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FRUITS OF THE GENUS *FAGUS* FROM THE NEOGENE OF THE  
WESTERN CARPATHIANS — BIOMETRICAL STUDY

Owoce rodzaju *Fagus* z miocenu Karpat Zachodnich — studium biometryczne

**ABSTRACT.** The beech nuts and cupules obtained from the Neogene deposits at Koniówka (Nowy Targ — Orawa Basin) were subject to a biometrical analysis. The results were compared with the measurements of nuts and cupules of 7 modern beech species. The use of Jentys-Szaferowa's graphic method for the whole of material from Koniówka shows its great similarity to the fruits of North American *Fagus grandifolia* Ehrh. and denies its relationships with the East Asiatic species.

#### INTRODUCTION

The beech was one of the trees that formed forest communities of the European Neogene, as evidenced by the macroscopic remains (leaves, nuts and cupules) found in the deposits of that age and by the frequently considerable proportion of the genus *Fagus* in pollen diagrams. As regards the Neogene of Poland, macroscopic remains of beech are known from at least 11 localities distributed in the south-west of the country. The fruits were most frequently described under the names of *Fagus ferruginea* Ait. and *F. decurrens* C. et E. M. Reid and compared with the North American species *F. grandifolia* Ehrh. Nuts of the *F. sylvatica* type were also described from Pliocene deposits.

Particularly abundant material of well-preserved beech nuts and cupules suitable for a biometrical study comes from a layer of grey clays exposed in the bed of the Czarny Dunajec River at Koniówka (Nowy Targ — Orawa Basin), in sediments included to the Neogene by the palynological method (Oszast & Stuchlik 1977). All these remains were collected and delivered to us for study by Prof. M. Łaniccka-Środoniowa.

## MATERIAL AND METHOD

Nowadays the genus *Fagus* occurs in Eurasia and North America (Meusel et al. 1965). *F. sylvatica* L. grows in Europe, *F. orientalis* Lipsky in Asia Minor, Crimea and Balkan Peninsula, *F. japonica* Maxim. and *F. crenata* Blume (= *F. sieboldii* Endl.) in Japan, *F. longipetiolata* Seemen, *F. engleriana* Seemen and *F. lucida* Rehder in China and *F. hayatae* Palib. in Formosa. Only *F. grandifolia* Ehrh. (= *F. ferruginea* Ait = *F. americana* Sweet) occurs in North America. The fruits of the genus *Fagus* have cupules which, in maturity, burst into four valves, exposing triangular nuts. The cupules are covered by numerous spiny processes.

The fossil material from Koniówka consists of cupules and nuts and in spite of their being compressed and strongly fossilized is in general well preserved. The spine bases can be seen on the surface of the valves. The best preserved specimens — 122 valves and 36 nuts — were picked out for this biometrical study; occasional whole cupules were not measured.

The guiding principle of this study was to get acquainted with the variability of the cupules and nuts of the now living beech species and to appraise the fossil material from Koniówka on this basis.

The present-day reference material consisted of samples collected specially for this study and samples from the collection of the Department of Palaeobotany of the Institute of Botany, Polish Academy of Sciences, in Kraków. The materials we had at our disposal are as follows:

1. *F. sylvatica* L. represented by the so-called general sample, comprising 7 local samples, 6 of which were from Poland and 1 from Denmark, gathered on cliffs near Copenhagen.
2. *F. grandifolia* Ehrh. — Canada; a sample from Venice, situated near the estuary of the St. Laurence River and 2 samples from the Quebec and Ontario Provinces.
3. *F. crenata* Blume — Japan, Hakkoda Mts. (c. 1000 m a. s. l.) in the northern part of Honshu Island.
4. *F. japonica* Maxim. — Japan, the central part of Honshu Island, the forest of Tokyo University at Chichibu (Saitama Prefecture).
5. *F. lucida* Rehder — China, Botanical Gardens in Peking; only nuts.
6. *F. longipetiolata* Seemen — China, Botanical Gardens in Peking; only nuts.
7. *F. engleriana* Seemen — Czechoslovakia, Arboretum at Průhonice.

The biometrical measurements cover the characters of the morphological structure of cupules and nuts.

**Cupules.** The material from Koniówka contained mostly detached valves of cupules, rarely whole specimens. In order to make the present-day material similar to the fossil remains, the cupules were divided into particular valves and next cleared of spines so that they should not impede the observation of the shape of the valves and boiled in water with an admixture of soda. After

a few hours they were removed from the water, dried on blotting paper and placed in a press to be given a shape resembling that of the fossil remains. After some dozen days the valves thus dried lost their moisture, which might have caused an increase in their size. The valves prepared in this way were drawn using a photographic enlarger. Measurements were taken on the drawings by means of a millimetre scale enlarged to the same degree as the drawings were. The following data characterize the size and shape of both modern and fossil valves: 1. valve length, 2. valve width, 3. apical angle of valve, 4. angle at the base of valve, 5. valve length : width ratio, 6. position of the greatest width expressed as a percentage of the valve length.

Nuts. The triangular nuts of modern beeches were divided into particular walls to make them similar to the fossil remains, which very rarely occurred as whole nuts. Measurements were taken on the drawings as in the case of valves. The morphological structure of nuts was determined by means of the following data: 1. nut length, 2. nut width, 3. apical angle of nut, 4. angle at the base of nut, 5. nut length : width ratio, and 6. the position of the greatest width expressed as a percentage of the nut length.

The fossil material was drawn and measured in the same way as was the present-day material.

The graphic method described by Jentys-Szaferowa (1959) was used to present the results of the biometrical analysis. It consists in comparing the arithmetic means of measurements from the samples examined with the arithmetic means from the sample selected as the comparative unit. The numerical material of the measurements is summarized in three Tables (1—3).

#### BIOMETRICAL ANALYSIS

The point of departure for the present study was the ascertainment of differences in the morphology of nuts and cupules of the now living species of *Fagus*. The tracing of the size and shape lines for particular modern species made the basis for the estimation of the analogously prepared fossil material. The question arises what relation exists between the fossil material and *Fagus sylvatica* growing now in the territory of Poland as well as other modern species of this genus. The cumulative sample of *F. sylvatica* was chosen as the comparative unit, with which all the available modern species and the fossil material were compared. The results of measurements are given in eight figures.

