenly thickened and have many narrow pits, so that the walls of the cell are often wider than its lumen. In the genus Carpinus, the cell walls may be either thin or more or less thickened, but they are always considerably narrower than the cell lumina, while their pits are less numerous, broader, and often irregular, so that the cell-wall in cross-section sometimes appears optically as if dentate (Pl. II—IV).

In the genus *Carpinus* the cells of the first layer of parenchyma are considerably larger than the epidermal cells, though in length they seldom exceed twice their breadth. In the genus *Ostrya* the cells under the epidermis are not only larger than the epidermal cells but as a rule are many times longer than their breadth.

The following descriptions of perigones of the genera *Carpinus* and *Ostrya* refer to their appearance before and after treatment with a soda solution and oxygenated water. They also give a general characterization of the walls of the cells of the epidermis and of the layer of parenchyma lying immediately below the epidermis.

# A. Genus Carpinus (Text-fig. 5; Pl. II, III, V, VI)

# 1. Carpinus betulus L.

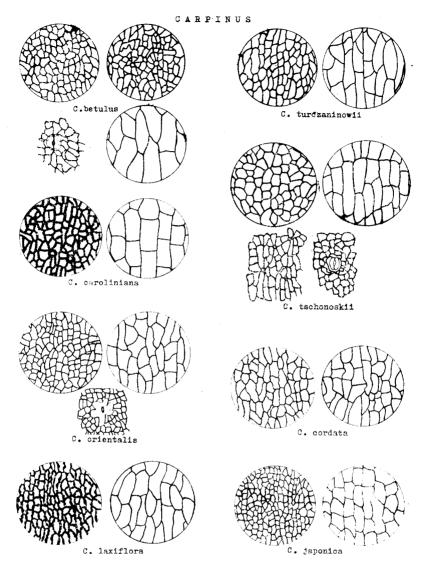
Surface of perigone glabrous or pilose. In the glabrous forms the epidermal cells have optically 3—6 sides, often unsymmetrical, usually slightly longer than broad in those parts of the perigone lying between the bundles, but above the bundles they are distinctly elongated in the direction in which these run. The cell wall is slightly thickened, with distinct pits. The stomata are mainly distributed at the ends of the leaflets of the perigone and along the bundles; they vary in number. The stomatal cells are raised slightly above the surface of the epidermis. Their walls, like those of the peristomatal cells, stain more weakly with iodine green than the other epidermal cells. At the ends of the leaflets of the perigone and on its surface, there are multicellular glands, which are not preserved in fossil material. The cells surrounding them do not differ from the other epidermal cells.

The hairs are unicellular and are found either at the ends of the perigone leaflets or covering the whole surface of the fruit except for the areas above the bundles, where they are sparser. Both these forms, the pilose and the glabrous or almost glabrous, appear in nature in the same populations in a ratio of  $\pm$  50 : 50%. The base of the hair is round, rarely elliptical, thin-walled, and markedly smaller than the cells surrounding it, which are longer than the other epidermal cells, and arranged in rays round the hair. The number of cells surrounding a hair is 5—9, most frequently 7. Seen from above they look like the petals of a ray-flower.

The cells of the parenchyma immediately underlying the epidermis are many times larger than the epidermal cells, irregular, often rhomboidal, elongated in the direction in which the bundles run, and are not arranged in rows. The thickness of their walls is like that of the epidermal cell walls, or slightly smaller, only they have not such distinct pits. One cell of the first layer of parenchyma most frequently corresponds to 7—9 cells of glabrous epidermis.

# 2. Carpinus caroliniana Walt.

The epidermal cells resemble those of *Carpinus betulus* in shape and size, but have much thicker walls. Many broad pits, hence in cross-section the cell-walls have a dentate appearance. The stomatal apparatuses resemble those in *Carpinus betulus*. The subsidiary cells are thick-walled and stain deeply with iodine green. All the perigones are densely pilose, and no glabrous form has been found. The hairs covering the whole surface of the perigone are longer and thicker than in *Carpinus betulus*.



Text-fig. 5. Cells of epidermis and underlying parenchyma of species belonging to the genus *Carpinus* 

Ryc. 5. Komórki epidermy i leżącej pod nią parenchymy gatunków należących do rodzaju *Carpinus* 

Their bases are also thick-walled, with pits. The cells surrounding the hairs are 5—9 but most often 7 in number, and show no distinct difference in shape or size from the epidermal cells. The glands resemble those in *C. betulus* and are similarly distributed. The parenchymal cells lying immediately beneath the epidermis are shorter than in *C. betulus*, often rectangular, sometimes as broad as they are long, and arranged in rows. These are characters by which the two species mentioned may be

easily distinguished. The walls of the parenchymal cells are thiner than those of the epidermal cells.

## 3. Carpinus orientalis Mill.

Perigone sparsely pilose only on the upper part of the fruit, though in the material studied a nutlet from China was found to have the whole surface covered with hairs. The epidermal cells are smaller than in the previously-mentioned species, thin-walled, without distinct pits, often undulating on the foliaceous terminations of the perigone. The first layer of parenchyma is composed of cells differing in shape and size, with walls sometimes thicker than those of the epidermal cells and distinct pits. The cells surrounding the hairs do not differ in shape or size from the epidermal cells in the vicinity, so that they do not stand out as clearly as in the species previously mentioned. They are usually 7—9 in number. The stomatal and subsidiary cells are remarkably thin-walled and do not stain with iodine green, so that they stand out from the stained epidermis as white patches on which it is difficult to observe the details of the walls of the individual cells.

# 4. Carpinus laxiflora (Sieb. et Zucc.) Blume

Epidermis with short hairs at the ends of the leaflets of the perigone, sometimes single hairs on the surface. No wholly pilose nutlets found. The epidermal cells are variously shaped, mainly elongated, fairly transparent, with unevenly thickened walls; in cross-section they appear to the eye as if tumid, with irregularly distributed pits. Stomata slightly raised on the surface. Subsidiary cells stain with iodine green the same as the whole of the epidermis. On the surface of the perigone there are gland hairs composed of a few cells, surrounded by roundish epidermal cells with thickened walls, so that even after the destruction of the glands their location is clearly marked. The first parenchymal layer is composed of cells much larger than the epidermal cells, thin-walled and irregular in shape, taking a deep stain, and sometimes arranged in rows.

# 5. Carpinus turczaninowii Hance

Delicate, transparent epidermis without visible pits in the cell-walls. The cells often have rounded walls. Hairs at the ends of the leaflets of the perigone and on their surface. Completely pilose nutlets have also been found, but more rarely than in *C. betulus*. Cells surrounding hairs 5—9 but usually 7 in number. Multicellular glands at the ends of the leaflets of the perigone (Text-fig. 4). Stomata not distinctly raised above

the surface. Subsidiary and epidermal cells have equally thin walls and both stain with iodine green. Cells of first parenchymal layer considerably larger than epidermal cells, but smaller than the analogous cells in *C. betulus*.

### 6. Carpinus tschonoskii Maxim.

The epidermal cells have distinctly outlined walls, evenly thickened, with rather wide pits, often arranged in longitudinal lines reaching right to the terminations of the perigone leaflets. This is a very typical character of this species. The stomatal apparatuses are markedly raised above the surface of the epidermis so that the subsidiary cells are hidden from the eye in cross-section and look like the petals of a full flower round the stoma (Text-fig. 3). The hairs, only in the upper part of the perigone, seldom in the lower, are surrounded by 5—8 cells usually stretching along the axis of the nutlet, so that the whole resembles a bow of ribbon. The last two characters clearly differentiate the species  $C.\ tschonoskii$  from other species of hornbeam which have hairs on the perigone. The cells under the epidermis are larger, with markedly delicate walls; they are usually rectangular and set in rows.

### 7. Carpinus cordata Blume

Perigone pilose only on the margins of the leaflets. Epidermal cells rather big thin-walled, with 4—6 walls, often elongated. Stomata slightly raised over surface, subsidiary cells stain like the epidermal cells. Cells of first parenchymal layer slightly larger, thin-walled, with cells or groups of cells with thick walls and numerous pits appearing sporadically between them. One of the most typical characters of this species is the small difference between the cells of the epidermis and those of the underlying parenchyma.

# 8. Carpinus japonica Sargent

Glabrous perigone, with hairs only on the margins of the leaflets. Small, rather regular, thin-walled cells, with no distinct pits. Stomata as a rule not raised above the surface; subsidiary cells stain like the rest of the epidermis. Cells of the first parenchymal layer small, regular, sometimes arranged in rows, approximately the same size as those of Carpinus cordata. The marked difference between the size of the epidermal cells and those of the first parenchymal layer is a character which clearly differentiates the species  $C.\ japonica$  from  $C.\ cordata$ .

# B. Genus Ostrya Scop. (Text-fig. 6; Pl. IV, VI)

#### 1. Ostrya carpinifolia Scop.

Epidermal cells irregular in shape and size, often elongated. Their thick walls with numerous pits are often as large as the cell lumen. The thickened part of the walls refracts light differently from the central lamina. Stomatal cells slightly elevated above the epidermis; under them is a small air chamber. The subsidiary cells are almost as thick-walled as the other epidermal cells and stain similarly with iodine green. Hairs only on the margins of the perigone leaflets. Cells of the first parenchymal layer scarcely three times longer than the epidermal cells, narrow, elongated, often distorted, with rather thin walls intersected by pits.

OSTRYA

Ostrya japonica

Text-fig. 6. Cells of epidermis and underlying parenchyma of species belonging to the genus Ostrya

Ryc. 6. Komórki epidermy i leżącej pod nią parenchymy gatunków należących do rodzaju Ostrya

Ostrya virginiana

Ostrya virginiana

#### 2. Ostrya virginiana (Mill.) K. Koch

Epidermal cells more or less as broad as long, with evenly thickened walls and numerous narrow pits. Seen from above, the central lamina is conspicuous, but the thickness of the very transparent walls gives these cells a lenticular appearance. Stomata mainly in the apical portion of the perigone, slightly elevated above the epidermis, with a small air chamber. The subsidiary cells have thickened walls and stain with iodine green. Hairs on the margins of the perigone leaflets and sometimes also at the base of the nutlet. Cells of the first parenchymal layer narrow, elongated, irregular in shape, with rather thick walls intersected with pits.

#### 3. Ostrya japonica Sargent

Epidermal cells slightly smaller than in *O. virginiana*, irregular in shape, with markedly thickened walls and numerous pits, stomatal cells slightly raised above the surface, subsidiary cells thin-walled on the side of the air-chamber, so that when stained with iodine green they quickly lose colour. Hairs only at the end of the perigone leaflets. Cells of the first parenchymal layer have walls slightly more delicate than those of the epidermal cells; elongated and markedly undulated. This character essentially differentiates the species *O. japonica* from *O. virginiana* and *O. carpinifolia*.

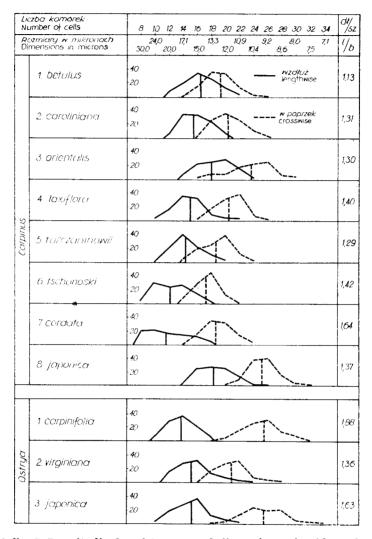
# II. DIMENSIONS AND SHAPE OF THE CELLS OF THE EPIDERMIS AND FIRST PARENCHYMAL LAYER

Since the descriptions of the cells of the epidermis and first parenchymal layer given above might have proved to be insufficient, especially when these species were differentiated chiefly by the cell dimensions, as in C. turczaninowii, C. japonica and C. cordata, in which the unaccustemed eye may perceive the differences only when these pictures are placed side by side in a photograph (Pl. III), detailed measurements were made of the cells both of the epidermis and the immediately underlying parenchymal layer. The cells, however, were usually so irregular that a search for more symmetrical specimens on which both the length and breadth could be measured would have resulted in selected and not random samples. The number of cells in the field of vision of the microscope was therefore counted in two directions, along and across the nut, always proceeding along the diameter of the field of vision. An ocular in which the field of vision was divided by a diagonal line, and which could be turned in appropriate directions, was helpful here. The diameter of the field of vision under high magnification (ocular  $8 \times$  and objective  $60 \times$ ) was 240  $\mu$ , or 480  $\mu$  under medium magnification (ocular 8 imes and

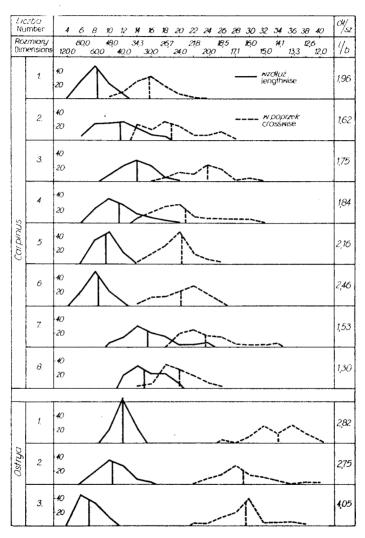
objective 30 X). This value was divided each time by the number of cells appearing along and across a given field of vision, so obtaining the mean breadth and mean length of the cells examined, E.g. if the diameter of the field of vision in the microscope under fairly high magnification intersected 10 cells of the perigone across and 8 cells along the perigone, then the mean breadth of these cells was 24 u (240:10), and the mean length was 30  $\mu$  (240:8), while the ratio of these two values was the gauge for the mean shape. It was shown that the epidermal cells studied were on the average 1.25 times longer than broad. A similar procedure was followed for the parenchymal cells lying immediately below the epidermis, except that these were counted not under high but medium magnification. Owing to the large dimensions, greater accuracy was then obtained in the measurement results. Measurements were made at the broadest part of the perigone, avoiding the areas situated over the bundles, which are distinctly marked on the epidermis in the form of bands of markedly elongated cells often arranged in rows. At least ten such measurements were attempted in each nutlet. This gave 10 mean values of the length and as many of the breadth, as well as 10 similar values for the parenchymal cells lying under the epidermis, and so resulted in the great accuracy of the observations made. Finally the ratios of the length and breadth of the epidermal cells to the length and breadth of the parenchymal cells were calculated. In this manner a further value was obtained, which gave the ratio of the dimensions of the epidermal cells to those of the parenchymal cells in a given nutlet. This proved to be an important character differentiating the species of the genera Carpinus and Ostrya. described, all this may seem complicated, but in reality it was very simple, since counting the cells on the diameter of the field of vision turned out to be very quick, although very tiring to the eyes.

The results of these studies are presented in graph form in Text-figs. 7 and 8. Text-fig. 7 illustrates the results of measurements of the epidermal cells of the species of *Carpinus* and *Ostrya* studied, and Text-fig. 8 gives those of the parenchymal cells lying immediately under the epidermis. The former were counted under high magnification, and the latter under medium.

In the captions to each of the graphs, the number of cells found on the diameter of the dield of vision in the microscope is given. This diameter measures 240  $\mu$  in Text-fig. 7, and 480  $\mu$  in Text-fig. 8. On the left side of the graphs is given the least number of cells and on the right the greatest number of cells found in the material investigated. The scale thus rises from left to right. In the next row, the relevant values are given in microns, and this scale of course diminishes in the same direction, for the greater the number of cells found, the smaller were their dimensions. If, for example, only 8 cells were seen on a diameter of a field of vision 240  $\mu$  in length, their mean size would be 30  $\mu$ , while if



Text-fig. 7. Longitudinal and transversal dimensions of epidermal cells Ryc. 7. Rozmiary komórek skórki wzdłuż i w poprzek



Text-fig. 8. Longitudinal and transversal dimensions of parenchymal cells Ryc. 8. Rozmiary komórek miękiszu wzdłuż i w poprzek

there were 34 cells, their mean size would be only about 7  $\mu.$  Thus, if the numbers of cells given in the first row in Text-figs. 7 and 8 are not directly comparable because they were counted under different magnifications, yet the relevant values in microns can be compared. We see that the sizes of the epidermal cells varied from 7 to 30  $\mu$  in the species investigated, while those of the cells in the first parenchymal layer varied from 12 to 120  $\mu.$ 

In Text-figs. 7 and 8 two curves have been plotted for each species. The curves drawn with a continuous line refer each time to the cells counted along the nutlets, and so characterize their length. The curves drawn with a dotted line refer to the similar measurements made across the perigone, and so illustrate the breadth of the cells. The greater the coincidence between these two curves, the less is the difference between the length and breadth of the given cells. The greater the divergence between these curves, the greater is the difference; the cells then become narrow and elongated. The species Carpinus betulus exemplifies the first type of epidermal cell, while the species Ostrya carpinifolia exemplifies the second type in Text-figs. 7 and 8. The last column in both figures gives the mean ratio of length to breadth of the cells in the species studied. From these figures the following data may be read off:

- 1. Distinct differences appear between the species studied, both in dimensions and in the breadth-length ratio in the cells of the epidermis and the first layer of parenchyma in the perigones of their fruits.
- 2. The dimensions of the epidermal cells were not correlated with those of the fruits; e.g. the species *Carpinus betulus* had nutlets strikingly larger than those in other species of hornbeam, as was shown in the studies of 1953, but did not differ at all in the size of the epidermal cells, while the species *C. tschonoskii*, of which the nutlets are among the smallest, had extremely large epidermal cells. The nutlets of the species *C. cordata* and *C. japonica* had almost the same dimensions, but the former had much larger epidermal cells than the latter (Text-fig. 9).
- 3. The genus Ostrya did not differ from the genus Carpinus in the shape or size of the epidermal cells in any significant manner, but there were striking differences between these two genera as regards the shape of the cells in the first layer of parenchyma (Text-fig. 8). The extremely narrow long parenchymal cells lying immediately below the epidermis were undoubtedly a typical character of the genus Ostrya.

The determination of the ratio of the dimensions of the cells of the epidermis to those of the parenchyma is also important in view of the specific classification of single nutlets, as though nutlets with epidermal and parenchymal cells slightly larger or smaller than the average may be found, the ratio of these remains unchanged. This character is of particular importance in the determination of fossil materials.

# Measurements of epidermal cells on the microscopes diameter = 240 $\mu$ Pomiary komórek skórki na średnicy pola mikroskopu = 240 $\mu$

Species Gatunek				Lengthy Wzdł	vise of					Ratio				
		n		mber of cells zba komórek	length in m długość w mil	n		umber of cells czba komórek		width in m szerokość w		1/w. Stosunek		
			$\left \begin{array}{c c} min\\ -max. \end{array}\right $ $M\pm m$ . $\pm$ $mi$		min.—max.	М		min.— —max.	M±m.	±	kronacl	h M	dł./szer.	
	betulus	100	11-21	15.89±0.22	2.23	11.4—21.8	15.1	200	1426	18.60±0.14	2.03	9.2—17.1	12.9	1.17
	caroliniana	50	1119	15.16±0.27	1.91	12.6—21.8	15.8	50	16—25	19. 9±0.29	2.08	9.0—15	12.1	1.31
SX	orientalis	67	13-23	$17.88 \pm 0.28$	2.34	10.4—18.5	13.4	90	1530	$23.27 \pm 0.32$	3.13	7.8—15	10.3	1.30
Carpinus	laxiflora	100	921	14.40±0.23	2.31	11.4—26.7	16.7	84	1625	$20.18 \pm 0.21$	1.90	9.215	11.9	1.40
ā	turczaninowii	70	10—19	$14.17 \pm 0.26$	2.17	12.6—24.0	16.9	80	1423	$18.19 \pm 0.23$	2.07	10.4—17.1	13.1	1.29
	tschonoskii	80	7—17	$11.84 \pm 0.27$	2.40	14.1-34.3	20.3	90	13-21	$16.78 \pm 0.17$	1.65	10.618.5	14.3	1.42
1	cordata	70	718	$11.27 \pm 0.32$	2.67	13.3—34.3	21.3	100	1424	$18.47 \pm 0.20$	2.05	10.015.5	13.0	1.64
	japonica	70	13—25	17.96±0.20	1.68	9.6—18.5	13.3	110	1931	$24.76\pm0.19$	1.99	7.4—12.0	9.7	1.37
ra Va	carpinifolia	86	918	13.15±0.21	1.96	13.3—26.7	18.2	86	1831	24.75±0.29	2.70	7.8—13.3	9.7	1.88
strya	virginiana	61	11—23	$15.10 \pm 0.35$	2.79	10.4-21.8	15.9	60	16—25	$20.53 \pm 0.26$	2.08	9.2—15.0	11.7	1.36
0	japonica	90	10—21	15.06±0.26	2.52	11.4—24.0	15.9	90	1834	$25.60 \pm 0.31$	3.00	7.1—13.3	9.8	1.63

 $\label{eq:Table 2} Table \ 2$  Measurements of the first layer of parenchyma cells on the diameter of the microscope field = 480  $\mu$ 

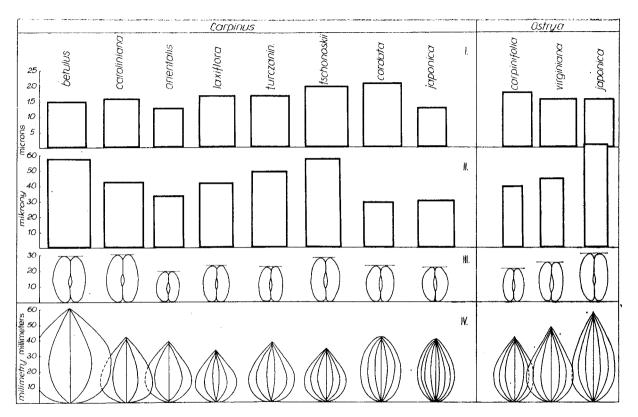
				Lengthwise Wzdłuż					Crosswise W poprze	/szer.	parenchy- ma			
	Species Gatunek	n		ber of cells a komórek		length in m długość w mik			ber of cells ba komórek		width in m szerokość w nach		I/w nek dł.	miękisz epider-
			min.— —max.	M±m		min.—max.	M	min.— —max.	M±m		min.—max.	M	Ratio Stosur	mis skórka
	betulus	175	414	8.16±0.64	1.70	30.0-120.0	56.9	1024	15.78 ± 2.12	2.80	18.5—48.0	28.9	1.96	8.44
	caroliniana	55	619	11.64±0.43	3.18	25.3— 88.0	41.2	1427	$18.88 \pm 0.56$	4.16	17.834.3	25.4	1.62	5.47
23	orientalis	90	919	$13.38 \pm 0.23$	2.23	25.3— 53.3	35.8	1631	$23.46 \pm 0.47$	4.47	15.5—30.0	20.5	1.75	5.31
inic	laxiflora	70	620	11.36±0.34	2.88	24.0 88.0	42.3	14-32	20.88 ±0.55	4.61	15.0—34.3	23.0	1.84	4.89
Carpinus	turczaninowii	40	6-12	9.10±0.23	1.46	40.0— 88.0	52.7	14—25	$19.72 \pm 0.35$	2.25	18.5—34.3	24.3	2.16	5.38
0	tschonoskii	24	6—12	8.34±0.34	1.68	40.0— 80.0	57.5	1426	$20.50 \pm 0.62$	3.02	18.5—34.3	23.4	2.46	4.63
	cordata	40	1024	$15.64 \pm 0.56$	3.56	20.0-48.0	30.6	18 - 34	$23.88 \pm 0.70$	4.08	14.1—26.7	20.1	1.52	2.22
	japonica	43	1220	15.30±0.36	2.40	24.0 40.0	31.4	1426	$19.82 \pm 0.38$	2.50	18.5—34.3	24.2	1.30	5.89
ä	carpinifolia	20	10—14	12.10±0.30	1.34	34.3— 48.0	39.7	2640	34.10±0.74	3.30	12.0—18.5	14.1	2.82	3.17
Ostrya	virginiana	50	6—16	$10.56 \pm 0.30$	2.22	30.0 80.0	45.5	22—40	Į.	3.56		16.5	2.75	4.03
Ó	japonica	40	410	7.20±0.24	1.60	48.0—120.0	66.7	22—38	29.20±0.52	3.40	12.6—21.8	16.45	4.05	7.02

Pomiary komórek pierwszej warstwy miękiszu na średnicy pola mikroskopu  $=480~\mu$ 

Table 3 Tabela 3

# List of localities of the fossil floras discussed in the paper Spis miejscowości flor kopalnych omawianych w pracy

				Epiderms investigated Skórki zbadane							
Age Wiek		Locality Miejscowość	Species Gatunek	number of speciments liczba okazów	naked in percentage nagie w %	hairy in percentage owłosione w %					
	Holocene	Krzeszów (Szafer 1939)	Carpinus betulus L.	2							
	Holocen	Raków (Kozłowska 1923)	",	5		_					
		Cimoszkowice (Kulczyński 1928)	,, ,,	6		_					
		Dzbanki Kościuszkowskie (Piech 1932)	,, ,,	5							
	Ę	Kalisz (Tołpa 1952)	,, ,,	6							
Quaternary Czwartorzęd	Riss-Würm	Nieciosy (Brem, Sobolewska 1950)	,, ,,	3							
ern tot	Λ-s	Rumlówka (Środoń 1950)	,, ,,	6		_					
uat wai	Ris	Rusinowo (Stark, Firbas, Overbeck 1932)	,, ,,	6	-						
Ōζ		Samostrzelniki (Szafer 1926)	,, ,,	8	<u> </u>	_					
		Szczerców (Piech 1932)	,, ,,	1							
	M. J.I D.	Ciechanki Krzesimowskie (Brem 1953)	,, ,,	3	· —						
	Mindel-Riss	Żydowszczyzna (Szafer 1926)	,, ,,	4	-						
	 :			55	47	53					
		Domański Wierch (Jentys-Szaferowa 1961)	C. betulus type	11	55	45					
		Mizerna, main layer — główny pokład (Szafer 1954)	Carpinus betulus L.	41	43	57					
•	Upper	Mizerna — Koprocz (Jentys-Szaferowa 1958)	,, ,,	2	(50)	(50)					
Pliocenc Pliocen	górny	Ruszów (Stachurska, Dyjor, Sadowska 1967)	•• ••	10	_	100					
Plic Plic			Ostrya sp.	10	_	100					
			C. betulus L. foss.	42	60	40					
	Lower		C. laxiflera Bl.	4	100						
	dolny	Krościenko (Szafer 1946)	C. tschonoskii Max.	10	100	_					
			O. carpinifolia Scop. foss.	10	100	_					
Miocene Miocen	Middle Upper środ- górny kowy	Gliwice Stare (Szafer 1961)	C. grandis Unger	12	42	58					
Mio Mio	Middle środ- kowy	Wieliczka (Zabłocki 1927, 1930)	C. polonica Zabł.	10	_	100					



Text-fig. 9. Morphograms of fruits of the genera *Carpinus* and *Ostrya*: I. Average length and breadth of epidermal cells; II. Average length and breadth of parenchymal cells; III. Average dimensions of stomata; IV. Dimensions of nutlets based on the arithmetical means of their characters

Ryc. 9. Morfogramy owoców rodzajów *Carpinus i Ostrya:* I. Przeciętna długość i szerokość komórek epidermy; II. Przeciętna długość i szerokość komórek parenchymy; III. Przeciętne rozmiary szparek; IV. Rozmiary orzeszków na podstawie średnich arytmetycznych ich cech

#### III. MENSURAL RESULTS

To facilitate a general orientation in the results of the biometric studies, these have been set out in the form of a morphograph in Textfig. 9. At the top are the schematic outlines of the epidermal cells of perigones of the species studied, drawn on the basis of the arithmetic means of their length and breadth. The scale used in this drawing is twice that used for the cells of the first parenchymal layer, drawn below. This was done deliberately, the better to bring out the differences between particular species in the shape of the epidermal cells. It should be remembered, however, that these are shown twice as large as the parenchymal cells. In the third row, the stomata of the given species are drawn on the basis of their mean length from the base up to the line drawn at the top of each pair of cells. At the bottom of the graph are shown contours of nutlets of the species studied drawn on the basis of the arithmetic means of the characters given in the treatise of 1953. Here the already-mentioned absence of correlation between the dimensions of the perigone epidermal cells and those of the nutlets themselves is fully apparent.

All that has been described, viz. the structure, shape and dimensions of the cell walls in the perigone and first parenchymal layer as well as the mutual relation between these elements, is presented in Text-figs. 5—9 and Plates II—VI. Together they form a key, the basis both for the systematic classification and for some biological properties of the fossil nutlets. When all these elements were in agreement and the similarity between the perigones of recent and fossil fruits with glabrous epidermis was complete, it was possible to assign fossil fruits to species known to us today. When all the characters described could not be detected in fossil nutlets, e.g. if only the epidermis was preserved and the parenchymal cells were missing, even then a determination of the specific classification of fossil nutlets could still be made with great probability.

#### PART II

# FOSSIL MATERIALS DETERMINATION OF FOSSIL FRUITS

#### CONTENTS

	Introduction	31
2.	List of materials studied	31
3.	Method of investigation	32
	A. Observations on the superficies of the epidermis	32
	B. Dimensions of the epidermal cells	34
4.	Individual studies on glabrous fossil nutlets	36
	A. Carpinus betulus type	41
	B. Carpinus turczaninowii type	43
	C. Carpinus tschonoskii type	44
	D. Carpinus orientalis type	45
	E. Genus Ostrya	48
5.	Fruits from Ruszów and Wieliczka	49
G	Summary of results	55

#### 1. INTRODUCTION

The aim of the second part of the study on variability in the epidermal cells of *Carpinus* and *Ostrya* fruits was to check whether the epidermal method elaborated by the author was useful in palaeobotanical investigations. An attempt was made to apply it to materials already studied by specialists who had assigned them to one or another systematic unit according to their opinions. From these materials nutlets with the epidermis undamaged were selected at random and an attempt was made to verify whether the determinations coincided with those of palaeobotanists based solely on the morphology of the nutlets.

#### 2. LIST OF MATERIALS STUDIED

The materials studied from the point of view of the structure of the epidermis of the perigone are listed in Table 3. This table contains a list of the fossil florae in which were found nutlets of the genera *Carpinus* and *Ostrya*, with the names of those who worked on these florae, the age to which they considered they should be assigned, and the names which

they gave the nutlets they segregated. The author worked on the greater part of these materials with respect to the morphology and anatomical structure (1960 and 1961). The materials found on the banks of the mountain stream Koprocz in Mizerna, the numerous Miocene materials from Wieliczka entrusted to the author by prof. J. Zabłocki and the fruits from Ruszów in Silesia received from doc. A. Stachurska and determined as Upper Pliocene are all new. Cordial thanks are expressed to both for the opportunity of examining these nutlets, since this has contributed to the greater thoroughness of the present study by the introduction of new problems. The author's gratitude is also due to prof. Shigeru Miki for sending some Pliocene nutlets of Ostrya japonica from Japan, which formed valuable comparative material, and to Miss Elizabeth Voges, who sent nutlets found by prof. F. Oldfield in early Quaternary deposits in the south of France.

Table 3 shows the materials studied in chronological order from the youngest to the oldest. On the right of the table is noted from how many nutlets it was possible to detach the perigone, and what were the proportions of glabrous to completely or at least half pilose nutlets in a given sample. The numbers in these samples varied, depending on the richness of the fossil material and the degree of its destruction. The author had at her disposal so many Quaternary nutlets that only a few were taken from each stand and mixed together in one sample (55 in all). The anatomical and morphological studies carried out in 1960 and 1961 showed that the sole species to appear was *Carpinus betulus*. The nutlets from Mizerna and Krościenko were also very numerous and comparatively thoroughly studied.

#### 3. METHOD OF INVESTIGATION

#### A. OBSERVATIONS ON THE SUPERFICIES OF THE EPIDERMIS

These were the first observations made on preparations of both recent and fossil nutlets. The question was whether the epidermis was bare or covered with hairs (Text-fig. 10). This shed light on the character of the trees studied. As follows from the descriptions of the fruits of the genera Carpinus and Ostrya on pages 16—22 their perigones differed in this respect, and whether the nutlets were glabrous or pilose was sometimes a specific character. The picture of this character is given on the lefthand side of Text-fig. 10, in which the recent species of the trees studied are illustrated. The white field shows the percentage of glabrous nutlets observed in the material examined, and the black field shows the percentage of entirely or partially pilose nutlets. The hairs appearing on the

<i>dzisiejsze</i> recent	kopalne fossil
1 & betulus	C. betulus L Quaternary
. 2 C. caroliniana	C.betulus L MIZERNA
3 Corientalis	C. betulus L. foss,-KROŚCIENKO
- Claxiflora	C. grandis UngGL/WICE
5 C turczaninowii	C.T. betulus L -DOM. WIERCH
6 C. tschonoskii	C. laxiflora BL-KROŚCIENKO
7 Licordata	C.cf, tschonoskii Maxım.
8 ^ japonica	C. betulus L RUSZOW
' 3 carpinifolia	C polonica Zabł -WIELICZKA
2 0 virginiana	0.carpinifolia-KROŚCIENKO
3 D japonica	Ostrya sp - RUSZÓW
owoce nagie frui	ts without hairs
owoce owłosione fr	uits with hairs
tylko szczyt owłesior	y hairy only on the top

Text-fig. 10. Proportion of pilose and glabrous nutlets in recent and fossil populations of the genera *Carpinus* and *Ostrya* 

Ryc. 10. Stosunek orzeszków owłosionych i nagich w populacjach dzisiejszych i kopalnych rodzajów *Carpinus* i *Ostrya* 

margins of the foliaceous terminations of the perigone and sometimes also on the surface of these leaflets were not taken into consideration, since this character appears in almost all the species examined. On the other hand, if hairs were found sporadically distributed here and there on the epidermis of a perigone, on the medial and lower parts of the nutlet, this was noted on the graph by cross-hatching.

As may be seen from Text-fig. 10, most of the recent species studied were glabrous. In three (nos. 3, 5 and 10), however, in each case among the many specimens examined, there was one which had nutlets pilose over the whole surface, so that in these species pilosity was a relative character. Only the American hornbeam *Carpinus caroliniana* Walt. had solely pilose nutlets. Even Winkler in his monograph on the family *Betulaceae* alludes to this characteristic feature, "nuculae pubescentes", while he writes of certain other species that they are "apice pilosae". Nutlets of the species *Carpinus betulus* had the specific character that in every population specimens with glabrous as well as pilose nutlets appeared, though Winkler paid no attention to this.