Graph I in Fig. 1 shows the differences and similarities occurring between the valves of five beech species living now. The valves of *F. sylvatica* (straight vertical line) are the comparative unit. The course of the curves shows that the valves of *F. sylvatica* have the greatest size (features 1 and 2) and are different from the remaining ones in shape. The cupule valves of *F. crenata* resemble them most, although they are smaller (features 1 and 2) and their

Table 1

Species	Length of cupule valve				Breadth of cupule valve				Apical angle of cupule valve			
	min.-max.	$M_0$	$M \pm m$	V	min.-max.	$M_0$	$M \pm m$	V	min.-max.	$M_0$	$M \pm m$	V
<i>Fagus sylvatica</i>	1.20—2.80	2.3	$2.06 \pm 0.04$	16.99	0.70—1.55	1.1	$1.12 \pm 0.02$	16.96	72—146	107	$105.68 \pm 2.29$	17.06
<i>F. crenata</i>	1.40—2.20	2.0	$1.91 \pm 0.02$	10.47	0.65—1.50	1.0	$1.02 \pm 0.02$	18.62	42—152	96	$90.50 \pm 2.20$	21.75
<i>F. japonica</i>	0.40—0.85	0.5	$0.59 \pm 0.01$	23.12	0.30—0.60	0.5	$0.44 \pm 0.01$	20.45	42—115	63	$72.90 \pm 2.85$	27.61
<i>F. engleriana</i>	1.20—1.90	1.4	$1.48 \pm 0.02$	10.81	0.55—0.75	0.6	$0.62 \pm 0.01$	8.06	32—72	52	$51.12 \pm 1.41$	19.58
<i>F. longipetiolata</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>F. lucida</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>F. grandifolia</i>	0.75—1.70	1.4	$1.29 \pm 0.01$	14.72	0.60—1.15	0.8	$0.82 \pm 0.01$	14.68	50—151	85	$86.65 \pm 1.09$	17.81
fossil (Koniówka)	0.80—1.80	1.1	$1.24 \pm 0.01$	15.32	0.50—1.10	0.8	$0.75 \pm 0.01$	17.33	41—150	74	$85.00 \pm 1.71$	22.51
Species	Basal angle of cupule angle				Ratio of length to breadth of cupule valve				Position of the broadest part of cupule valve in %% of its length			
	min.-max.	$M_0$	$M \pm m$	V	min.-max.	$M_0$	$M \pm m$	V	min.-max.	$M_0$	$M \pm m$	V
<i>Fagus sylvatica</i>	57—160	125	$104.87 \pm 3.66$	27.50	1.20—2.86	1.9	$1.88 \pm 0.04$	20.74	31.4—76.6	50	$52.70 \pm 1.28$	19.16
<i>F. crenata</i>	63—180	114	$119.17 \pm 2.74$	20.58	1.30—2.85	1.6	$1.88 \pm 0.02$	18.08	31.5—61.5	45	$47.00 \pm 0.80$	15.31
<i>F. japonica</i>	95—180	125	$144.80 \pm 3.37$	16.48	0.90—2.16	1.3	$1.38 \pm 0.04$	21.01	20.0—66.7	35	$36.20 \pm 1.06$	20.85
<i>F. engleriana</i>	92—180	147	$143.70 \pm 3.20$	15.76	1.92—2.77	2.2	$2.29 \pm 0.03$	9.60	23.5—44.8	40	$33.60 \pm 0.76$	16.07
<i>F. longipetiolata</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>F. lucida</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>F. grandifolia</i>	85—180	125	$129.84 \pm 1.25$	13.38	1.00—2.45	1.6	$1.55 \pm 0.01$	16.12	23.0—73.3	45	$41.95 \pm 0.51$	17.52
fossil (Koniówka)	65—180	125	$126.54 \pm 2.55$	22.25	1.10—2.60	1.6	$1.56 \pm 0.03$	21.79	20.0—57.1	40	$40.90 \pm 0.65$	17.60

Table 2

Species	Length of nutlet				Breadth of nutlet				Apical angle			
	min.-max.	M <sub>0</sub>	M±m	V	min.-max.	M <sub>0</sub>	M±m	V	min.-max.	M <sub>0</sub>	M±m	V
<i>Fagus sylvatica</i>	1.05—1.80	1.50	1.47±0.02	9.52	0.65—1.00	0.70	0.79±0.01	11.39	40—105	75	74.15±0.91	15.50
<i>F. crenata</i>	1.10—1.40	1.10	1.20±0.03	10.00	0.65—0.90	0.70	0.77±0.02	11.68	80—111	80	90.80±2.70	10.27
<i>F. japonica</i>	0.90—1.35	1.10	1.12±0.01	8.03	0.45—0.70	0.60	0.60±0.01	13.33	46—73	55	58.30±0.96	11.74
<i>F. engleriana</i>	0.80—1.15	1.00	0.98±0.01	6.12	0.35—0.60	0.50	0.51±0.01	13.72	36—66	50	52.00±1.42	15.00
<i>F. longipetiolata</i>	1.00—1.40	1.30	1.28±0.01	7.03	0.50—0.65	0.60	0.57±0.01	8.77	44—70	60	58.00±1.38	11.89
<i>F. lucida</i>	0.80—1.20	1.10	1.07±0.01	6.54	0.30—0.50	0.40	0.43±0.01	11.62	46—75	60	60.80±1.06	9.62
<i>F. grandifolia</i>	0.80—1.40	1.10	1.07±0.01	11.21	0.45—1.10	0.70	0.72±0.01	15.27	51—107	75	77.50±1.13	17.03
fossil (Koniówka)	0.75—1.25	1.10	0.95±0.02	12.63	0.45—0.75	0.60	0.64±0.01	9.37	63—100	90	83.85±1.73	12.40
Species	Basal angle				Ratio of length to breadth of nutlet				Position of the broadest part in %% of length			
	min.-max.	M <sub>0</sub>	M±m	V	min.-max.	M <sub>0</sub>	M±m	V	min.-max.	M <sub>0</sub>	M±m	V
<i>Fagus sylvatica</i>	108—180	140	144.3±2.51	10.70	1.40—2.46	1.90	1.89±0.04	14.28	26.6—46.6	35	35.55±0.80	13.47
<i>F. crenata</i>	135—180	165	155.8±4.29	9.53	1.22—1.76	1.60	1.57±0.04	10.19	26.9—50.0	35	34.55±1.92	19.24
<i>F. japonica</i>	97—180	140	137.3±2.73	14.09	1.63—2.30	1.80	1.89±0.02	8.46	23.8—54.5	35	32.90±0.74	16.10
<i>F. engleriana</i>	118—180	180	161.9±3.26	11.02	1.60—3.00	1.90	1.97±0.05	14.72	10.0—42.1	25	27.80±0.96	19.06
<i>F. longipetiolata</i>	113—180	130	142.6±3.60	12.62	1.83—2.80	2.10	2.31±0.04	10.38	14.8—38.4	35	29.80±1.37	22.98
<i>F. lucida</i>	62—180	125	131.5±4.43	18.44	2.10—3.14	2.40	2.51±0.04	9.96	22.7—39.1	35	31.15±0.93	16.37
<i>F. grandifolia</i>	100—180	165	163.1±1.41	10.14	0.75—2.20	1.50	1.52±0.01	14.47	16.6—38.4	25	27.45±0.32	13.66
fossil (Koniówka)	133—180	165	153.7±2.00	7.80	1.14—2.00	1.50	1.50±0.03	12.66	18.1—44.4	30	30.25±1.15	22.97

Table 3

*Fagus grandifolia* Ehrh.