The nutlets found in fossil florae presented an entirely different picture. In contradistinction to the left side of Text-fig. 10 those on the right-hand side have been arranged on the basis of their possible systematic classification. The materials which not only other authors have determined to the side of their possible systematic classification.

ined as approximating the recent species *C. betulus* but which the present author has confirmed as belonging to the *betulus* type by investigating their anatomy and morphology have been placed in the upper part of Text-fig. 10. In the lower part of the Text-figure specific names given by the authors who discovered or elaborated the mentioned flora have been kept for nutlets of the genera *Carpinus* and *Ostrya*.

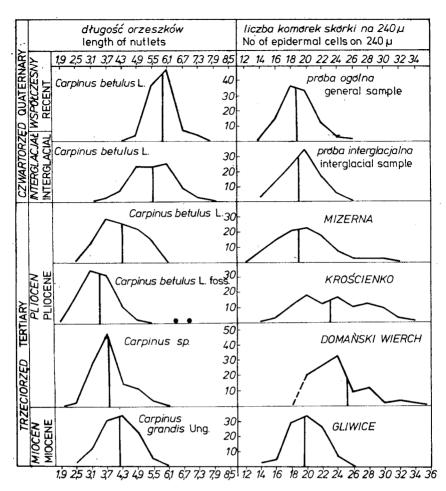
Even a superficial glance at Text-fig. 10 will show that only in the fossil samples nos. 1, 2 and 4 was the ratio of glabrous to pilose nutlets similar to that in recent populations of the species *C. betulus*. In the samples of nutlets from Krościenko and Domański Wierch both types were also found, but glabrous nutlets predominated. The fossil florae in the lower half of Text-fig. 10 are of an entirely different character. There the nutlets examined were either all glabrous or all pilose.

#### B. DIMENSIONS OF THE EPIDERMAL CELLS

The next information on the character of the fossil nutlets was provided by the results of calculating the number of epidermal cells across the nutlet on a section 240  $\mu$  long. This of course was done only on glabrous nutlets, since only in these was the distribution of the cells comparatively regular.

The example in Text-fig. 11 shows the value of the information gained in this way. In this figure are set out to the right the polygons of variability of the number of epidermal cells in nutlets from fossil florae studied morphologically in 1960 and anatomically in 1961 and in which the presence of nutlets of the *C. betulus* type was demonstrated. For better orientation on the character of the nutlets studied, a graph of their length on the basis of the 1960 data has been placed on the left-hand side of the Text-figure.

We shall now try to interpret Text-fig. 11 without allowing ourselves to be influenced by morphological or anatomical studies. We see from the right-hand side of the Text-figure that the Quaternary nutlets coming from various florae of the younger and older interglacial do not differ at all in the number of epidermal cells per 240  $\mu$  and so do not differ, as far as cell-breadth is concerned, from the nutlets of recent hornbeams belonging to the species. C. betulus. We do not observe here even that insignificant diminution in size which we see on the graph showing the length of the whole nutlets (left-hand side of Text-figure) caused by the slight contraction of the nutlets which must have already lost part of their organic matter though not yet flattened. This is confirmed by what has previously been said, that the epidermis of hornbeam fruits prepared by the method given in Part I of this treatise straightens out and its cells are comparable with those of recent species.



Text-fig. 11. Left: length of hornbeam nutlets of the Carpinus betulus type from the Tertiary to the present day. Right: number of epidermal cells of these fruits counted across the perigone in the field of vision of a microscope 240  $\mu$  in diameter Ryc. 11. Na lewo długość orzeszków grabu typu Carpinus betulus od trzeciorzędu po dzień dzisiejszy. Na prawo liczba komórek skórki tych owoców, liczona w poprzek perigonu w polu widzenia mikroskopu o średnicy 240  $\mu$ 

After the transition from the Quaternary to the Tertiary distinct changes occur on both sides of Text-fig. 11. The dimensions of the nutlets become smaller (1960), although their anatomical structure shows that the great majority belonged to the C. betulus type (1961). This diminution in size is not seen in the epidermal cells from Mizerna and Gliwice. In the sample from Mizerna, however, we see something new. Although the majority of these nutlets had epidermal cells similar to those in the species C. betulus there was a certain inconsiderable percentage with smaller epidermal cells, since there were 20 - 30 on a diameter  $240~\mu$  in length. This appeared much more strongly in the sample from Krościenko, and still

more so in that from Domański Wierch. This indicates that the nutlets found there did not represent one species, but at least two and possibly more. This is also a proof of how misleading it may be to sort out hornbeam nutlets on the basis of their appearance when the differences in the dimensions of *C. betulus* and the other species begin to be effaced.

After obtaining proof that in a sample studied there are nutlets which might be assigned to more than one species, nothing else remained but to analyse them in detail, i.e. to determine the nutlets individually.

#### 4. INDIVIDUAL STUDIES ON GLABROUS FOSSIL NUTLETS

Before beginning the individual studies of fossil nutlets it was necessary to gain knowledge of the variability of the epidermal cells in the individual nutlets of recent species. Since in the material used nutlets determined as the fossil equivalent of the species *Carpinus betulus* predominated, these were studied in the first place. Other species were examined in a similar manner.

Text-fig. 12 may be taken as an example. On the lefthand side is illustrated the number of epidermal cells counted along and across nine nutlets of *C. betulus* from various parts of Europe. On the righthand side the analogous values are given for their first layer of parenchymal cells.

skórka epidermis											<i>miękisz</i> parenchyma															
Γ	liczba k	~~~~	ek ni	a 24	0 μ	No	of ce	lls o	n 24	цC			liczl	oa ko	mør	ek n	a 48	10 µ	No	of c	ells o	n 48	0 N		-	
l	12 14 wzdłuż		18 + busis		22	14	16 20 prz	- 1	20			26	4	6	8	-	-	14	10				-1	20 2	2 24	dt/sz l∕b
	W20102	ieng	LINVIS		T	-	70 pr 2	er	CIO	55 W	rise		WZC	łłuż	ien	gthw	ise		"	pop	orzek	çn	ossw	rise		1.96
recent	2. 3.				•	_			_	_				_							=		_	_		1,93 2,10 1,88 1,85 1,87
Je.	3. — 4. —								_		-			_	_		_			_				_		1,85
SZe				_	ļ				_					_	_			1		-		_				2,00
dzisieisze	8. —— 9. ——								_					_	_	_					_					2,00 223 2,05 1,90
20	-								_				Ц.						$\perp$						M-	1,98
	1.			_											_			-								2,02 1,75
J.S	3. 4							_			_			_				-								2,60 1,89
fossil	I D.		-			-	_			_			-	_		_										2,05 1,54
a/ne	7. 8							_									_		-							1,81
KOD	7. 8. 9. 10.					-					-,	-		_	_			ŀ		**						2.09 1.85
L					L	⊥																			M=	1,96

Text-fig. 12. Individual variability in dimensions of epidermal and parenchymal cells in nine recent and ten interglacial fruits of the species *Carpinus betulus* Ryc. 12. Zmienność indywidualna rozmiarów komórek skórki i miękiszu u dziewięciu owoców dzisiejszych i dziesięciu interglacjalnych należących do gatunku *Carpinus betulus* 

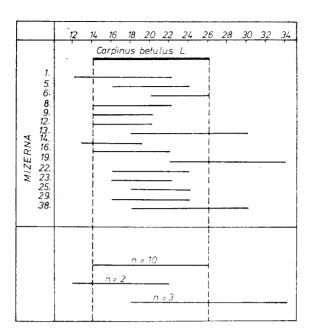
Under these are given the same values for ten nutlets from various Polish interglacial florae. Besides the graph are given data on the lenght: breadth ratio of the parenchymal cells.

In the upper part of the graph there is a scale of variability in length and breadth of the cells of the epidermis and the first layer of the parenchyma in perigones from a general sample of *C. betulus*, drawn up from 200 observations made on recent hornbeams over the whole range of Europe.

From the upper part of Text-fig. 12 we may see that although the cells of recent hornbeams from various parts of Europe differed both in size and shape, yet they never went beyond the scale proper to the species C. betulus. The same is seen in the lower part of the figure, which illustrates ten nutlets from various interglacial florae. It was therefore incontrovertible that they belonged to the species C. betulus. The numerical data on the righthand side of Text-fig. 12 are also characteristic. The average shape, i.e. the length: breadth ratio of the parenchymal cells of nine recent and ten fossil nutlets were almost identical, as in the general sample (1.96, 1.98, 1.96). This was a convincing proof that if the scale of variability of the cells of the epidermis and parenchyma in fruits of recent species is known, the specific classification of similar fossil forms may be determined with great probability on the basis of individual nutlets.

Text-fig. 13 exemplifies the method of determination of the fossil materials. This was a detailed analysis of a sample composed of 40 nutlets, selected at random from 200 nutlets from Mizerna, described by W. S z afer as Carpinus betulus L. In this sample the perigones were pilose completely of to a considerable extent in 22 nutlets, while in 18 the epidermis was glabrous; among the latter there were three in which it was not possible to detach the epidermis in the preparation so that accurate measurements could be made. The epidermal cells in the others were measured. The graph in Text-fig. 13 refers to these, showing the individual variability of only one character, viz., the number of epidermal cells per 240  $\mu$  counted across the perigone. This is sufficient for the first segregation of the nutlets.

At the top of Text-fig. 13 the scale of variability of this character in the general sample of *C. betulus* has been marked by a thicker line (Text-fig. 12). Among the 15 nutlets illustrated below, in only two (nos. 1 and 14) were there found some cells larger than is typical of the species *C. betulus*; there were only 12-13 on the diameter of the field of vision in the microscope. In three nutlets (nos. 13, 19, and 38) there was a large percentage of small cells. The other ten nutlets fitted into the scale of variability in breadth for the epidermis of the species *C. betulus*. It also turned out that they had the same shape of cell, only slightly longer than broad, the same character of cell-wall, and even the same dimensions of



Text-fig. 13. Number of epidermal cells appearing per 240 μ across glabrous perigones of 15 nutlets from Mizerna. The thick line at the top of the graph denotes the scale of variability of these cells in the recent species Carpinus betulus (cf. Text-fig. 12) Ryc. 13. Liczba komórek skórki, występujących na 240 μ w poprzek nagich perigonów 15 orzeszków z Mizernej. Gruba linia u góry wykresu zaznacza skalę zmienności tych komórek u dzisiejszego gatunku Carpinus betulus (por. ryc. 12)

the stomata is in the species *C. betulus*, so that nothing prevented them from being assigned to this species. The nutlets in which the scale of variability exceeded that characteristic of the species *C. betulus* were divided into two groups with larger or smaller epidermal cells, and each group was then examined in detail, taking all the characters studied into consideration.

Of the three nutlets which had small epidermal cells, the parenchymal cells of one (no. 19) were so damaged that they could not be examined in detail, but the others, i.e. nos. 13 and 38, were thoroughly studied. Biometric studies were also made of the epidermis and parenchyma of nutlet no. 1, which had larger epidermal cells than *C.betulus*. In nutlet no. 14 the epidermis was similar.

Text-fig. 14 illustrates the length and breadth of the cells of the epidermis and first parenchymal layer in recent species of *C. betulus*, *C. orientalis* and *C. turczaninowii*, and below these of the fossil nutlets nos. 1, 13 and 38. Nutlet no. 13 completely corresponds to the species *C. orientalis*, and the length: breadth ratio of the parenchymal cells is also approximately the same. Nutlet no. 38 is quite different, and the character of its markedly narrow but long parenchymal cells, about three times

			skol	ka	epi	derm	is							nięk	isz	par	enc	hym	a							dt/sz.
8	10	12	14	16	18	20	22	24	26.	28	30	4	6	8	10	12	14	16	18	20	22	2	4 26	28	30	1/6
C)	C. betulus											C. betulus										1,96				
dzisiejsze recent	C. orientalis									_	C. orientalis										1,75					
9.2ρ s:2ρ	C turczaninowii								C. turczaninowii									2,16								
4.					Nr	13					_					Nr 1	3									1,62
pliocen górny upper pliocene	Nr 38								_											2,94						
phiocen upper	_		r 1	=_			_						_		,	٧r	1									2,44
-				- wz	dłu	ż ler	ngth	wise				L			_		- w	ро	prze	ek c	ross	wis	e	-		

Text-fig. 14. Length and breadth of epidermal and parenchymal cells compared in three recent species of the genus *Carpinus* and in three nutlets from Mizerna. The long narrow parenchymal cells of nutlet No. 38 gives evidence against its classification in the genus *Carpinus* (cf. Text-figs. 8, 15)

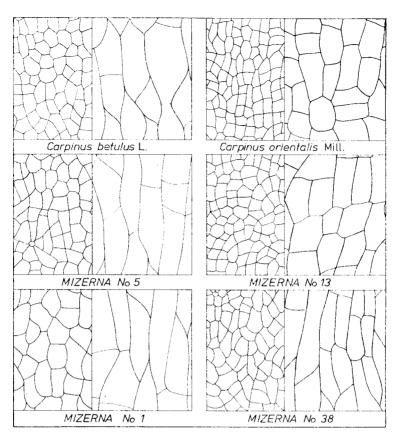
Ryc. 14. Porównanie długości i szerokości komórek skórki i miękiszu u trzech dzisiejszych gatunków rodzaju *Carpinus* i u trzech orzeszków z Mizernej. Wąskie a długie komórki miękiszu orzeszka nr 38 świadczą przeciw jego przynależności do rodzaju *Carpinus* (por. ryc. 8, 15)

as long as they are broad, suggests that it does not belong to the genus *Carpinus*. We shall return to this nutlet when discussing the fossil genus *Ostrya*.

In the lower part of the graph are illustrated the cells of nutlet no. 1, one of the two fruits with long epidermal cells. This cannot belong to the species *C. betulus*, not only because the epidermal cells are larger, but also because the parenchymal cells are of a different shape, as shown in the last column of the graph. Nutlet no. 14 was similar.

Text-fig. 14 gives an idea of the dimensions of the cells and to a certain extent of their shape, and is supplemented by Text-fig. 15, showing the exact contours of the cells of the epidermis and parenchyma of the nutlets studied by means of a drawing apparatus.

In Text-fig. 15 (left) are shown the cells of the epidermis and underlying parenchyma in a randomly selected recent nutlet of *C. betulus* L, with the similar nutlet no. 5 from Text-fig. 13 below it. Beneath is nutlet no. 1, which is different, since its epidermal cells are not only large but have a characteristic shape and slightly undulating walls, not found in the species *C. betulus*; the parenchymal cells are also different. This kind of epidermis and parenchyma are now found only in the species *C. turczaninowii*. In Text-fig. 15 (right) the recent species *C. orientalis* is shown and below are the very similar nutlet no. 13 from Text-fig. 13 and nutlet



Text-fig. 15. Epidermal and parenchymal cells of two recent species of hornbeam and four nutlets from Mizerna (cf. Text-figs. 13, 14)

Ryc. 15. Komórki skórki i miękiszu dwóch dzisiejszych gatunków grabu i czterech orzeszków z Mizernej (por. ryc. 13, 14)

no. 38, which has not only small epidermal cells but very narrow elongated parenchymal cells, so that it cannot belong to the species *C. orientalis* and indeed cannot belong to the genus *Carpinus* at all.

Only the contours of the cells have been drawn in these figures, going by their medial lamella, since a faithful representation of the character of the cell-walls, their thickness, and the distribution of the pits was impossible at the magnification used. The character of the cell-walls may be seen in the photographs (Pl. VII) which supplement the two preceding Text-figures and dispel any doubts as to the specificity of nutlets nos. 1 and 14 on the one hand and on the other of nutlet no. 19, which on the basis of the epidermis should be included in the species *C. orientalis*, like nutlet no. 13.

Only now can we determine the composition of the sample of 40 nutlets from Mizerna. If we accept of the 15 nutlets with a glabrous perigone 10 belong to the species *C. betulus* and to these add the three

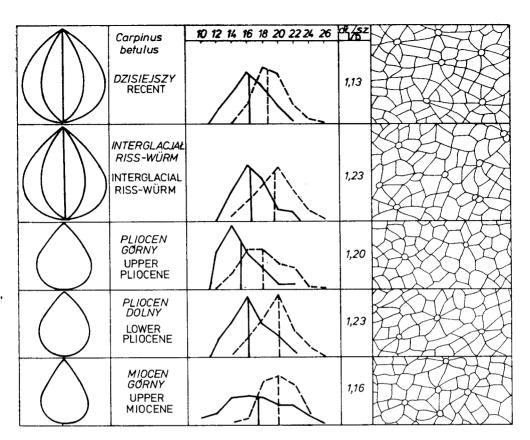
exactly similar nutlets which could not be measured, as well as 22 pilose nutlets also certainly belonging to the species *C. betulus*, we have 35 nutlets in which the proportion of glabrous to pilose fruits is as 37 to 63, i. e. similar to that found today in a population of this species (Text-fig. 10). If the sample of 40 nutlets from Mizerna represents this fossil flora adequately, it gives evidence that about 88 per cent of the horn-beams growing there were of the *C. betulus* type and about 12 per cent were trees or bushes belonging to other species of the genus *Carpinus* or possibly *Ostrya*. Among these the species *C. orientalis* is certain, and the determination of the species *C. turczaninowii* is also very probable.