Locality	Length of cupule valve				Breadth of cupule valve				Apical angle of cupule valve			
	min.-max.	$M_0$	$M \pm m$	V	min.-max.	$M_0$	$M \pm m$	V	min.-max.	$M_0$	$M \pm m$	V
Quebec	0.75—1.45	1.1	$1.16 \pm 0.02$	18.10	0.60—1.05	0.7	$0.75 \pm 0.01$	14.66	50—118	85	$85.88 \pm 2.14$	17.67
Ontario	1.20—1.45	1.4	$1.35 \pm 0.01$	8.14	0.65—0.90	0.8	$0.77 \pm 0.01$	7.79	59—100	74	$77.74 \pm 1.41$	12.87
Venice	1.00—1.70	1.4	$1.31 \pm 0.01$	10.52	0.65—1.15	0.9	$0.89 \pm 0.01$	11.35	59—151	85	$93.60 \pm 1.57$	16.80
Locality	Basal angle of cupule valve				Ratio of length to breadth of cupule valve				Position of the broadest part of cupule valve in %% of its length			
Quebec	103—158	125	$130.94 \pm 1.82$	9.82	1.00—2.00	1.6	$1.52 \pm 0.03$	16.44	23.0—50.0	35	$37.20 \pm 0.91$	17.33
Ontario	87—153	136	$127.86 \pm 1.85$	10.23	1.41—2.00	1.6	$1.70 \pm 0.02$	9.41	26.9—48.1	40	$40.10 \pm 0.72$	12.71
Venice	85—180	125	$130.39 \pm 2.05$	15.77	1.13—2.45	1.3	$1.50 \pm 0.09$	16.66	32.0—73.3	45	$45.15 \pm 0.73$	16.27
Locality	Length of nutlet				Breadth of nutlet				Apical angle of nutlet			
Quebec	0.90—1.40	1.0	$1.09 \pm 0.01$	11.92	0.45—1.10	0.7	$0.77 \pm 0.03$	36.06	57—107	80	$83.10 \pm 1.83$	15.64
Ontario	1.10—1.30	1.1	$1.16 \pm 0.02$	12.06	0.50—0.90	0.7	$0.69 \pm 0.01$	13.04	51—97	75	$67.20 \pm 1.86$	16.66
Venice	0.80—1.10	1.0	$1.00 \pm 0.01$	8.00	0.45—0.90	0.7	$0.69 \pm 0.01$	13.04	61—102	85	$79.40 \pm 1.38$	12.34
Locality	Basal angle of nutlet				Ratio of length to breadth of nutlet				Position of the broadest part in %% of length			
Quebec	100—180	165	$161.40 \pm 2.44$	10.71	0.75—2.16	1.4	$1.41 \pm 0.03$	18.43	18.1—34.4	30	$29.30 \pm 0.69$	16.38
Ontario	127—180	140	$159.85 \pm 2.75$	9.88	1.44—2.20	1.6	$1.69 \pm 0.03$	11.83	18.1—37.5	25	$26.80 \pm 0.79$	17.72
Venice	130—180	160	$167.30 \pm 2.01$	8.51	1.11—2.20	1.5	$1.48 \pm 0.02$	12.16	16.6—35.0	25	$25.10 \pm 0.53$	15.13

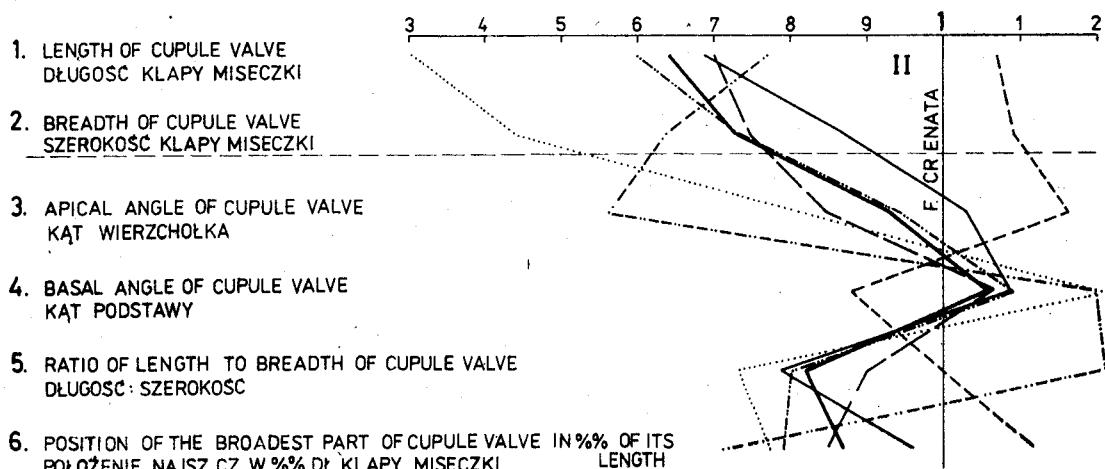
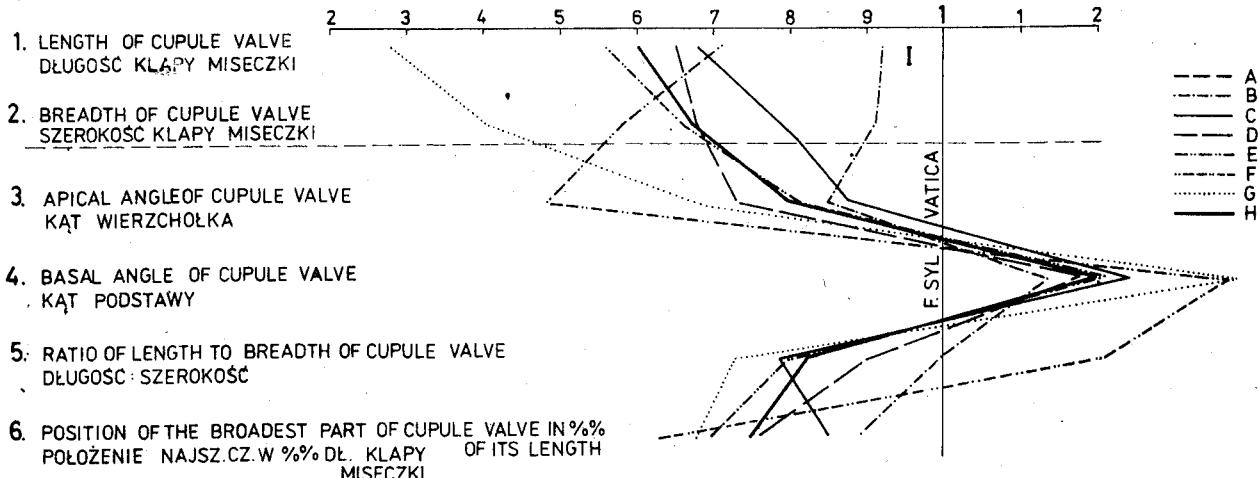


Fig. 1. Graph I. A comparison of the size and shape of cupule valves in various species of *Fagus* with those of the valves of *F. sylvatica*: A — *F. sylvatica*; B — *F. crenata*; C — *F. grandifolia* from Venice; D — *F. grandifolia* from Ontario; E — *F. grandifolia* from Quebec; F — *F. engleriana*; G — *F. japonica*; H — fossil specimens from Koniówka. Graph II. The same species compared with *F. crenata*.

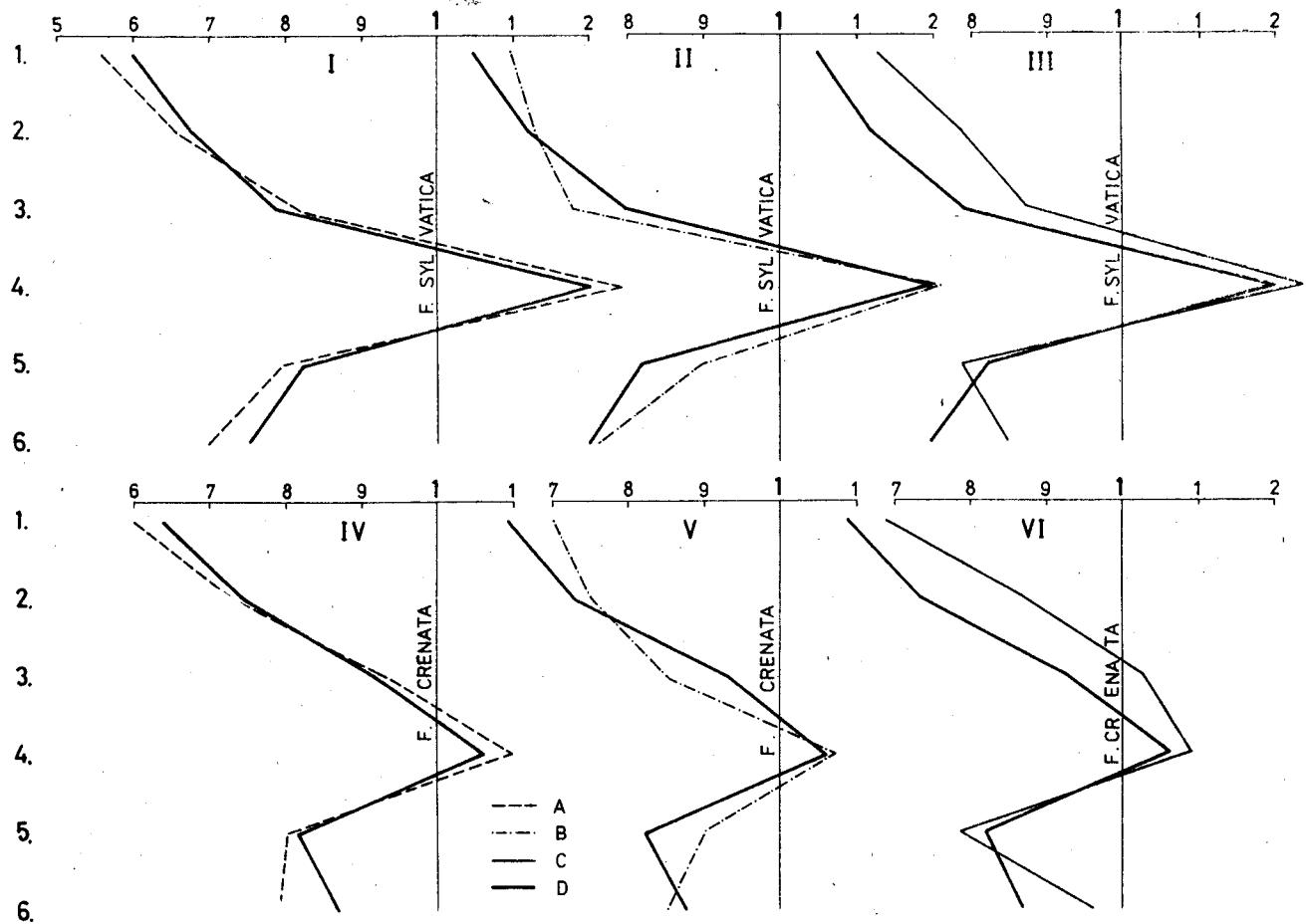


Fig. 2. Graphs I, II and III. A comparison of the cupule valves of *Fagus grandifolia* and fossil specimens from Koniówka with the cumulative sample of *F. sylvatica*: A — from Quebec; B — from Ontario; C — from Venice; D — from Koniówka. Graphs IV, V and VI. The same species compared with *F. crenata*

apex is more acute (feature 3). The curve of the second species growing in Japan, *F. japonica*, has the farthest position in relation to the comparative unit line, this species being characterized by the smallest size of valves (features 1 and 2) of all the species examined. The valve curve for *F. engleriana* is noteworthy. These valves are narrow (feature 2) and their apical angle is very acute (feature 3). Their slenderness is confirmed by feature 5, which emphasizes their different shape in comparison with other species of *Fagus*. It should further be stated that the cupule valves of all the species examined have a more pointed apex, less acute angles at the base (notably, in *F. japonica* and *F. engleriana*) and more rounded shape (except in the above-mentioned *F. engleriana*) than have the valves of *F. sylvatica*. The increase in the value of the basal angle (feature 4) seems to be connected to a certain extent with the lowering of the position of the greatest valve width (feature 6). An analysis of this graph shows also that the lines representing the features of size and shape for three local samples of *F. grandifolia* and forming a group in which they run close to each other, occupy an intermediate position between the cupule lines of *F. sylvatica* and *F. crenata* and those of *F. japonica* and *F. engleriana*. The foregoing results are confirmed by graph II in Fig. 1, in which the cupules of *F. crenata* are used as the comparative unit.

The size and shape lines for the fossil material from Koniówka are also traced out in these figures. Their course does not need any extensive comments. It shows a great similarity to that of *F. grandifolia*. To be sure, the fossil cupule valves are somewhat smaller, but their shape is nearly identical. This fact is illustrated additionally and still more clearly in Fig. 2, which comprises 6 graphs. The first three graphs (I—III) represent the local samples of *F. grandifolia* and the material from Koniówka compared with *F. sylvatica*, the remaining graphs (IV—VI) the same samples compared with *F. crenata*. The change of the comparative unit appears to have no effect on the relations between *F. sylvatica* and the fossil remains. The similarity of the fossil beech

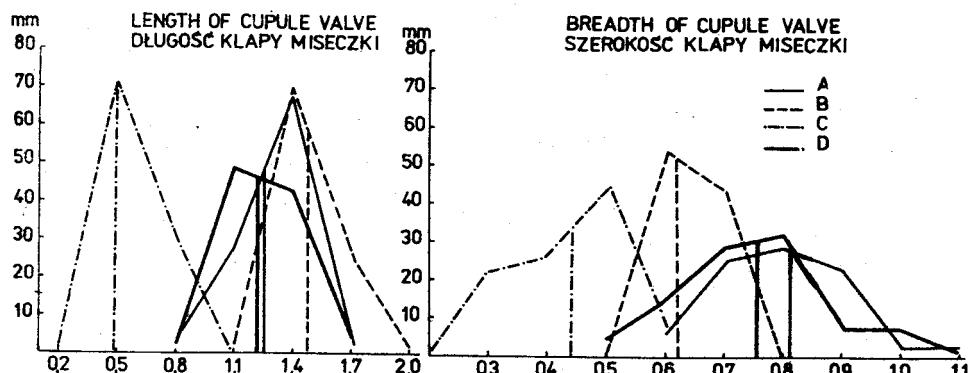


Fig. 3. Polygons of frequency for two features characterizing the size of cupule valves:  
A — *F. grandifolia* (cumulative sample); B — *F. engleriana*; C — *F. japonica*; D — fossil  
*Fagus* (Koniówka)

to the North-American species *F. grandifolia* and at the same time the distinctness of its cupule valves in respect of size and shape from those of both *F. sylvatica* and *F. crenata* are striking in both cases. The variation range of the length and width of cupules from Koniówka lies nearly exactly within this range of the American beech (cf. Fig. 3).