Here it may be recalled that in the morphological studies on fossil hornbeam nutlets published in 1960 the author suggested that in the fossil flora of Mizerna there was a small percentage of hornbeams belonging to species which no longer grow in Poland, as well as trees of the C. betulus type. Anatomical studies then showed that the percentage of nutlets similar in structure to C. orientalis should be determined as about 4 per cent in Mizerna. These studies would thus be in agreement with the epidermal studies.

## A. Carpinus betulus type

A species of hornbeam very near to the present *C. betulus* was that most frequently appearing in Central Europe in the Neogene. This was shown as early as 1959 on the basis of the numbers of fruit involucres found in Tertiary deposits, and confirmed by studies of the morphology and in particular of the anatomy of the fruits. Typical characters of the species *C. betulus* were found even in some old and badly damaged nutlets.

Text-fig. 16 illustrates the epidermal characters of a number of nutlets, determined by the author as a type of *C. betulus* appearing from the Upper Miocene up to the present day. The middle column shows the variability in the length and breadth of their epidermal cells. If we recall Text-fig. 7 in Part I of this treatise, showing the differences which appear in this respect in particular species, we must acknowledge that in Text-fig. 16 the dimensions and shape of the epidermal cells completely agree in all samples. Only in the Miocene sample from Gliwice is there a slightly greater variability in the length of the cells, though this is not reflected in their shape, since the proportion of the length to the breadth of the cells is the same in all samples. The epidermal cells were on the average 1·13 to 1·23 times longer than broad; this is not found in any other species of hornbeam. A photograph of the epidermis of a fruit of the *C. betulus* type from the Miocene deposits in Gliwice is shown in Plate VIII, as are also parenchymal cells characteristic of this species.



Text-fig. 16. Left: shape and dimensions of nutlets of the Carpinus betulus type from the Miocene to the present day, drawn on the basis of the arithmetical means of their characters. In the centre of the polygon, variability of length and breadth in cells of the glabrous epidermis of these nutlets. Right: epidermis of pilose nutlets from the same populations drawn with the aid of an Abbe apparatus

Ryc. 16. Na lewo kształt i rozmiary orzeszków typu *Carpinus betulus* od miocenu po dzień dzisiejszy, narysowane na podstawie średnich arytmetycznych ich cech. W środku wieloboki zmienności długości i szerokości komórek nagiej skórki tych orzeszków. Na prawo rysunki skórki orzeszków owłosionych z tych samych populacji, narysowane za pomocą aparatu Abbego

On the left side of Text-fig. 16 are shown the contours of hornbeam nutlets from the corresponding samples drawn on the basis of the arithmetic means of six characters. Here it comes out quite clearly that the size and shape of the epidermal cells is connected with the species and not with the dimensions of the nutlet.

The picture given in the middle column of Text-fig. 16 refers to a series of measurements made on a larger number of glabrous nutlets. This is why we see such a scale of variability; it was possible to check the arithmetic means of the length: breadth ratio in the nutlets; in all samples this is approximately the same. In every fossil flora in which the species

C. betulus appeared, however, a certain percentage of pilose nutlets with characters also appropriate to this species was found as well as glabrous nutlets. In the last column, therefore, fragments of the epidermis of these nutlets, selected at random, and which could not be studied biometrically (see p. 50), have been sketched by means of a drawing apparatus. Both the shape and dimensions of the epidermal cells, as well as the characteristic arrangement by which the cells surrounding hairs, rayed out like petals, of a flower divided transversely, could be observed in all the specimens studied.

Text-fig. 16 also suggests a remark on the history of the species C. betulus, as the problem of the relation of the recent species with large fruits and the Tertiary species with small fruits is very interesting. From the author's previous publications it is known that the large-fruited type of C. betulus existed as early as the Upper Tertiary, although the small--fruited type was numerically predominant. The complete morphological and anatomical similarity of the two forms suggests that they had a common origin, or that one of these forms originated from the other. It is now known that the appearance of large forms is often connected with an increase in the number of chromosomes. This is usually accompanied, however, by an increase in the cell dimensions, as is easily seen in the epidermal cells of some plant species. Wettstein (1942) established this in his study on the epidermis of the diploidal and tretraploidal poplar. In our case we cannot assume that the recent species C. betulus is polyploidal as compared with its Tertiary small-fruited counterpart, since the dimensions of its epidermal cells were not correlated with those of the nutlets. It should be added that the present species of the genus Carpinus do not on the whole differ from one another in the chromosome number, which is very low, since 2n = 16; only in C. betulus do some authors give 32 and 64 besides the number 16.

# B. Carpinus turczaninowii type

Among the recent species studied by the author there were only two, *C. betulus* and *C. turczaninowii*, which exhibited similarity ich the perigone structure of their fruits. The author was often struck by this similarity during her studies, and the thought occurred that it was perhaps this which made it difficult to differentiate these species in the fossil state. Careful observation of Text-figs. 1 and 5 and then of the graphs in Text-figs. 7 and 8 and the photographs in Plates III, V and VI convinced her that in the structure of the epidermal cells of *C. turczaninowii* there is a unique character, which consists not only in their dimensions but also in the stream-lined shape of their walls, markedly bullate and with almost no angularities. In addition, the pits in the walls are so small

that they are almost invisible and are not revealed even under high magnifications. A certain similarity in the epidermal structure may be found only between the species C. turczaninowii and the East Asiatic C. cordata and C. japonica. The former, however, has unequally larger epidermal cells, while the latter has very small cells. Passing over the fact that it could scarcely be assumed that they grew in the Polish Pliocene, a mere glance at Text-fig. 7 excludes such a hypothesis. This was also the reason why it was decided that nutlet no. 1 from Text-fig. 13 and the similar nutlet no. 14 belonged to the species C. turczaninowii this was then confirmed by a more careful examination of the epidermis and parenchyma in Text-fig. 14 and especially in Text-fig. 15, where in detailed drawings made under high magnification the correct determination of nutlet no. 1 from Mizerna was quite evident. This achievement, the result of analysing the sample of 40 nutlets from Mizerna, was of importance in the further course of work. It may be added that the material of recent nutlets of C. turczaninowii studied by the author was composed of 16 specimens, of which 13 had glabrous perigones in the lower part of the nutlet, while the whole perigone was profusely pilose only in three nutlets from China. A drawing of one of these perigones made with the aid of an Abbe apparatus will be found in Text-fig. 21.

# C. Carpinus tschonoskii type

The possibility that hornbeams similar to the recent species *C. tschonoskii* grew in the Polish Neogene was suggested by Prof. W. Szafer when describing the fossil flora from the Lower Pliocene in Krościenko. He provisionally included 200 nutlets a little smaller than those of *C. betulus* in the species *C. cf. tschonoskii* Maxim., at the same time making it clear that this determination might be erroneous and that a small-fruited form of *C. betulus* might be distinguished as *C. cf. tschonoskii*. Since Berger found 14 fruit involucres of the *C. tschonoskii* type from the Lower Pliocene at Laarberg near Vienna, however, the chances of finding this species also in the Polish fossil flora have increased. In 1959 the present author ventured the hypothesis that the fruit involucre found by Steger at Kokoszyce near Rybnik should also be included in this species.

Among the nutlets of the *C. tschonoskii* type from Krościenko, 10 were subjected to epidermal investigations. Unfortunately only fragments of the perigones were preserved, though the epidermis of two nutlets strongly resembled that in the species *C. cf. tschonoskii*, and measurements of the epidermal and parenchymal cells, when these could be made, also indicated that they belonged to this species. Two nutlets found among those segregated as *Ostrya carpinofolia* were incontrovertibly so. The similarity of their epidermis to the very characteristic epidermis of *C. tschonoskii* was so great that no comment need be made. A photograph

of the epidermis of a recent *C. tschonoskii* fruit and of one fruit from the Pliocene in Krościenko may be seen in Plate IX. Epidermal investigations thus made it certain that hornbeams approximating the recent *C. tschonoskii* grew in the Polish Pliocene, though they could not have been common, since among the numerous hornbeam nutlets studied by the epidermal method only four have been found which could be included in this species with certainty.

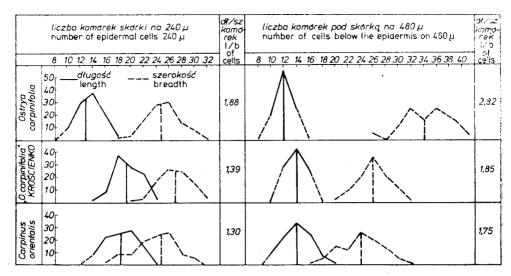
## D. Carpinus orientalis type.

The species *Carpinus orientalis* has not so far been reported in the Polish fossil flora by palaeobotanists, nor have its fruit involucres been found in Poland. None the less prof. J. Zabłocki, when describing hornbeam nutlets from Wieliczka as *C. polonica*, noted their similarity to the species *C. orientalis*, and even in the collection of these nutlets which he prepared for the Cracow Botanical Institute the recent *C. orientalis* nutlets below those from Wieliczka actually appear very similar to the fossil specimens in shape. It was not until the present authors anatomical studies in 1961 that the presence of *C. orientalis* nutlets in the Pliocene at Mizerna and Krościenko was demonstrated (see 1961, Pl. XI).

The finding of epidermis of fruits of the orientalis type in the materials from Mizerna has already been mentioned (Text-figs. 13, 14, 15). Still more were found by the present author among the nutlets from the Lower Pliocene in Krościenko sorted out and classified by Prof. W. Szafer as C. betulus L. fossilis. They have also been found among Lower Pliocene materials and described as C. tschonoskii and, what is extremely interesting, epidermal investigations on some of the nutlets from Krościenko, which on account of their small breadth were described as Ostrya carpinofolia Scop. fossilis, have shown that they should be included in the species C. orientalis. Three of these nutlets have been carefully studied by the epidermal method.

Text-fig. 17 shows in the centre of the graph the polygons of variability plotted on the basis of the results of measurements of the cells of the epidermis and first parenchymal layer in these three nutlets from Krościenko. In spite of the inaccuracy of the measurements of the parenchymal cells, which were not easily visible in all the preparations, it is quite certain that these nutlets belong to the species *C. orientalis*, and not to *Ostrya carpinofolia*. This is confirmed by the drawing in Text-fig. 18, the morphogram in Text-fig. 19 and the photograph of the epidermis of one of these nutlets in Plate IX.

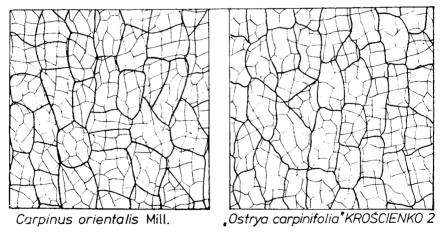
At the bottom of Text-fig. 19 are drawn the contours of recent nutlets of Ostrya carpinofolia Scop. and C. orientalis Mill. on the basis of the arithmetic means of their characters. Text-fig. 20 shows the scale of



Text-fig. 17. Variability of epidermal and parenchymal cells in three fruits from the Pliocene in Krościenko compared with recent fruits of the species Carpinus orientalis Mill. and Ostrya carpinifolia Scop.

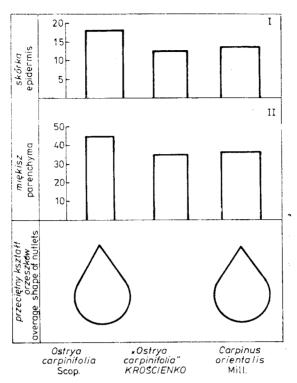
Ryc. 17. Porównanie zmienności komórek skórki i miękiszu trzech owoców z pliocenu w Krościenku z dzisiejszymi owocami gatunków Carpinus orientalis Mill.

i Ostrya carpinifolia Scop.



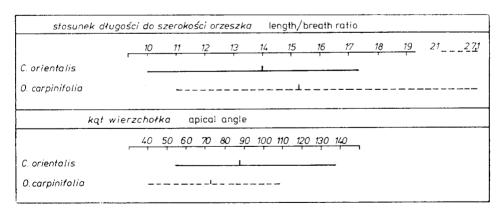
Text-fig. 18. Drawing of the epidermis and parenchyma of a recent fruit of Carpinus orientalis Mill. and one of the three fruits from the Pliocene in Krościenko, determined on the basis of the morphology as Ostrya carpinifolia Scop. fossilis Ryc. 18. Rysunek skórki i miękiszu dzisiejszego owocu Carpinus orientalis Mill i jednego z trzech owoców z pliocenu w Krościenku, określonych na podstawie morfologii jako Ostrya carpinifolia Scop. fossilis

variability in their most specific morphological characters, i. e. the lenghtbreadth ratio and the apical angle. These values coincide so markedly that the author, in spite of an extensive acquaintance with nutlets of



Text-fig. 19. Morphogram of the nutlets of which the variability is illustrated in Text-fig. 17

Ryc. 19. Morfogram orzeszków, których zmienność obrazuje ryc. 17



Text-fig. 20. Variability of the most important characters differentiating the nutlets of Carpinus orientalis Mill. and Ostrya carpinifolia Scop.

Ryc. 20. Zmienność najważniejszych cech odróżniających orzeszki Carpinus orientalis Mill. od Ostrya carpinifolia Scop.

both these types, would not undertake to separate a mixture of them into its component parts. None the less, the genus Ostrya has been found

among the Pliocene nutlets from Krościenko. This will be discussed in the next section.

## E. Genus Ostrya

If the epidermal structure of fruits of the recent species Carpinus orientalis Mill. and Ostrya carpinifolia Scop. are compared, it seems very simple to differentiate them, as the epidermis in each is fundamentally different. In C. orientalis the cell-walls are thin, while in O. carpini folia these walls are markedly thickened and full of pits, through which the cell contents may communicate (Text-fig. 5, 6; Pl. V, VI). It cannot be supposed that any doubt should arise in determining these fossil fruits by the epidermal method. Yet a persistent search for analogous pictures among the narrow elongated fossil fruits gave no result. In some of them indeed the epidermal cell walls were thickened here and there, but the usual picture seen was that of a pentagonal or hexagonal central lamella giving off only in the interior of the cells a sort of sparse brush, which might be compared with the pits in the markedly translucent cell-wall of the genus Ostrya (Pl. IX, D, E; Pl. XI, B) This suggested that the thick cell-walls in these fruits were constructed of some other substance than the medial lamella and the ducts, and that this substance was less resistant and underwent destruction more rapidly during fossilization. This led the author to look for fossil materials which might confirm her hypothesis. Materials of this description could only be found in Japan, where the fruits of the only species now growing in this country, Ostrya japonica Sargent, are so large and characteristic as compared with the hornbeams growing there that their correct determination in the fossil state presents no difficulties. The author turned to prof. Shigeru Miki, an eminent Japanese palaeobotanist, with a request for help. Unfortunately the materials received from prof. Miki were rather scanty and younger than the fruits from Krościenko, as they came from the Pleistocene. They were very valuable, however, with respect to the results of the study, as they had the same characters as some of the fruits from Krościenko which the author was inclined to recognize as belonging to the genus Ostrya.

In order to make an accurate study of the epidermal cells of the species Ostrya japonica and the structure of their walls, the following method was used. The epidermis, together with the strongly adherent first parenchymal, layer, was detached from the fruit and immersed in some drops of a strong solution of iodine green for a few minutes so that the solution had time to permeate the interior of the cells. The preparation was then very quickly washed first in alcohol and then in xylol and immersed in Canadian balsam. The pictures then obtained are illustrated in photographs

A and B in Plate X. In photograph A it may be seen that only some of the epidermal cells are filled with stain, while the others are pierced by the first layer of long narrow parenchymal cells with a shape very characteristic of Carpinus japonica, which confirms the systematic classification of this nutlet. In photograph B the epidermal cells are completely filled with stain and a very clear outline of their walls is obtained against this background. Comparison of these photographs will show both the dimensions and the shape of the epidermal and parenchymal cells of Ostrua iaponica, as well as the structure of their walls. It was not possible to fill the cells in the preparations of the perigones of these Japanese Pleistocene fruits with a strong solution of stain before immersing them in Canadian balsam, as this rose from the cells even when very quickly rinsed with alcohol, but all the elements characterizing the epidermis of the recent species O. japonica could be discerned in the preparations (Pl. X, C, D). The epidermal cell-walls of the Pleistocene fruits were so markedly translucent that in spite of their thickness the medial lamella was very evident. From the lamella branched out here and there striae, the remains of the pits in the thick cell-walls. These fruits were entirely similar to some of those found at Krościenko. A photograph of the epidermis of one of them may be seen in Plate XI, baside that of a recent fruit filled with stain. The epidermis of the two fruits D and E, of which photographs are shown in Plate IX, also probably belong to the genus Ostrya. It should be added that all the fruits from Krościenko determined by Prof. W. Szafer as belonging to the species Ostrya carpinifolia Scop. fossilis, both those which after epidermal tests were included in Carpinus orientalis and those which were classified as Ostrya, were completely glabrous.

#### 5. FRUITS FROM RUSZÓW AND WIELICZKA

In the preceding chapter much attention has been given to the structure of the epidermis and perigone of recent fruits of the genus Ostrya, and in particular to the Japanese species Ostrya japonica Sargent, since it is very characteristic and there is no fear that it might not be distinguished in the fossil state from fruits of the genus Carpinus. Thanks to the Japanese fossil material received from prof. Shigeru Miki, it was possible to conclude by analogy what the fossil fruits of this genus must have looked like in the European Pliocene deposits, where most probably we met the recent European species Ostrya carpinifolia Scop. This was the more important since the presence of fruits of Carpinus orientalis, of which the present area in Europe coincides with that of O. carpinifolia, has been established in the Polish Pliocene. If the area of the former

in the Pliocene extended to the south of Poland, it is very probable that the area of the latter, a species with the same climatic requirements today, also reached there. It should be repeated yet again that all the fruits studied by the author in her materials, both recent and fossil, classified as *Ostrya*, irrespective of whether they came from Europe or Japan, had glabrous fruits.

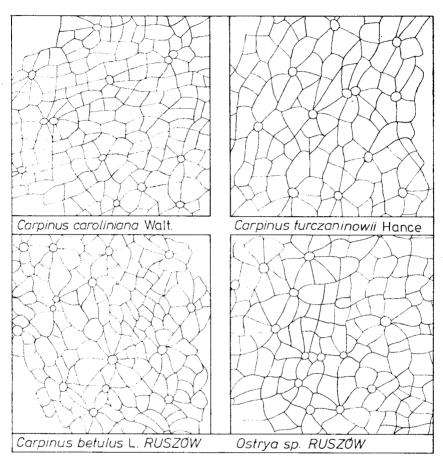
Since it has been ascertained that the genus Ostrya occurred in the Polish Pliocene, it is not in the least surprising that doc. A. Stachurska churska found in Ruszow in Silesia deposits, containing numerous fossil fruits, among which she determined 111 as belonging to the species Carpinus betulus and 33 to "Ostrya sp". Doc. A. Stachurska, to whom cordial thanks are again extended, kindly sent some of these fruits to the author to be studied by the epidermal method; they brought some interesting new problems into the investigation.

The determinations made by doc. A. Stachurska on the basis of the morphology of the fruits would have raised no doubts, if it had not been for the fact that examination of ten nutlets which she had included in the genus Carpinus and ten determined as belonging to the genus Ostrya showed that the epidermis was identical in both that this epidermis was constructed of cells with very delicate walls, so transparent that not one but several layers of parenchyma could be seen through them, and what was most important, this epidermis was thickly covered with hairs. The long narrow fruits of the Ostrya type and the short broad fruits of the Carpinus type did not differ at all in this respect. This was the first time that the author had met with a fossil material in which all the fruits were pilose. On the basis of their epidermis it might be assumed that all these fruits, both those with a rather broad lower part resembling Carpinus fruits in shape, and the narrow fruits resembling those of Ostrya in shape, belonged to the same population (Pl. XI, C, D; Text-fig. 21), a population without a counterpart in the recent flora.

The author's researches up to the present have shown that among the recent fruits of the genus Carpinus only in the American species C. caroliniana are the fruits always pilose. The presence of both pilose and glabrous fruits in the same population is characteristic of the species C. betulus. This is probably a genetic character connected with this species. It also appears in populations of C. betulus from the Miocene up to the present day (Text-fig. 16), and with this is connected the shape of the cells surrounding the hairs, as mentioned on page 43. Such cell shapes were not observed in the fruits from Ruszów. This led the author to make a thorough examination of both the recent and the fossil pilose fruits of the genus Carpinus from the point of view of the shapes of their epidermal cells. Since, however, the biometric method cannot be applied to pilose epidermis, other means were used, which may be called the visual method. This consisted in the accurate drawing of the cells of

the pilose epidermis by means of an Abbe apparatus and the comparison of these drawings, referring to Text-fig. 16.

Text-fig. 21 shows a fragment of epidermis of *C. caroliniana* with distinctly angular cells drawn under the same magnification as in Text-fig. 16. The "pseudo-flower petals" already described did not stand out



Text-fig. 21. Drawings of pilose perigones made with the aid of the Abbe apparatus. Top, nutlets of the recent Carpinus caroliniana Walt. from North America and nutlets of Carpinus turczaninowii from China. Bottom, epidermal cells of two fossil fruits, one determined by A. Stachurska as Carpinus betulus L. and the other as Ostrya sp.

Ryc. 21. Rysunki perigonów owłosionych wykonane za pomocą aparatu Abbego. U góry orzeszek dzisiejszego Carpinus caroliniana Walt. z Ameryki Północnej oraz orzeszek Carpinus turczaninowii pochodzący z Chin. U dołu komórki skórki dwóch owoców kopalnych, jednego oznaczonego przez A. Stachurską jako Carpinus betulus L. i drugiego, oznaczonego jako Ostrya sp.

so clearly from the other epidermal cells. This was an entirely different type of epidermis from that in the species *C. betulus*. There was, however, a great similarity between the epidermis of the nutlets from Ruszów and

that of the pilose fruits of the species *C. turczaninowii* from China. The author does not now remember the origin of this material, but it was certainly included in her collections while she was working on the morphology and then the anatomy of hornbeam nutlets from herbaria and arboreta in Poland and abroad. It was composed of only a few specimens, and in any case did not represent a larger native population of this species. All the other fruits of the species *C. turczaninowii* examined by the author had glabrous nutlets.

It has already been suggested in a previous chapter, when describing the glabrous perigones of hornbeams from Mizerna (see p. 39), that some fruits from the Polish Pliocene exhibit great similarity to the species C. turczaninowii. It should now be considered how the materials from Ruszów determined as belonging to the genus Ostrya may be brought into relation with the Pliocene materials from Mizerna and Krościenko. The morphology of the last-mentioned fruits, as well as the character of the flora, indicates that the determination of the nutlets found there as Ostrya carpinifolia Scop. fossilis was often correct, and the only error might lie in their confusion with the fruits of C. orientalis, as mentioned in the previous chapter. The fruits found at Ruszów were determined by doc. A. Stachurska as belonging to the genus Ostrya, but she did not attempt do identify them with the only species now living in Europe, O. carpinifolia, while the hornbeams found there have been identified by the present author without hesitation as belonging to the species C. betulus L. Nutlet no. 1 in Plate XIX has even the dimensions of a nutlet of our recent C. betulus, while the others of which photographs have been given resemble both in dimensions and shape the Tertiary nutlets determined by the author on the basis of their morphology and anatomy (1960 and 1961) as typical of the Polish Pliocene.

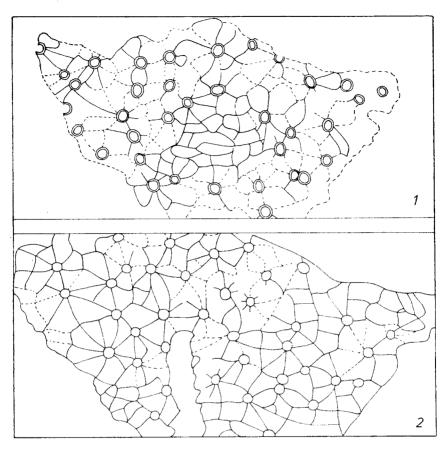
A second striking fact in the material from Ruszów is the large number of Carpinus and Ostrya nutlets found there. Fossil deposits of this kind, containing numerous fruits of two species belonging to two different genera (144 speciments in all), and in addition 78 remains representing 30 species or genera of mainly exotic plants, must be a palaeobotanical rarity. It would be evidence that the given plants bave been found "in situ". The present author will not attempt to comment on this, but will merely note that the complete similarity of the epidermis in the nutlets from Ruszów, 20 of which have been examined, all pilose and completely similar to one another, does not permit her to connect them either with any of the recent hornbeams of the species C. betulus or with recent species of the genus Ostrya. From the point of view of their epidermis, the whole of the materials from Ruszów should be reckoned as belonging to the same population which, however, was quite different from the Tertiary population of the genus Carpinus hitherto known and described in the present

treatise. In the latter population glabrous and pilose nutlets were found side by side, just as in the recent species C. betulus.

Since it was impossible to determine the specific classification of the nutlets by the biometrical method, which can only be applied to glabrous fruits, the only thing the author could do was to make very accurate drawings of pilose perigones from a population of recent hornbeams. Many photographs were taken, but were unsuitable for study, because too many layers of thin-walled cells were seen in them and it was difficult to distinguish the epidermis from the parenchyma (Pl. XI, C, D). The similarity on the basis of the structure of the epidermis was therefore determined by purely visual means.

The necessity of a more thorough study of the shape of the epidermal cells surrounding the hairs in the fruits from Ruszów compelled the author to go back a little and study the pilose materials which had been left out of consideration in the biometrical investigations. The starting point was Text-fig. 16, in which it was shown that C. betulus has not only not exhibited any differences in the structure of the glabrous epidermis from the Miocene up to the present day, but has also had typical specific characters in the pilose fruits, i. e. the cells surrounding the hairs frequently had the appearance of being divided transversely, and so did not clearly differ in size from the other epidermal cells. With reference to this figure a number of drawings were made of the epidermis in C. caroliniana, a species which today has (as already mentioned) always pilose fruits, and then drawings of fruits of C. turczaninowii from China, the only pilose fruits of this species which the author possessed in her materials. Parts of these drawings are shown in Text-fig. 21, where it is seen that the cells surrounding the hairs in the species C. caroliniana differ little either in size or shape from the other epidermal cells. The cells of the pilose epidermis of C. turczaninowii from China were quite different. They resembled in their stream-lined shape the cells of the glabrous epidermis of nutlet no. 1 from Mizerna, which on the basis of a thorough analysis had been classified as belonging to the species C. turczaninowii (Text-figs. 13—15). Yet again, this time on the basis of the pilose epidermis, the probability was ascertained of the appearance in the Polish Neogene of a species approximating the recent C. turczaninowii.

This observation on the specificity of the nutlets found in the Pliocene deposits at Ruszów is supported by comparing them with the epidermis of the two nutlets from Wieliczka drawn in Text-fig. 22. It was comletely similar to the materials from Ruszów as regards both the dimensions of the cells and their stream-lined contours, as may be seen by comparing Text-figs. 21 and 22. Unfortunately the nutlets from Wieliczka, which came from deposits not of soil but of salt, were extremely brittle and the perigones were badly cracked. Preparations could be obtained only by



Text-fig. 22. Epidermis of two fruits from the Miocene in Wieliczka, described by Zabłocki as Carpinus polonica

Ryc. 22. Skórki dwóch owoców z miocenu w Wieliczce, opisanych przez Zabłockiego jako Carpinus polonica

carrying out the whole procedure of separating the epidermis on a slide, when as a rule the nutlet itself disintegrated. For this reason not many of these preparations were made, and distinct fragments of their epidermis were obtained only from comparatively undamaged nutlets. They all looked exactly alike. The possibility of relating the materials from Ruszów, which the author could not connect with the Tertiary materials from Mizerna, Krościenko, Gliwice or Domański Wierch, with the materials from Wieliczka seems to be very valuable for the history of the genus *Carpinus* in **Poland**.

#### 6. SUMMARY OF RESULTS

The application of the epidermal method in the determination of fossil fruits of the genera Carpinus and Ostrya has shown that this method may be successfully used for the elaboration of materials previously segregated by palaeobotanists on the basis of their morphology. In some cases it has enabled the determinations of specialists to be confirmed, and in others it has made further segregation possible, or the demonstration of similarities between materials coming from different geological eras. It has also enabled conclusions to be drawn as to the character of the populations from which the given remains originated. Again, it has led to the possibility of making incontrovertible statements on materials of species already studied by palaeobotanists but which could not be distinguished on the basis of their morphology alone, as for example the occurrence of the species Carpinus orientalis in the Polish Pliocene. In this way confirmation has been obtained of what the author had already, demonstrated in 1961 on the basis of anatomical studies on the genus Carpinus. The epidermal method has also made it possible to show that in the Polish Pliocene there were populations, such as the population from Ruszów, which have no counterparts in recent flora and to draw conclusions as to their history and their connections with materials from the earlier Tertiary.

This ends the description of the attempt to apply epidermal investigations to Polish fossil materials. The author repeats once more that these studies on fossil materials were made only in order to test the value of the epidermal method in investigations on the fossil fruits of the horn-beams and Ostrya. She has tried to carry out these studies as objectively as possible, and to note the results precisely. In summarizing them it should be stated that while the epidermal method, extremely laborious and time-consuming, cannot or rather should not be applied to materials which have not yet been studied by palaeobotanists or sorted out on the basis of the morphology of the fossil remains, the possibility of confirming the results of their determinations by the epidermal method may not only facilitate some determinations but also indicate the relationship or the path of evolution of species or genera in past ages.

Institute of Botany of the Polish Academy of Sciences Department of the Variability of Plants 31-512 Kraków, ul. Lubicz 46

Instytut Botaniki Polskiej Akademii Nauk Zaklad Zmienności Roślin

#### REFERENCES

- Brem M. 1953. Flora interglacjalna z Ciechanek Krzesimowskich. Interglacial flora from Ciechanki Krzesimowskie by Łęczna. Acta Geol. Polon. 3: 475—480.
- Brem M., Sobolewska M. 1950. Wyniki badań botanicznych osadów interglacjalnych w dorzeczu Niemna. The results of botanical investigations of interglacial deposits in the Niemen basin. Acta Geol. Polon. 1: 335—364.
- Jentys Szaferowa J. 1958. Znaczenie materiałów czwartorzędowych dla badań nad ewolucją historyczną roślin. Kosmos A. 7(1): 3—8.
- 1958. Importance of the Quaternary materials for research on the historical evolution of plants. In: Ver. Geobot. Inst. Rübel 34: 67—73.
- 1958. The genus Carpinus in the palaeobotanical literature. Monogr. Bot. 7: 3-59.
- 1960. Morphological investigations of the fossil Carpinus nutlets from Poland. Badania morfologiczne nad kopalnymi orzeszkami rodzaju Carpinus w Polsce. Acta Palaeob. 1: 1—41.
- 1961. Anatomical investigations on fossil fruits of the genus Carpinus in Poland. Badania anatomiczne nad kopalnymi owocami rodzaju Carpinus w Polsce. Acta Palaeob. 2: 1—33.
- Jentys Szaferowa J., Białobrzeska M. 1953. Owoce rodzajów Carpinus i Ostrya. Fruits of the genera Carpinus and Ostrya. Prace Inst. Geol. 10: 5—35.
- Kozłowska A. 1923. Flora międzylodowcowa spod Rakowa. La flore interglaciaire des environs de Raków. Acta Soc. Bot. Polon. 1(4): 213—232.
- Pięch K. 1932. Das Interglazial von Szczerców (östlich v. Wieluń Wojewodschaft Łódź). Rocz. Polsk, Tow. Geol. 8: 51—132.
- Stachurska A., Dyjor S., Sadowska A. 1967. Plioceński profil z Ruszowa w świetle analizy botanicznej. Pliocene section at Ruszów in the light of botanical analysis. Kw. Geol. 2: 353—371.
- Stark P., Firbas F., Overbeck F. 1932. Die Vegetationsentwicklung des Interglazials von Rinnersdorf in der östlichen Mark Brandenburg. Abh. Naturw. Ver. Bremen. 28: 105—130.
- Szafer W. 1926. O florze i klimacie okresu międzylodowcowego pod Grodnem. Über den charakter der Flora und des Klimas der letzten Interglazialzeit bei Grodno in Polen. Spraw. Kom. Fizjogr. PAU. 60: 1—40.
- 1939. Nowe znalezienia flory plejstoceńskiej w Polsce. Neue Fundorte der pleistozänen Flora in Polen. Biul. Państw. Inst. Geol. 9: 1—3.
- 1946—1947. Flora plioceńska z Krościenka n. Dunajcem. The Pliocene flora of Krościenko in Poland. I. Część ogólna. General part. II. Część opisowa. Descriptive part. Rozpr. Wydz. Mat.-Przyr. PAU. 72, (1): 1—162, (2): 1—213.
- 1954. Plioceńska flora okolic Czorsztyna i jej stosunek do plejstocenu. Pliocene flora from the vicinity of Czorsztyn (West Carpathians) and its relationship to the Pleistocene. Prace Inst. Geol. 11: 5—224.
- 1961. Mioceńska flora ze Starych Gliwic na Sląsku. Miocene flora from Stare Gliwice in Upper Silesia. Prace Inst. Geol. 33: 5—205.
- Środoń A. 1950. Rozwój roślinności pod Grodnem w czasie ostatniego interglacjału. The development of vegetation in the Grodno area during the last interglacial period. Acta Geol. Polon. 1: 365—400.
- Tołpa S. 1952. Flora interglacjalna w Kaliszu. Interglacial flora at Kalisz. Biul. Inst. Geol., 68: 73—120.
- Zabłocki J. 1927. Tertiäre Flora des Salzlagers von Wieliczka (Erster Teil). Acta Soc. Bot. Pol. 5 (1): 174—208.

- 1930. Tertiäre Flora des Salzlagers von Wieliczka (Zweiter Teil). Acta Soc. Bot. Pol. 7 (1): 139—163.
- 1930. Flora kopalna Wieliczki na tle ogólnych zagadnień paleobotaniki trzeciorzędu. Die fossile Flora von Wieliczka und die Allgemeinen Probleme der Paläobotanik des Tertiärs. Acta Soc. Bot. Pol. 7 (2): 215—240.