The second part of the modern and fossil materials examined consisted of triangular nuts or rather their walls. In this case the material being compared was more abundant, since it included also 2 samples of nuts of the Chinese species *F. longipetiolata* Seemen and *F. lucida* Rehder. As in the study of cupules, *F. sylvatica* was the comparative unit, which is presented in Fig. 4 (graphs I and III). The differences in the morphological structure of nuts in the species under study seem to be smaller than in the case of cupules, nevertheless they are quite distinct. These differences are well seen in the graphs in which three local samples of *F. grandifolia* have been reduced into one cumulative sample. The comparative units in these graphs are *F. sylvatica* (Fig. 4, graph III) and *F. crenata* (Fig. 4, graph IV).

As in the case of cupules, the nuts of *F. sylvatica* are characterized by their greatest size (features 1 and 2). The three Chinese species (*F. lucida*, *F. engleriana* and *F. longipetiolata*) have very narrow nuts, and then very slender (features 2 and 5) with acute apical angles (feature 3). They differ much from the fossil material. Considerable differences, notably in size, relative to the comparative unit (*F. sylvatica* and *F. grandifolia*) can be observed on the nuts of *F. japonica*. The least variable feature is the position of the greatest width expressed in a percentage of the nut length. In all the species examined it lies in the lower half of the nut and ranges from 27 to 35% of its length. And again, as in the case of the cupules, the course of the size and shape lines of the fossil nuts most resembles that of the lines of *F. grandifolia* in respect of all the six features. Although the shape lines (features 4, 5 and 6) of the second Japanese species *F. crenata* have a similar course to that for the nuts of Koniówka, this species differs more from them than *F. grandifolia* as regards size (features 1 and 2). The nuts of *F. crenata* are much longer and broader. The inclusion of the fossil nuts from Koniówka in *F. grandifolia* is also supported by the polygons of variation for the length and width of nuts (Fig. 5), notably their length: width ratio, which constitutes a reliable diagnostic character. The fact that the size of the fossil nuts is somewhat smaller than that of modern *F. grandifolia* may have been caused by fossilization. Writing about the presence of two morphological types of beech nuts in the Miocene of Stare Gliwice, Szafer (1961) is inclined to think that the East Asiatic species *F. japonica* may have occurred in the Tertiary of Poland. The supposition that the beeches occurring in the Tertiary of Europe resembled the East Asiatic species finds no confirmation in the material from Koniówka. The inclusion of the beech fruits from Koniówka in *F. japonica* must be ruled out on the basis of the graphs in Fig. 6 and in *F. engleriana* on the basis of the graphs in Fig. 7. Figure 6 shows a nearly identical arrangement of the size and shape lines for the nuts and valves of *F. japonica*

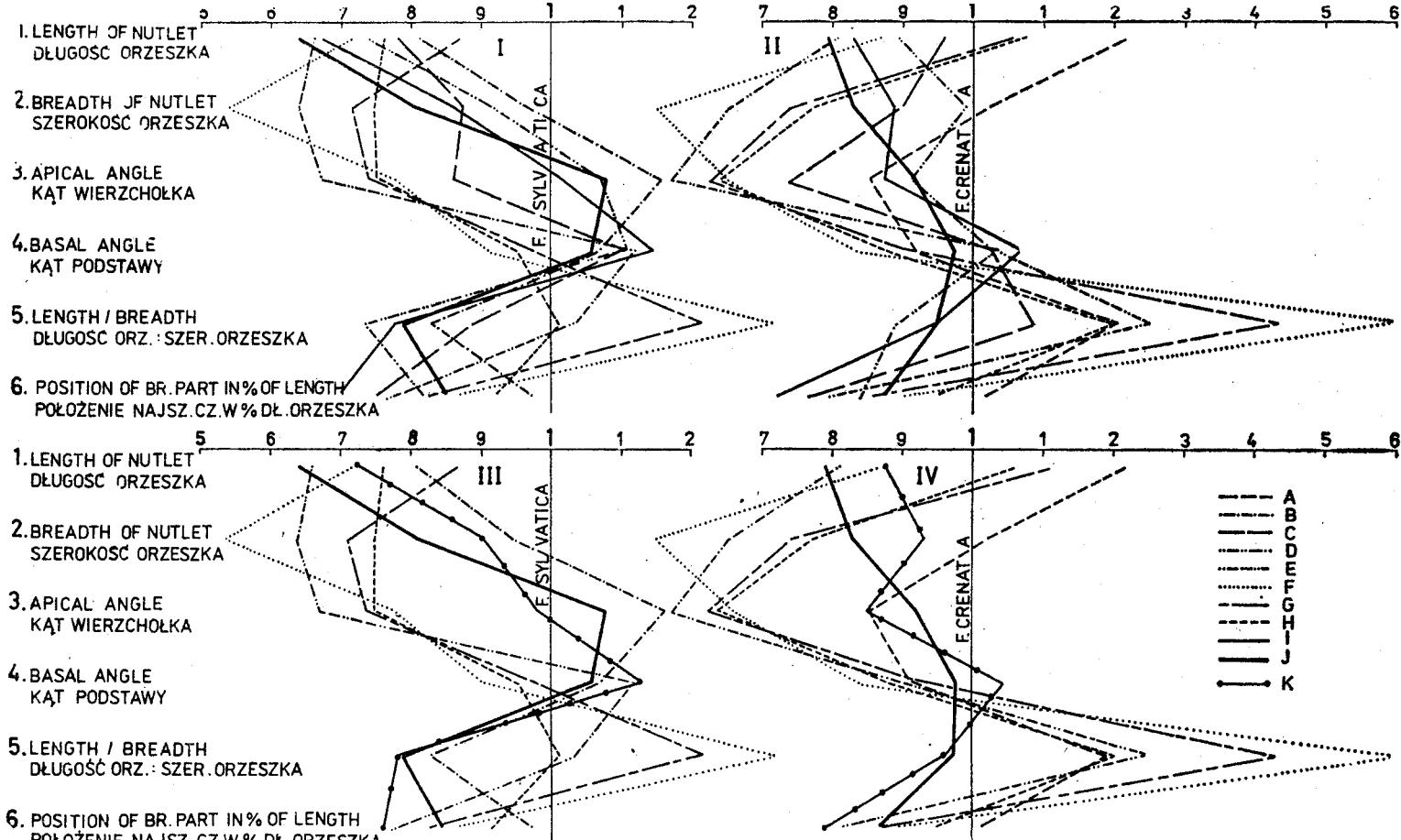
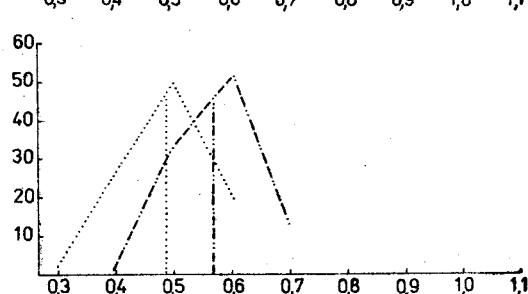
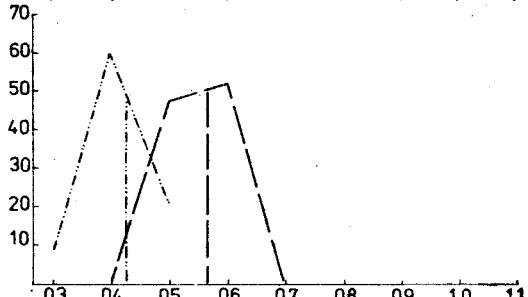
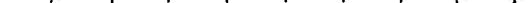
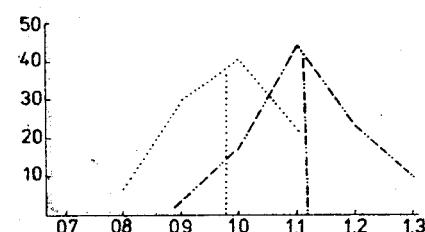
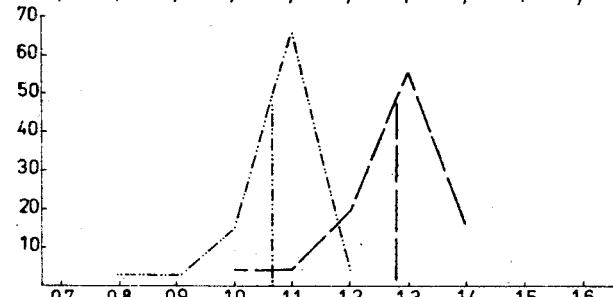
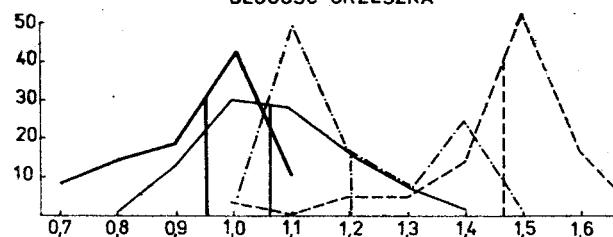