#### STRESZCZENIE

BADANIA NAD SKÓRKĄ DZISIEJSZYCH I KOPALNYCH OWOCÓW CARPINUS I OSTRYA ORAZ ICH ZNACZENIE DLA SYSTEMATYKI I HISTORII TYCH RODZAJÓW

Część I

## PERIGONY DZIŚ ŻYJĄCYCH GATUNKOW

#### OZNACZANIE GATUNKÓW NA PODSTAWIE PRZEKROJÓW PERIGONÓW

W czasie badań anatomicznych nad kopalnymi orzeszkami rodzaju Carpinus (Jentys-Szaferowa 1961) zwrócono uwagę, że często na poprzecznych przekrojach tych owoców widać resztki zewnętrznej części ich ścian. czyli tak zwanego perigonu, który składa się ze skórki i kilku warstw cienkościennych komórek. Nasuneło to myśl, że gdyby gatunki należące do rodzajów Carpinus i Ostrya różniły się między sobą pod względem budowy perigonów, można by spróbować określać na tej podstawie przynależność systematyczną materiałów kopalnych. W tym celu przebadano dokładnie dzisiejsze owoce i wykonano przekroje perigonów w najszerszej części orzeszków, zwracając specjalną uwagę na budowę skórki i pierwszych warstw miękiszu. Zarówno bowiem skórka, jak i pierwsza warstwa miękiszu mają błony skutynizowane, co widać przy barwieniu preparatów zielenią jodową. Barwią się one wtedy na intensywny zielony kolor, podczas gdy pozostałe komórki miękiszu barwią się na fioletowo. Skórka i część miękiszu mają więc szanse zachowania się w materiale kopalnym.

Różnice w budowie poprzecznych przekrojów perigonów dzisiejszych orzeszków okazały się dostatecznie duże, aby można było ułożyć na ich podstawie klucz do oznaczania gatunków, który przytaczam. Wprawdzie klucz ten znalazł małe zastosowanie przy oznaczaniu materiałów kopalnych, ale uzupełniony rysunkami na ryc. 1 - 4 i fotografiami na Tablicy I ułatwia zrozumienie budowy perigonu widzianego z góry.

Klucz do oznaczania gatunków rodzajów *Carpinus* i *Ostrya* na podstawie poprzecznych przekrojów perigonów (ryc. 1 i 2, Tab. I)

1.	Komórki skórki nie różnią się wyraźnie od leżących pod nią komór miękiszowych. Wiązki eliptyczne silnie wydłużone.	·ek
	Perigon w miejscu wiązki nie poszerzony	2
1.		_
	grubością błony od leżących pod nią komórek miękiszowych	3
2.	Naczynia są mniejsze w przekroju od komórek skórki	Ū
	Ostrya virginiana	
2.	Naczynia nie są mniejsze w przekroju od komórek skórki	
	Ostrya japonica	
3.	- · · ·	4
3.		5
4.		
	i zgrubieniem zewnętrznej części błony od prostokątnych, często	
	spłaszczonych komórek miękiszowych. Kutykula wyraźna	
	· · · ·	
4.	Komórki skórki znacznie mniejsze od komórek miękiszowych, ale	
	nie różniące się od nich kształtem ani grubością błony. Kutykula	
	cienka, niewyraźna	
<b>5</b> .	Wiązki bardzo małe, okrągłe. Średnica ich odpowiada ± połowie	
	szerokości perigonu	6
5.	Wiązki o średnicy znacznie większej od połowy szerokości peri-	
	gonu	7
6.	- G	
	podkowiasto wypukła, często szersza od światła komórek, kuty-	
	kula wyraźna	
6.	Błona komórek skórki równomiernie zgrubiała, węższa od świa-	
	tła komórek, kutykula cienka, mało widoczna . Ostrya carpinifolia	
7.	the state of the s	
	wyraźnie odcinających się od reszty komórek perigonu	
	· · · · · · · · · Carpinus laxiflora	
7.	or o	
	cych się od reszty komórek perigonu	8
8.	The state of the s	
	kulą, z wierzchu wypukłe, dzięki czemu brzeg przekroju jest kar-	
_	bowany	
8.		9
9.	Wiązki umieszczone w dolnej części perigonu. Włosy obfite, dłu-	
	gie, często dłuższe od średnicy wiazek Carpinus caroliniana	

10

9.	Wiązka umieszczona w środkowej części perigonu, wiosy, o lie
	są, bardzo krótkie
l 0.	Komórki skórki wielokrotnie mniejsze od komórek miękiszowych.
	Parigon w miejscu wiązki silnie poszerzony. Liczba szeregów ko-
	mórek miękiszu dochodzi tam do 14 Carpinus betulus
10.	Komórki skórki zaledwie dwa do trzech razy mniejsze od komó-
	rek miękiszowych. Perigon w miejscu wiązki słabo poszerzony,

liczba szeregów komórek miękiszu nie przekracza siedmiu . . Carpinus turczanowii

#### OZNACZANIE GATUNKÓW NA PODSTAWIE PERIGONÓW WIDZIANYCH Z GÓRY

### Charakterystyka ogólna i metody pracy

Następną czynnością, po poznaniu budowy anatomicznej perigonu na podstawie przekrojów poprzecznych, było zrobienie preparatów, na których można było obserwować z góry epidermę oraz leżące pod nią warstwy miękiszu.

Próbowano różnych sposobów badania. Przede wszystkim próbowano oddzielić samą kutykulę metodą acetolizy, okazało się to jednak bezcelowe. Chociaż można było wtedy obserwować na kutykuli zarys komórek skórki i zorientować się w ich rozmiarach, nie dawało to pojęcia o budowie ich ścian, a tym bardziej leżącej pod nią warstwy miękiszu, które to cechy mają znaczenie diagnostyczne dla gatunków w obrębie rodzajów Carpinus i Ostrya. Postępowano więc dwojako. Jednym ze sposobów było wygotowanie orzeszków w wodzie z sodą, aby wywołać zmiękczenie perigonu, po czym zdzierano jego zewnętrzną warstwę tak, aby oddzielić stosunkowo jak najcieńsze skrawki. Można było wtedy obserwować nie zmienioną powierzchnię perigonu, a więc zarówno włoski pokrywające często jego powierzchnię lub brzegi jego listków, jak i gruczoły żywiczne oraz kryształy szczawianu wapnia zawarte w komórkach skórki. Trudno jednak było obserwować w tych warunkach budowę ścian komórek perigonu, tym bardziej że komórki nie pozbawione treści źle przepuszczały światło.

Lepsze wyniki otrzymano badając epidermę oraz leżącą pod nią warstwę miękiszu następującą metodą: orzeszek przeznaczony do badania gotowano w probówce przez około 5 minut w małej ilości wody z rozpuszczonym w niej kryształkiem sody (Na<sub>2</sub>CO<sub>3</sub>). Po szybkim zdekantowaniu wody (niezupełnym, tak aby zostało na dnie trochę płynu) wprowadzano do probówki parę kropel perhydrolu (H<sub>2</sub>O<sub>2</sub>) i przez chwilę podgrzewano. Wywoływało to początkowo lekkie burzenie, a następnie gwałtowną reakcję, połączoną z wydzielaniem banieczek gazu, po czym zewnętrzna część perigonu, złożona zwykle ze skórki i jednej lub dwóch warstw miękiszu, zsuwała się z owocu jak rękawiczka. Wtedy wylewano płyn z probówki na szalkę z zimną wodą, skąd przenoszono pływającą w wodzie skórkę na

szkielko podstawowe, na którym można było zrobić trwały preparat do badań mikroskopowych. Analogicznie można było postępować z orzeszkami kopalnymi, na których zachował się perigon. Nie niszczyło się przy tym samego orzeszka, chyba że był popękany i rozleciał się przy gotowaniu. Było to pierwsze, o ile autorce wiadomo, zastosowanie metody epidermalnej do badania owoców kopalnych.

## Badania szczegółowe

Szczegółowe badanie perigonów widzianych z góry składa się z trzech części. Są to: I. Opisy zewnętrznego wyglądu oraz szczegółów budowy ścian komórek, skórki i miękiszu, poparte rysunkami i fotografiami (ryc. 5 i 6 oraz Tablice II – IV). II. Pomiary długości i szerokości komórek skórki oraz pierwszej warstwy miękiszu (ryc. 7 i 8, tabele 1 i 2). III. Wzajemne ustosunkowanie tych elementów uzupełnione średnimi rozmiarami szparek i całych orzeszków (ryc. 9). Wszystko to tworzy jakby klucz do określania materiałów kopalnych.

Spomiędzy wymienionych wyżej metod oznaczania przynależności gatunkowej orzeszków, należących do rodzajów Carpinus i Ostrya, najważniejsze okazały się pomiary wielkości komórek skórki i pierwszej warstwy miękiszu i one to odgrywały dużą rolę przy oznaczaniu materiałów kopalnych. Metoda ta mogła być zastosowana jednak tylko do owoców o skórkach nie pokrytych włosami, bo tylko te miały mniej więcej regularne kształty. Pomiary wykonywano bowiem w ten sposób, że liczono liczbę komórek napotkanych wzdłuż i w poprzek perigonu na średnicy pola widzenia mikroskopu. Długość zaś tej średnicy obliczona w mikronach odpowiadała 240  $\mu$  przy większym powiększeniu, zaś 480  $\mu$  przy mniejszym powiększeniu. Jeżeli więc na średnicy 240 μ znajdowało się 10 komórek perigonu, to przeciętne ich wymiary wynosiły 24 μ. Jeżeli jednak skórka była pokryta włosami, które są zawsze otoczone silnie wydłużonymi komórkami, to liczby komórek ich skórki o charakterystycznych dla niektórych gatunków kształtach spotkanych na średnicy pola widzenia mikroskopu nie były porównywalne ani w obrębie tego samego orzeszka, ani też między poszczególnymi orzeszkami.

Przystępując do powyższej pracy autorka sugerowała się informacją, którą podaje W i n k l e r w swojej monografii rodziny Betulaceae. Pisze on bowiem, że jedynie gatunek Carpinus caroliniana ma owoce owłosione, u innych występują tylko na listkach perigonów lub na ich brzegach (ryc. 1 i 4). Dlatego autorka oparła się w badaniach biometrycznych na orzeszkach nagich, licząc u C. caroliniana komórki tylko w nielicznych miejscach perigonu, gdzie nie natrafiono na włosy. W czasie badań okazało się jednak, że informacja W i n k l e r a dotycząca owłosienia orzeszków grabów nie okazała się ścisła i że nie można jej uważać za cechę związaną tylko z gatunkiem C. caroliniana. Dlatego do oznaczania orzeszków zarów-

no dzisiejszych, jak kopalnych, pokrytych włosami, zastosowano inną metodę, nazwaną wizualną, która jest opisana w rozdziale 5 drugiej części pracy i zilustrowana na ryc. 16—22.

Na ryc. 7 i 8 zamieszczono wieloboki zmienności, będące wynikiem obliczania ilości komórek na średnicy pola widzenia mikroskopu wzdłuż i w poprzek orzeszka. Dla każdego z gatunków narysowano charakterystyczne dla niego wieloboki zmienności szerokości i długości komórek skórki (ryc. 7) i miękiszu (ryc. 8). Odpowiednia skala rośnie od lewej do prawej. Pod nią zamieszczono drugą skalę po przeliczeniu górnej skali na mikrony i ta skala maleje oczywiście od lewej do prawej. Jeżeli bowiem spotkamy u jakiegoś gatunku tylko 8 komórek na średnicy pola widzenia 240 μ, to przeciętny ich wymiar na szerokość względnie na długość będzie 30 μ. Jeżeli jednak tych komórek będzie na takiej samej średnicy aż 34, to ich przeciętny wymiar będzie tylko około 7 μ. Stosunek długości do szerokości komórek skórki i miękiszu dla każdego z badanych gatunków podano w ostatniej kolumnie ryc. 7 i 8.

Opisane wyżej ryciny, poza ścisłością informacji, dają szybką orientację w charakterze komórek skórki i miękiszu. Rzut oka na zamieszczone tam wykresy informuje nas, że np. gatunek Carpinus betulus ma komórki skórki nieznacznie tylko dłuższe od swej szerokości, podczas gdy u Ostrya carpinifolia są one wybitnie długie i wąskie. Znacznie silniej zaznacza się to na miękiszu (ryc. 8), gdzie wyraźnie można odróżnić za pomocą tej cechy rodzaj Carpinus od rodzaju Ostrya. Na ryc. 9 mamy wszystkie powyższe wiadomości przedstawione w schematach, przy czym, aby uwidocznić lepiej różnice w kształcie komórek skórki, narysowano je tam w dwa razy większej niż komórki miękiszu podziałce. Rycinę 9 uzupełniono przeciętnym kształtem komórek szparek oraz rozmiarami i kształtem odpowiednich orzeszków, narysowanych na podstawie średnich arytmetycznych ich cech, podanych w rozprawie autorki z r. 1960. Wszystko zaś tworzy jakby klucz do oznaczania przynależności gatunkowej nagich orzeszków kopalnych.

#### Część II

#### MATERIAŁY KOPALNE

Zastosowanie metody epidermalnej do oznaczania przynależności systematycznej materiałów kopalnych wypróbowano na owocach *Carpinus* i *Ostrya*, znajdujących się w zbiorach Zakładu Paleobotaniki Instytutu Botaniki PAN. Wykaz zbadanych materiałów zestawiono w tabeli 3.

Badania rozpoczynano zawsze od obserwacji nad powierzchnią skórki (rozdz. 3 A), co dawało pierwsze wskazówki ewentualnej przynależności systematycznej owoców. Jak bowiem wynika z ryc. 10, skórka owoców

zarówno dzisiejszych, jak kopalnych może być, w zależności od gatunku wzglednie od znaleziska (jeżeli chodzi o materiały kopalne), albo naga albo owłosiona, albo też owoce owłosione i nagie występują obok siebie w tym samym materiale. Jest to czasem jego cechą charakterystyczną, jak to jest w przypadku materiałów zawierających prawie wyłącznie owoce Carpinus betulus. Właściwości skórki orzeszków dziś żyjących gatunków opisała autorka na podstawie zgromadzonych przez nią materiałów prawidłowo określonych przez systematyków. Charakteryzowały one więc dobrze dziś żyjące rośliny. Materiały kopalne, choć oznaczone przez paleobotaników, rzadko kiedy zawierały jedna jednostkę systematyczną. Zdarza sie to w polskich materiałach czwartorzędowych, reprezentujących florę mało różniącą się od dzisiejszej, gdzie według wszelkiego prawdopodobieństwa występował tylko gatunek Carpinus betulus (ryc. 10). Zadanie autorki polegało więc w pierwszym rzędzie na tym, aby jeżeli opracowujący paleobotanik podawał tylko jeden gatunek, potwierdzić to oznaczenie, a poza tym odszukać w jego materiałach ewentualną domieszkę innych gatunków badanych rodzajów, usiłować je oznaczyć lub też dowieść, że materiał kopalny nie miał odpowiedników wśród żyjących dziś w Polsce roślinności.

Następną czynnością po obserwacji powierzchni skórki było zbadanie rozmiarów jej komórek (rozdz. 3 B). Określano je w sposób podany w części pierwszej, a mianowicie licząc komórki spotkane w poprzek perigonu na średnicy pola widzenia mikroskopu o znanych wymiarach. Wyniki badań epidermalnych nad niektórymi orzeszkami opisanymi przez paleobotaników ilustruje ryc. 11. Z lewej strony tej ryciny zobrazowano długość orzeszków typu Carpinus betulus wyodrebnionych z flor kopalnych, z prawej strony zaś mamy liczbę komórek ich skórki. Z lewej strony ryciny widzimy, że owoce z interglacjałów mało różniły się rozmiarami od dzisiejszych, dopiero w trzeciorzędzie pojawia się forma małoowocowa obok sporadycznie tylko spotykanej formy o dużych owocach (Jentys-Szaferowa 1960). Z prawej strony ryc. 11 widzimy, że zmniejszenie rozmiarów trzeciorzędowych orzeszków nie wpłynęło zupełnie na rozmiary komórek ich skórki. Były one równie duże wszędzie tam, gdzie występował gatunek Carpinus betulus lub jego trzeciorzędowy odpowiednik, Rozmiary komórek skórki są tu widocznie związane z gatunkiem. W Mizernej jednak pojawia się mały procent orzeszków o drobnych komórkach skórki, co świadczyłoby, iż mimo że Prof. Szafer zaliczył wszystkie znalezione tam orzeszki do gatunku C. betulus L., to jednak w pliocenie górnym była domieszka orzeszków innych gatunków. Bedzie o tym mowa szerzej w rozdziale 4. Obecność orzeszków o małych komórkach skórki zarysowuje się jeszcze wyraźniej na wykresie z Krościenka i Domańskiego Wierchu.

Autorka pomija tu świadomie owoce opisane przez Prof. Szafera w plioceńskiej florze z okolic Czorsztyna jako Carpinus minima, gdyż

zdaniem jej mają one inną budowę anatomiczną niż owoce rodzaju *Carpinus* (Jentys-Szaferowa 1958, 1960). Ważną jej cechą jest rozmieszczenie wiązek nie w zewnętrznej, niezdrewniałej części owocni, czyli w perigonie, którego nie znaleziono na żadnym z badanych orzeszków "*Carpinus minima*", ale wewnątrz zdrewniałych ścian jego owocni. Owoce te wymagają osobnego opracowania i dlatego nie zostały włączone do badań autorki nad owocami rodzaju *Carpinus* (1958, 1960).

Rozdział 4 jest poświecony indywidualnym badaniom nagich orzeszków kopalnych. Przed przystąpieniem do tych badań starała się autorka zorientować w zmienności indywidualnej rozmiarów komórek skórki i miekiszu owoców najcześciej podawanego przez paleobotaników gatunku Carpinus betulus. Wyniki tych badań zestawiono na ryc. 12. Na górze tego wykresu zamieszczono długość i szerokość komórek skórki, określoną na podstawie 200 spostrzeżeń robionych na dzisiejszych orzeszkach tego gatunku z różnych stron Europy. Zamieszczone poniżej wartości, znalezione u losowo wybranych dziewięciu współczesnych i dziesięciu kopalnych orzeszków tego gatunku, nigdzie poza tę zmienność nie wykraczają. Opierając się na tym wybrano z 200 orzeszków z Mizernej losowo próbę złożoną z 40 orzeszków i zanalizowano ją szczegółowo na podstawie ich epiderm. Między nimi 22 miało perigony owłosione, a 18 nagie. Z tych ostatnich trzy nie nadawały się do pomiarów, analizę pozostałych piętnastu przedstawia ryc. 13. Budzą tam zainteresowanie dwa orzeszki o komórkach większych od spotykanych u C. betulus (nr 1 i 14) i trzy o komórkach mniejszych (nr 13, 16 i 38); ogółem było ich tam 28—34 na polu widzenia mikroskopu, licząc w poprzek epidermy. Szczegółowa ich analizę pokazano na ryc. 14. Komórki większe od komórek gatunku C. betulus, lecz podobne do niego kształtem, ma dziś tylko gatunek C. turczanowii (Tablice II, III, V), mniejsze możemy spotkać u Carpinus orientalis i w rodzaju Ostrya (ryc. 7 i 8). Do ostatecznego rozstrzygniecia dopomogły badania skórki jak i miękiszu, i to zarówno wzdłuż, jak na szerokość, na ryc. 14. Co do orzeszka nr 1, nie ma wątpliwości. Może być to tylko gatunek C. turczaninowii. Orzeszek nr 14 był zupełnie do niego podobny, więc go nie zamieszczono na wykresie. Orzeszek nr 13, to Carpinus orientalis, zaś orzeszek nr 38 nie należy w ogóle do rodzaju Carpinus, bo tak wąskie a długie komórki miękiszu występują jedynie w rodzaju Ostrya. Rysunki epiderm tych orzeszków wykonane na ryc. 15 za pomocą aparatu Abbego potwierdzają te oznaczenia. W ten sposób dowiedziono, że rodzaj Ostrya, choć nielicznie, rósł jeszcze w Mizernej w pliocenie. Potwierdzono też tu metodą epidermalną to samo, co autorka pisała już o gatunku C. orientalis, badając w r. 1960 morfologię i w r. 1961 anatomię orzeszków z Mizernej.

Zatrzymano się dłużej nad opisem sposobu, w jaki oznaczano orzeszki kopalne. Obecnie zajmiemy się opisem form, jakie udało się wyróżnić za pomocą metody epidermalnej. Najważniejszy jest tu gatunek *C. betulus*,

gdyż graby zbliżone do tego gatunku opisywano najczęściej z neogenu Europy Środkowej.

## A. Typ Carpinus betulus

W neogenie Europy Środkowej najczęściej występował gatunek grabów podobny do dzisiejszego *Carpinus betulus*. Wykazano to jeszcze w rozprawie z r. 1959, opisując ich okrywy owocowe, a potwierdzono w badaniach anatomicznych (1960). Obecnie korzystając z dużego materiału owoców kopalnych można było zbadać biometrycznie komórki skórki ich perigonów z rozmaitych okresów geologicznych od miocenu po dzień dzisiejszy. Wykresy długości i szerokości tych komórek przedstawia ryc. 16. Widzimy na niej, że chociaż orzeszki trzeciorzędowe były znacznie mniejsze od czwartorzędowych, nie odbiło się to jednak zupełnie na rozmiarach komórek ich skórki zarówno z owoców nagich, jak i z owoców pokrytych włosami, które zilustrowano w ostatniej kolumnie ryc. 16, rysując je za pomocą aparatu Abbego. Rozmiary skórki są więc niechybnie u tego grabu cechą gatunkową. Komórki nagiej skórki były we wszystkich próbach 1·13—1·23 razy dłuższe od swej szerokości, czego nie spotykano u żadnego innego gatunku grabu.

Wyniki powyższych badań nasuwają jeszcze jedną uwagę co do historii gatunku *C. betulus*. Występowanie sporadyczne począwszy od dolnego pliocenu owoców grabu o rozmiarach nie różniących się od dzisiejszych nasunęło myśl, że *C. betulus* o dużych owocach mógł powstać drogą poliploidalności. Pomnożenie liczby chromosomów pociąga za sobą jednak zwykle zwiększenie liczby komórek skórki, czego nie zaobserwowano w naszym przypadku. Dodać należy, że dzisiejsze gatunki rodzaju *Carpinus* nie różnią się między sobą liczbą chromosomów, która jest bardzo niska, gdyż 2n=16, a tylko w gatunku *C. betulus* podają niektórzy autorzy obok liczby 16 także 32 i 64.

# B. Typ Carpinus turczaninowii

Pomiędzy zbadanymi przez autorkę dzisiejszymi gatunkami grabu tylko dwa wykazują niejakie podobieństwo w budowie perigonów swoich owoców. Są to *C. betulus* i *C. turczaninowii*. Podobieństwo to nieraz uderzało autorkę w czasie jej badań i nasuwało myśl, że może z tego powodu napotkać trudności przy odróżnieniu tych gatunków w stanie kopalnym. Dokładna obserwacja ryc. 1, a następnie ryc. 5, wykresów na ryc. 7 i 8 i fotografii na Tablicy III przekonała autorkę, że w budowie komórek skórki *C. turczaninowii* jest jakaś niepowtarzalna właściwość, która polega nie tylko na rozmiarach komórek, ale również na opływowym ich

kształcie, pełnym uwypukleń i omal pozbawionym kanciastości. Do tego w ich ścianach nie widać prawie zupełnie przetchlinek, a jeśli są, to tak drobne, że nie uwydatniają się na powiększeniach. Niejakie podobieństwo w budowie skórki można znaleźć jedynie między gatunkiem C. turczaninowii a południowoazjatyckimi C. cordata i C. japonica. Pierwszy z nich ma jednak nierównie wieksze komórki skórki, drugi zaś bardzo małe. Pomijając wiec to, że trudno przypuścić, aby rosły one u nas w pliocenie, sam rzut oka na ryc. 7 wyklucza podobną możliwość. To też było przyczyną zaliczenia orzeszka nr 1 z ryc. 13 i podobnego do niego nr 14 do gatunku C. turczaninowii. Potem zostało to udowodnione dokładniejszym zbadaniem skórki i miękiszu na ryc. 14, a przede wszystkim na ryc. 15, gdzie na szczegółowych rysunkach w dużym powiekszeniu okazało się w całej pełni trafne określenie orzeszka z Mizernej naznaczonego numerem 1. Ta zdobycz, będąca wynikiem analizy próby 40 orzeszków z Mizernej, będzie miała znaczenie dla dalszego ciągu badań autorki. Należy dodać, że materiał dzisiejszych orzeszków C. turczaninowii, przebadany przez autorkę, składał się z 16 okazów, oraz że miały one wszystkie perigony w środkowej i dolnej części nagie, z wyjątkiem trzech, pochodzących z Chin. Skórke jednego z nich narysowano za pomoca aparatu Abbego, nie mogąc go włączyć do materiałów zbadanych za pomoca pomiarów. Fragment tego rysunku zamieszczonego na ryc. 21. O owłosionych orzeszkach gatunku C. turczaninowii bedzie mowa w dalszym ciagu pracy.

# C. Typ Carpinus tschonoskii

Możliwość występowania w polskim neogenie grabów podobnych do żyjącego dziś gatunku *C. tschonoskii* zasugerował Prof. S z a f e r, opisując florę z Krościenka. Zaliczył nawet do tego gatunku prowizorycznie 200 orzeszków, zastrzegając się, że może to być błędne. Możliwość występowania owoców *C. tschonoskii* w polskich florach kopalnych stała się bardziej prawdopodobna od czasu znalezienia przez Bergera (1955) w dolnym pliocenie pod Wiedniem 14 okryw tego typu. Niestety perigony orzeszków z Krościenka typu *C. tschonoskii* zachowały się tylko w fragmentach trudnych do oznaczenia. Bezspornie do tego gatunku można było zaliczyć dwa orzeszki spomiędzy wysegregowanych przez Prof. Szafera pod nazwą *Carpinus* cf. *tschonoskii* Maxim. i dwa oznaczone jako *Ostrya carpinifolia* Scop. *fossilis*. Fotografię skórki jednego z nich zamieszczono na Tablicy IX.

# D. Typ Carpinus orientalis

Możność występowania gatunku *C. orientalis* w polskim neogenie nie była poruszana przez naszych paleobotaników, mimo że prof. Zabłocki, opisując pod nazwą *Carpinus polonica* owocki rodzaju *Carpinus* z Wielicz-

ki, zwrócił uwagę na ich morfologiczne podobieństwo do gatunku *C. orientalis*. W zestawie tych orzeszków, sporządzonym jego ręką dla zbiorów Instytutu Botaniki w Krakowie, widnieją pod orzeszkami z Wieliczki dzisiejsze orzeszki *C. orientalis*, rzeczywiście bardzo do kopalnych podobne. Dopiero badania anatomiczne autorki z r. 1961 wykazały bezsporną obecność gatunku *C. orientalis* w materiałach z Mizernej i Krościenka. Obecnie gatunek ten odnaleziono metodą epidermalną zarówno między orzeszkami określonymi przez Prof. S z a f e r a jako *C. betulus* L. fossilis, jak i określonymi jako *C. tschonoskii* oraz — co ciekawsze — jako *Ostrya carpinifolia* Scop. fossilis.

Spomiędzy tych ostatnich trzy zostały określone metodą epidermalną. Wyniki tych badań przedstawiono na ryc. 17. Przynależność badanych trzech orzeszków z Krościenka do gatunku *Carpinus orientalis*, a nie do *Ostrya carpinifolia* nie ulega wątpliwości. Potwierdza to ryc. 18 i morfogram na ryc. 19.

### E. Rodzaj Ostrya

Stwierdzenie, że niektóre orzeszki z pliocenu w Krościenku, określone przez Prof. Szafera jako Ostrya carpinifolia, należały do gatunku C. orientalis, nie wyklucza obecności rodzaju Ostrya w tym materiale. Autorkę intrygowało tylko to, że nigdy nie spotkała w badanych materialach plioceńskich orzeszków, których epiderma miałaby tak grube ściany komórek, jak to obserwowano u dzisiejszych owoców rodzajów Ostrya. Nasuneło to myśl, że ściany te były zbudowane z innej substancji niż ściany komórek rodzaju Carpinus i ulegały zmianom w czasie fosylizacji. Dla potwierdzenia swoich przypuszczeń przebadała zmiany, jakie zachodziły w epidermie plejstoceńskich owoców Ostrya japonica, otrzymanych od prof. Shigeru Miki. Poprzedziła to zbadaniem budowy epidermy owoców tego gatunku z dziś rosnących w Japonii okazów. Fotografie ich epidermy zamieszczono na Tablicy X. Budowe błon komórek skórki uwidoczniono zanurzając ją na parę minut w roztworze zieleni jodowej, aby roztwór ten miał czas wejść do wnętrza komórek. Ten sam zabieg powtórzono na epidermie zdjętej z dzisiejszych i z plejstoceńskich owoców z Japonii. Wprawdzie nie udało się u okazów plejstoceńskich utrzymać w komórkach barwika, który wypływał z nich w czasie przepłukiwania preparatu alkoholem, niemniej na rycinach C i D Tablicy X można zauważyć zgrubienia na ścianach komórek z rysującymi się na nich wyraźnie przetchlinkami. Zupełnie analogiczne obrazy można zauważyć na fotografiach A i B Tablicy XI, gdzie znajduje się obok skórki dzisiejszego gatunku Ostrya carpinifolia Scop. skórka owocu z pliocenu w Krościenku. Dodać należy, że wszystkie owoce z Krościenka zarówno określone jako Carpinus orientalis, jak i określone jako Ostrya carpinifolia miały skórkę nie pokrytą włosami.

#### Owoce z Ruszowa i Wieliczki

Plioceńskie owoce z Ruszowa na Śląsku (Ś tachurska, Dyjor, Ś adowska 1967), złożone z 111 orzeszków opisanych pod nazwą *Carpinus betulus* L. i 33 opisanych jako *Ostrya* sp., wzbudziły specjalne zainteresowanie autorki niniejszej rozprawy. Po raz pierwszy spotkała się bowiem w swoich badaniach z owocami kopalnymi zaliczonymi na podstawie morfologii do dwóch odrębnych nie tylko gatunków, ale rodzajów, które to owoce miały zupełnie identyczną skórkę nie spotykaną ani u dzisiejszego gatunku *Carpinus betulus*, ani u żadnego ze współczesnych nam gatunków rodzaju *Ostrya*. Wszystkie te owoce zarówno przypominające kształtem owoce *Carpinus betulus* L. *fossilis*, opisane przez autorkę w r. 1960, jak i opisane z Ruszowa jako *Ostrya* sp. miały identyczną epidermę pokrytą całkowicie włosami. Z punktu widzenia epidermy trzeba by wszystkie te owoce zarówno krótkie, stosunkowo szerokie, jak i wąskie i wydłużone zaliczyć do tej samej populacji, i to do populacji, która nie ma odpowiednika w dzisiejszej florze.

Wszystkie dotychczasowe badania autorki były wykonywane na owocach nagich, a ich podstawą były badania biometryczne, które można wykonywać tylko na owocach nie pokrytych włosami. Zachodzi przeto konieczność powrotu do zbadanych już poprzednio flor, zaczynając od owoców Carpinus betulus, których cechą gatunkową było występowanie w tych samych populacjach owoców owłosionych obok nagich. W badaniach tych okazy owłosione zostały pominięte. Ponieważ owoców owłosionych nie można badać metodą ścisłą, o czym wspomniano już wyżej, ograniczono się więc tylko do wykonania szeregu rysunków owoców o epidermie owłosionej, występujących w dzisiejszej florze i porównanie z nimi obrazów owoców kopalnych. Punktem wyjściowym była ryc. 16, na której obok szczegółowego opracowania orzeszków nagich, zamieszczono niejako dla orientacji rysunki epidermy owłosionej owoców z różnych epok geologicznych, zaliczonych do gatunku — mówiąc ogólnie — Carpinus cf. betulus. Wspólną cechą charakterystyczną tych owoców są komórki skórki, otaczające włosy, które w ogólnym charakterze są podobne do innych komórek tego perigonu, ale nieco większe i często jakby podzielone poprzecznie. Ta cecha nie zmieniła się od miocenu po dzień dzisiejszy, przy czym wielkość komórek nie koreluje z rozmiarami owocu (ryc. 16).

W porównaniu z *C. betulus* gatunek *C. caroliniana*, jedyny dzisiejszy grab o zawsze owłosionych owocach, miał komórki skórki zupełnie inne, co widać na ryc. 21. Podobne komórki skórki, jak u owoców z Ruszowa

spotkała autorka tylko u dzisiejszych owoców *Carpinus turczaninowii*, pochodzących z Chin, jedynych w jej obfitych zbiorach, które miały owoce pokryte włosami. Autorka nie komentuje tej zbieżności, wychodziłoby to bowiem poza ramy obecnej pracy, zwraca jednak uwagę, że w materiałach, które miała do swojej dyspozycji, podobną skórkę jak u owoców z Ruszowa spotkała jeszcze w materiałach z Wieliczki, przysłanych jej uprzejmie przez prof. Zabłockiego. Epidermę dwóch takich owoców narysowano na ryc. 22. Zwiększa to zainteresowanie owocami z Ruszowa.

Wyniki badań nad epidermami owoców rodzajów *Carpinus* i *Ostrya* pozwalają stwierdzić, że o ile metodę epidermalną trudno jest stosować do materiałów nie opracowanych, jeszcze przez paleobotaników, to dzięki możności skontrolowania tą drogą wyników ich badań można nie tylko sprostować niektóre oznaczenia, ale wskazać na pokrewieństwa i drogi ewolucji gatunków lub rodzajów w czasach minionych.

Badania nad epidermami dzisiejszych i kopalnych owoców rodzajów *Carpinus* i *Ostrya* zamykają cykl prac autorki, zapoczątkowany w r. 1953 rozprawą pt.: "Owoce rodzajów *Carpinus* i *Ostrya*" (wykonaną wspólnie z M. Białobrzeską), a kontynuowany planowo przez autorkę w latach 1958—1961.