Fig. 4. Graphs I and III. A comparison of the nuts of the *Fagus* species examined with the cumulative sample of *F. sylvatica* (in graph III three local samples of *F. grandifolia* are cumulated into one). Graphs II and IV. A comparison of the nuts of all the *Fagus* species examined with those of *F. crenata* (in graph IV the three local samples of *F. grandifolia* are combined into one cumulative sample). A — *F. sylvatica*; B — *F. crenata*; C — *F. grandifolia* (Ontario); D — *F. grandifolia* (Quebec); E — *F. engleriana*; F — *F. lucida*; G — *F. longipetiolata*; H — *F. japonica*; I — *F. grandifolia* (Venice); J — Koniówka; K — *F. grandifolia* (cumulative sample)

LENGTH OF NUTLET  
DŁUGOSC ORZESZKA

FAGUS

BREADTH OF NUTLET  
SZEROKOSC ORZESZKALENGTH / BREADTH  
STOSUNEK DŁUGOSCI DO SZEROKOSCI ORZESZKA

- A
- - - B
- C
- D
- E
- F
- G
- H

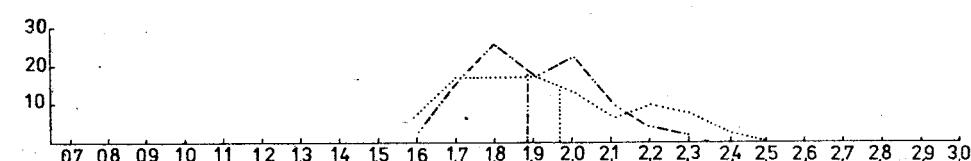
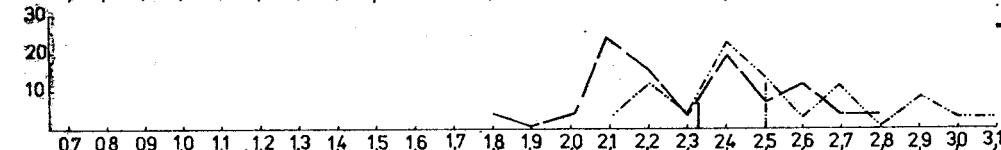
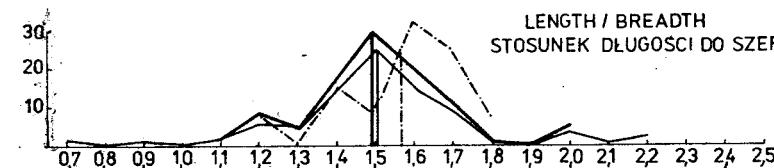


Fig. 5. Polygons of variation for three features of nuts: A — *F. sylvatica*; B — *F. crenata*, C — *F. grandifolia* (cumulative sample); D — *F. longipetiolata*; E — *F. lucida*; F — *F. japonica*; G — *F. engleriana*; H — fossil *Fagus* (Koniówka)

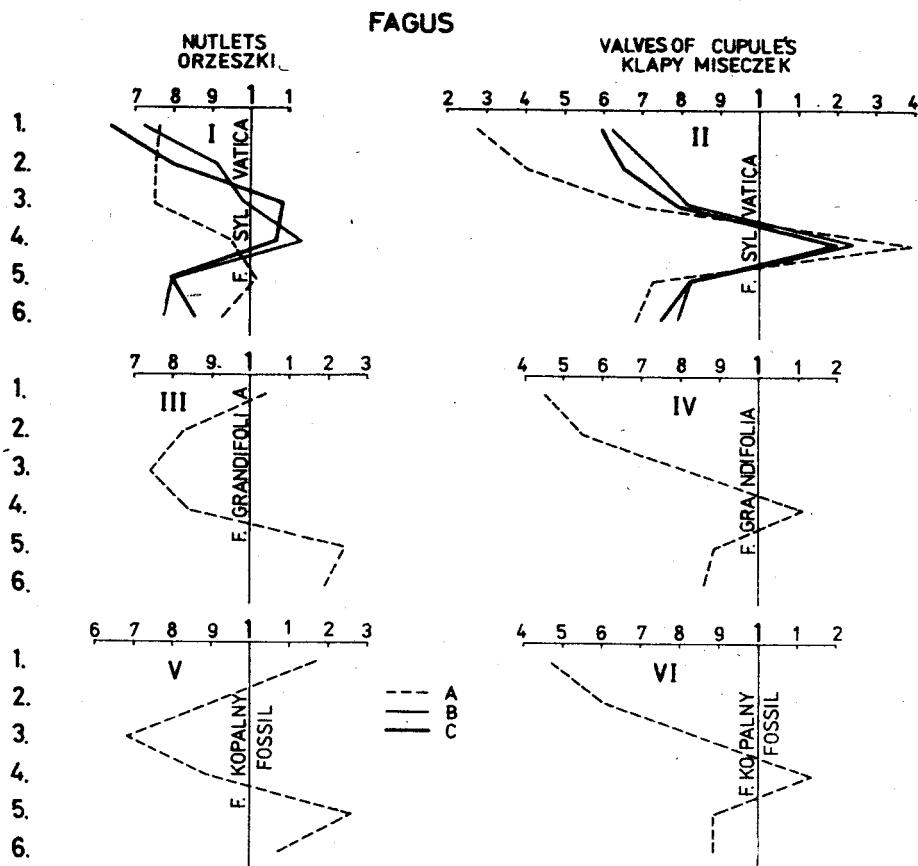


Fig. 6. Graphs I and II. A comparison of the nuts and cupule valves of *Fagus japonica* (A), *F. grandifolia* (B) and Miocene fruits (C) with the cumulative sample of *F. sylvatica*. Graphs III and IV. A comparison of the nuts and cupule valves of *F. japonica* with *F. grandifolia*, (cumulative sample). Graphs V and VI. A comparison of the nuts and cupule valves of *F. japonica* with the fossil material from Koniówka

in relation to the comparative unit represented once by *F. grandifolia* (cumulative sample) and then by the material from Koniówka.

Attention should also be drawn to the fact that in all the species examined and in the material from Koniówka the length of cupule valves always exceeds the length of nuts, the cupules of *F. japonica* being the only exception (Tables 1 and 2).

The surface sculpture of cupules is an important character which has proved helpful in palaeobotanical studies; here, however, it has not been approached numerically. In describing the cupules from the Pliocene of Krościenko, Szafer (1947) emphasized the significance of this feature as one of the diagnostic characters. Three types of cupule surface are observed in the available reference material. After the removal of the spines the surface of the cupules of *F. sylvatica* and *F. crenata* is smooth, marked only with the scars of spine bases. After the

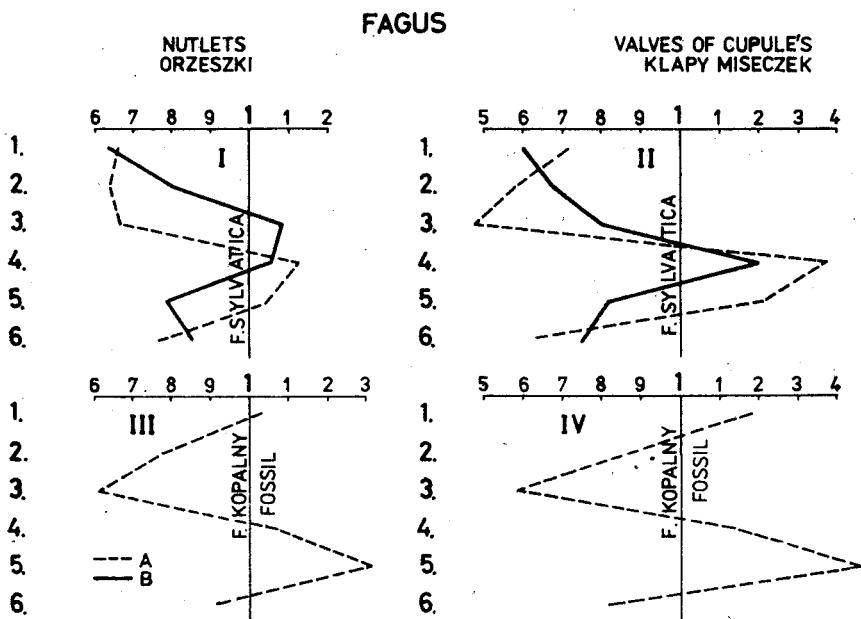


Fig. 7. Graphs I and II. A comparison of the size and shape lines for the nuts and cupule valves of *Fagus engleriana* (A) and Miocene specimens from Koniówka (B) with the cumulative sample of *F. sylvatica*. Graphs III and IV. A comparison of the nuts and cupule valves of *F. engleriana* with the Miocene sample from Koniówka

spines have been removed, longitudinal grooves extend on the surface of the cupules of *F. grandifolia*, the scars of spine bases being preserved on the ridges alternating with the grooves. The surface of cupules differentiated in this way occurs also in *F. japonica* and *F. engleriana*, but usually only in the apical portion of the valves. In the material from Koniówka the grooves run from the base to the very top and so in the same way as in *F. grandifolia*.

#### CONCLUSIONS

The results of this biometrical study show that in shape the nuts and cupules of the genus *Fagus* obtained from the Neogene clays at Koniówka very much resemble the fruits of *F. grandifolia* Ehrh. (= *F. ferruginea* Ait. = *F. americana* Sweet), now growing in the Atlantic part of North America. This statement is besides confirmed by the similarity of the surface sculpture of cupules (Pls. I and II). The fossil fruits differ from the modern ones only in their somewhat smaller size, particularly that of nuts, which is probably connected with the process of fossilization. It is worth noticing that the differences between the species of the genus *Fagus* are more distinct in the morphological structure of cupule valves than in that of nuts.

The referring of the beech fruits from Koniówka to the species *F. grandifolia*

Ehrh. is not an isolated case in the studies on the Tertiary. This species was reported with more or less serious reservations among other localities, from the Miocene of Wieliczka (Zabłocki 1928), the Miocene of Stare Gliwice (Szafer 1961), the Pliocene of Krościenko (Szafer 1947) and the Pliocene of Frankfurt am Main (Mädler 1939). In the Mio-Pliocene deposits of Gozdnica in Lower Silesia 613 cupules were found (Stachurska et al. 1971), which, to be sure, show some likeness in shape and surface sculpture to those of the species *F. grandifolia*, but are characterized by their strikingly small size. A close investigation of this rich material will be the objective of our further work on the genus *Fagus* in the Tertiary.

### FAGUS

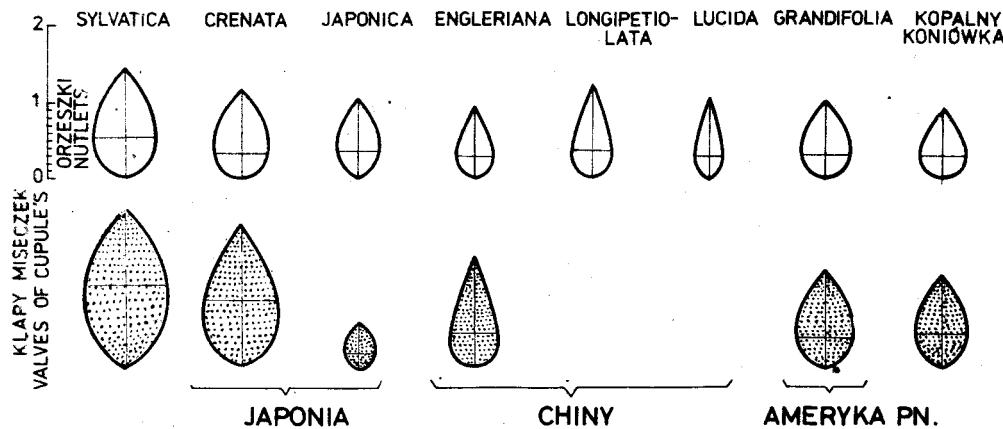


Fig. 8. The nuts and cupule valves of the *Fagus* species examined, drawn on the basis of the arithmetic means of the characters ( $\times 2$ )

The size of the fossil fruits both from all the above-mentioned localities and from Koniówka has been found smaller than that of the fruits of the modern species *F. grandifolia*. On this basis the supposition was put forward that in the European Neogene there lived a species similar to *F. japonica*, whose fruits are characterized by small dimensions (Szafer 1961). The results of the study carried out on the material from Koniówka do not confirm this supposition. The length of cupules is 4—8 mm in *F. japonica* (Ohwi 1965) and 8—17 mm in *F. grandifolia* (cf. Fig. 3). The length ratio of cupules to nuts is also noteworthy. In *F. grandifolia* and the material from Koniówka the nuts are hidden in the cupule, their dimensions being smaller than those of the cupule valves *F. japonica* is marked by its exceedingly short valves their length is hardly a half and sometimes two-thirds of the nut length.