# PLATES

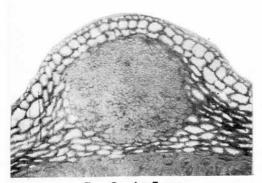
# TABLICE

#### PlateI

Transverse sections through the perigones of recent fruits of the genera Carpinus and Ostrya

#### TablicaI

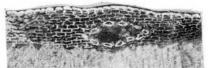
Przekroje poprzeczne przez perigony dzisiejszych owoców należących do rodzajów Carpinus i Ostrya



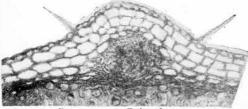
C. betulus



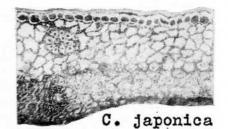
C. tschonoskii



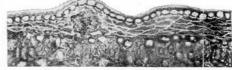
C. cordata



C. caroliniana



C. orientalis



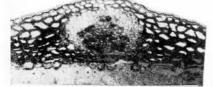
0. carpinifolia



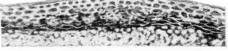
C. laxiflora



0. virginiana



C. turczaninowii



0. japonica

J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

#### Plate II

Perigones of fruits of the genus Carpinus seen from above:

A<sub>1</sub>, A<sub>2</sub> — Carpinus betulus; glabrous and pilose

 $B_1,\ B_2$  — C. caroliniana; glabrous and pilose parts of the same fruit

C<sub>1</sub>, C<sub>2</sub> — C. orientalis

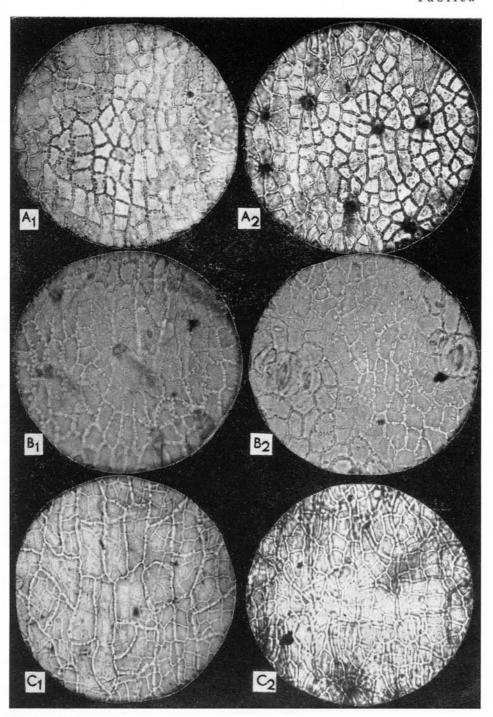
#### Tablica II

Perigony owoców rodzaju Carpinus widziane z góry:

A<sub>1</sub>, A<sub>2</sub> — Carpinus betulus; nagi i owłosiony

 $\mathrm{B_{i},\ B_{2}}$  — C. caroliniana; część owłosiona i naga tego samego owocu

C<sub>1</sub>, C<sub>2</sub> — C. orientalis



J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

## Plate III

A - Carpinus laxiflora

B — C. turczaninowii

 $C_1$ ,  $C_2$  — C. tschonoskii; partly glabrous and partly pilose

D - C. cordata

E - C. japonica

### Tablica III

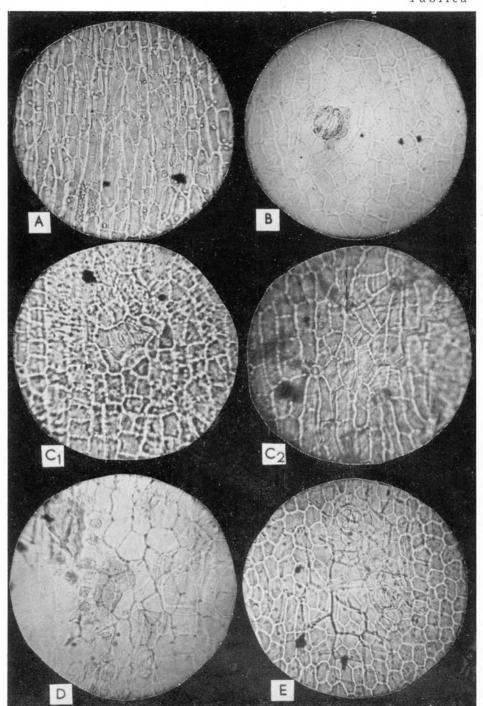
A — Carpinus laxiflora

B — C. turczaninowii

 $C_1$ ,  $C_2$  — C. tschonoskii; część naga i owłosiona

D — C. cordata

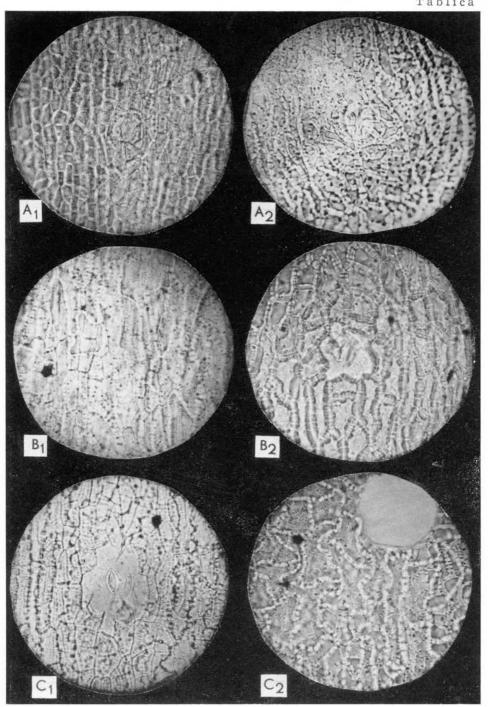
E — C. japonica



J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

# Plate IV Tablica IV

 $A_1$ ,  $A_2$  — Ostrya carpinifolia  $B_1$ ,  $B_2$  — O. virginiana  $C_1$ ,  $C_2$  — O. japonica



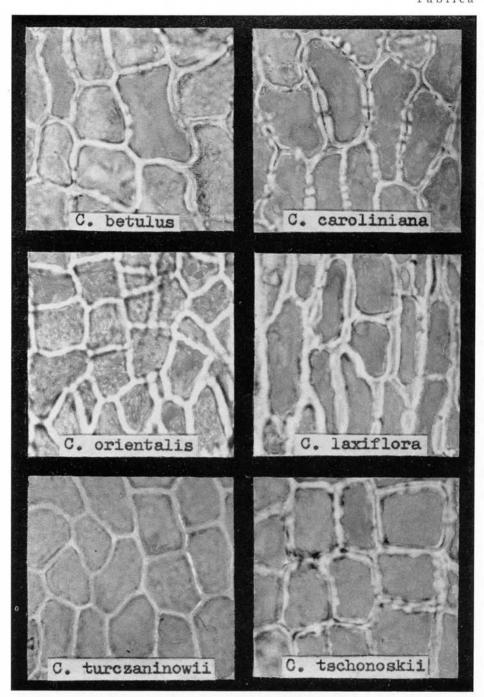
J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

## Plate V

Fragments of epidermal cells of species of the genus Carpinus

# Tablica V

Fragmenty komórek skórki gatunków należących do rodzaju Carpinus



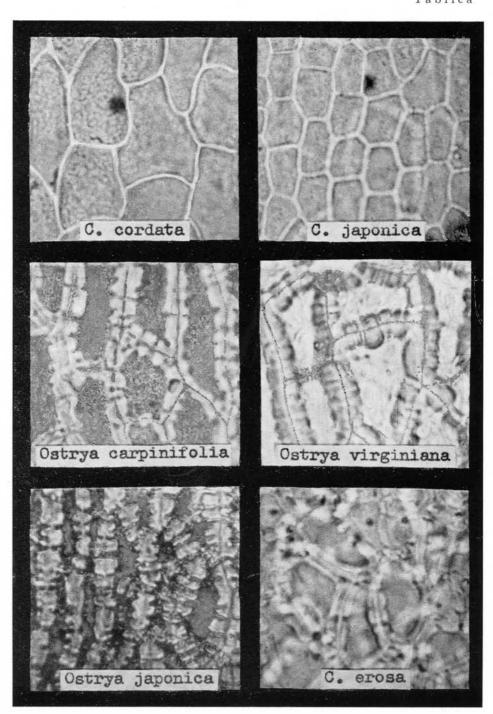
J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

## Plate VI

Fragments of epidermal cells of species of the genera Carpinus and Ostrya

## Tablica VI

Fragmenty komórek skórki gatunków należących do rodzajów Carpinus i Ostrya



J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

## Plate VII

Epidermis of nutlets from Mizerna:

A — No. 1

B — No. 14

C - No. 5 (cf. Text-figs. 13-15)

D — No. 19

Tablica VII

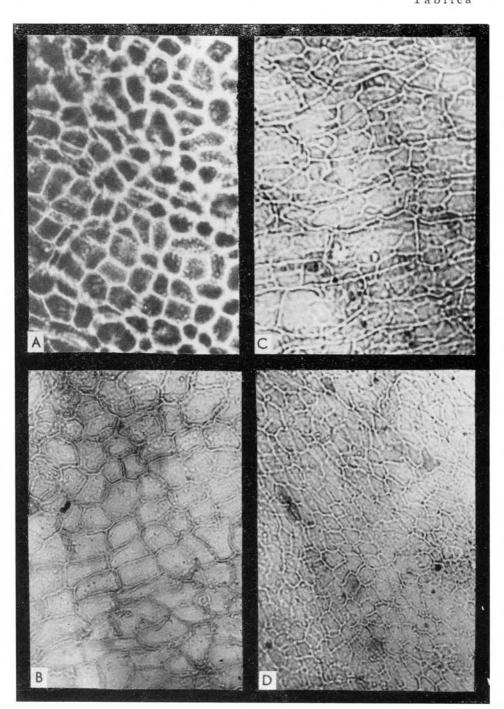
Skórki orzeszków z Mizernej:

A — No. 1

B — No. 14

C — No. 5 (por. ryc. 13—15)

D - No. 19



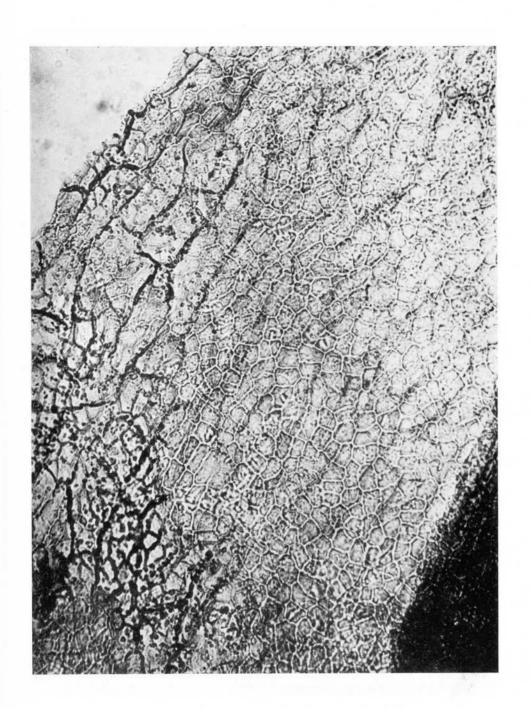
J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

## Plate VIII

Epidermal and parenchymal cells of a fruit of Carpinus cf. betulus from the Upper Miocene in Gliwice

## Tablica VIII

Komórki skórki i miękiszu owocu Carpinus cf. betulus z górnego miocenu w Gliwicach



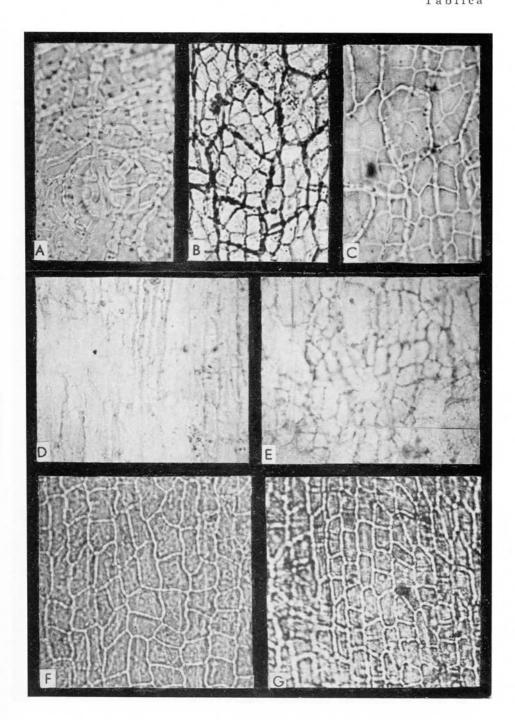
J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

#### Plate IX

- A Epidermis of a recent fruit of Ostrya carpinifolia
- B Epidermis and parenchyma of a fruit from the Pliocene in Krościenko
- C Epidermis and parenchyma of a recent fruit of Carpinus orientalis
- D, E Epidermises of fruits from the Pliocene in Krościenko, possibly belonging to the species Ostrya cf. carpinifolia
- F, G Epidermises of fruits of the recent and Pliocene species Carpinus tschonoskii

### Tablica IX

- A Skórka dzisiejszego owocu Ostrya carpinifolia
- B Skórka i miękisz owocu z pliocenu w Krościenku
- C Skórka i miękisz dzisiejszego owocu Carpinus orientalis
- D, E Skórki owoców z pliocenu w Krościenku mogące należeć do gatunku Ostrya cf. carpinifolia
- F, G Skórki owoców dzisiejszego i plioceńskiego gatunku Carpinus tschonoskii



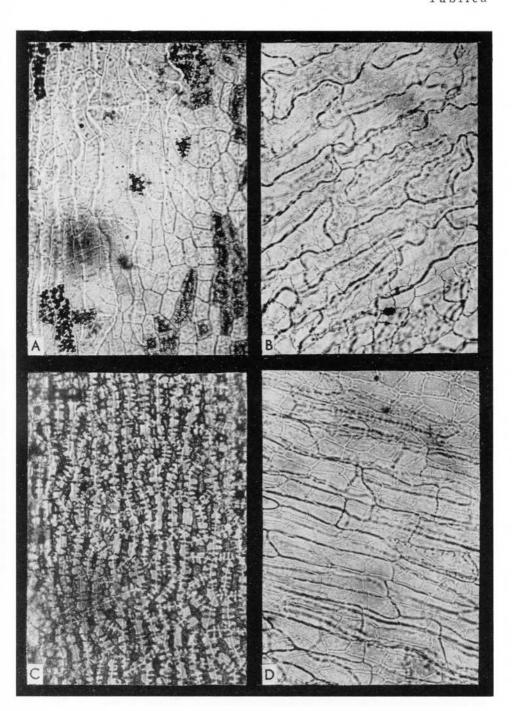
J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

### Plate X

- A, C Epidermal cells of a fruit of  $Ostrya\ japonica$  partially or wholly saturated with methylene blue
- B, D Epidermal and parenchymal cells of a fruit of Ostrya japonica from the Pleistocene in Japan

### Tablica X

- A. C Komórki skórki owocu Ostrya japonica całkowicie lub częściowo wypełnione błękitem metylenowym
- B, D Komórki skórki i miękiszu owocu Ostrya japonica z plejstocenu w Japonii



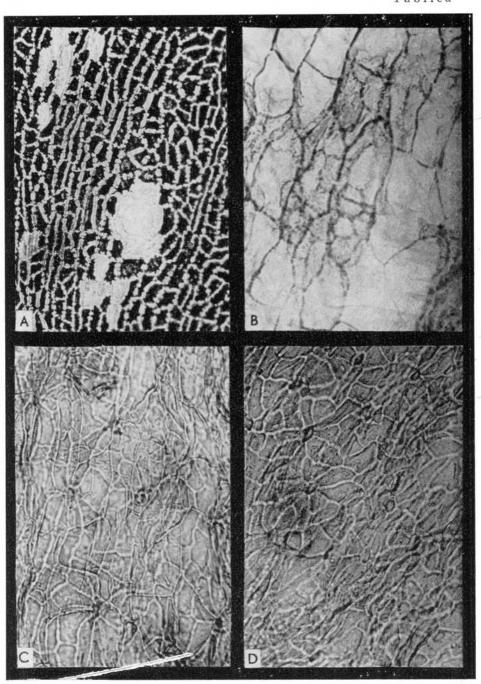
J. Jentys-Szaferowa Acta Palaeobotanica XVI/1

### Plate XI

- A Epidermis of a fruit of Ostrya carpinifolia with cells saturated with methylene blue
- B Epidermis and parenchyma of a fruit of Ostrya carpinifolia from the Pliocene in Krościenko
- C Epidermis and parenchyma of a fruit of "Carpinus betulus L." from Ruszów
- D Epidermis and parenchyma of a fruit of "Ostrya sp." from Ruszów

### Tablica XI

- A Dzisiejsza skórka owocu Ostrya carpinifolia z komórkami wypełnionymi błękitem metylenowym
- B Skórka i miękisz owocu Ostrya carpinifolia z pliocenu w Krościenku
- C Skórka i miękisz owocu "Carpinus betulus L." z Ruszowa
- D Skórka i miękisz owocu "Ostrya sp." z Ruszowa



J. Jentys-Szaferowa Acta Palaeobotanica XVI/1