Neither can we see any similarity of the fossil remains from Koniówka to the fruits of other Asiatic species, like *F. lucida* and *F. longipetiolata*. The available reference material was limited to nuts, which in their slim shape differ distinctly from the fossil nuts. The nuts and cupules of *F. engleriana*

also differ from the fossil specimens from Koniówka (Fig. 5). The results of the present biometrical study are well illustrated in Fig. 8, which shows the outlines of the nuts and cupule valves of the species under study, reconstructed on the basis of the arithmetic means obtained from the measurements taken.

#### ACKNOWLEDGMENTS

We wish to express our heartfelt thanks to Prof. Maria Łaniccka-Środoniowa for the fruits of *Fagus* from Koniówka delivered to us for study and for pains she took to provide us with modern materials for comparisons. We thank Assist. Prof. Jerzy Staszkiewicz for his valuable remarks on the draft of this paper. We are also indebted to Assist. Prof. Krystyna Grodzińska for the fruits of *F. crenata* brought from Japan, to Mrs. Ilona Zgierska for the material collected in the Quebece and Ontario Provinces in Canada and to Mr. Antoni Svoboda F. E. for the fruits of *F. engleriana*.

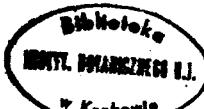
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#### STRESZCZENIE

Buk był drzewem wchodzącym w skład zbiorowisk leśnych neogenu europejskiego. Z polskiego neogenu szczątki makroskopowe buka znane są co najmniej z 11 stanowisk. Owoce były najczęściej opisywane pod nazwą *Fagus ferruginea* Ait. i *F. decurrentis* C. et E. M. Reid. i porównywane do północno-



amerykańskiego gatunku *F. grandifolia* Ehrh. Z plioceńskich osadów opisywane były również owoce typu *F. sylvatica* L.

Materiał dobrze zachowanych orzechów i kupul buka, nadających się do opracowania metodą biometryczną, pochodził z neogenickich złóż szarych ilów w miejscowości Koniówka (Kotlina Nowotarsko-Orawska).

Do badań biometrycznych wybrano najlepiej zachowane okazy w liczbie 122 klap i 36 orzechów. Założeniem podjętych studiów było poznanie zmienności kupul i orzechów współcześnie żyjących gatunków buka i na tym tle ocena materiału kopalnego z Koniówki.

Morfologię kupul i orzechów zarówno współczesnych, jak i kopalnych charakteryzowano za pomocą następujących cech:

**Kupule:** 1. Długość klapy; 2. Szerokość klapy; 3. Kąt wierzchołka klapy;  
4. Kąt podstawy klapy; 5. Stosunek długości do szerokości klapy; 6. Położenie najszerszej części w % % długości klapy.

**Orzechy:** 1. Długość orzecha; 2. Szerokość orzecha; 3. Kąt wierzchołka orzecha;  
4. Kąt podstawy orzecha; 5. Stosunek długości do szerokości orzecha;  
6. Położenie najszerszej części w % % długości orzecha.

Wyniki analizy biometrycznej przedstawiono stosując metodę graficzną Jentys-Szaferowej (1959). Materiał liczbowy zestawiony jest w 3 tabelach (tabele 1–3).

Na podstawie wyników badań biometrycznych stwierdzono, że kopalne orzechy i kupule rodzaju *Fagus* z Koniówki są bardzo podobne w swoim kształcie do orzechów *F. grandifolia* Ehrh. (= *F. ferruginea* Ait. = *F. americanus* Sweet.), gatunku rosnącego dziś w atlantyckiej części Ameryki Północnej. Oznaczenie to potwierdza podobna skulptura powierzchni kupul (tablice I i II). Owoce kopalne różnią się od współczesnych jedynie nieco mniejszymi rozmiarami, zwłaszcza orzechów, co prawdopodobnie wiąże się z procesem fosylizacji.

*Fagus grandifolia* Ehrh. był podawany z większymi lub mniejszymi zastrzeżeniami m. in. z miocenu Wieliczki (Zabłocki 1928), miocenu Starych Gliwic (Szafer 1961), pliocenu Krościenka (Szafer 1947) i z pliocenu Frankfurtu nad Menem (Mädler 1939). Również na Dolnym Śląsku (Stachurska et al. 1971) znaleziono 613 kupul, które pod względem kształtu i skulptury powierzchni wykazują podobieństwo do *F. grandifolia*, ale odznaczają się uderzająco małymi rozmiarami. Na wszystkich tych stanowiskach stwierdzono, podobnie jak w Koniówce, mniejsze rozmiary owoców kopalnych od współczesnych owoców *F. grandifolia*. Na tej podstawie były wysuwane przypuszczenia, że w europejskim neogenie występował także gatunek podobny do *F. japonica*, którego owoce odznaczają się małymi rozmiarami (Szafer 1961). Wyniki badań nad materiałem z Koniówki tej sugestii nie potwierdzają. Długość kupul u *F. japonica* wynosi 4–8 mm (Ohwi 1965), a u *F. grandifolia* (materiały współczesne i kopalne z Koniówki) 8–17 mm (por. ryc. 3). Ponadto u *F. grandifolia* i w materiale kopalnym z Koniówki orzechy są ukryte w kupuli, ponieważ ich rozmiary

są mniejsze od klap kupul. *F. japonica* charakteryzuje się wybitnie krótkimi klapami, których długość wynosi zaledwie 1/2, a czasem 2/3 długości orzechu. Nie można również dopatrywać się podobieństwa między szczątkami kopalnymi z Koniówki a innymi gatunkami azjatyckimi, takimi jak *F. lucida* i *F. longipetiolata*. Posiadany materiał porównawczy ograniczony był do orzechów, które swoim smukłym kształtem różnią się wyraźnie od okazów kopalnych. Odmienne od kopalnych z Koniówki są również orzechy i kupule *F. engleriana* (ryc. 5.) Wyniki badań biometrycznych ilustruje dobrze ryc. 8, na której przedstawione są narysy orzechów i klap kupul badanych gatunków, sporządzone na podstawie średnich arytmetycznych uzyskanych w wyniku przeprowadzonych pomiarów.

## **PLATES**

Plate I

Cupules and nuts of the genus *Fagus*

- A — *F. sylvatica* L., recent
- B — *F. crenata* Blume, recent
- C — *F. japonica* Maxim., recent
- D — *F. engleriana* Seemen, recent
- E — *F. longipetiolata* Seemen, recent
- F — *F. lucida* Rehder, recent
- G — *F. grandifolia* Ehrh., recent
- H — *F. aff. grandifolia* Ehrh., Miocene (Koniówka)

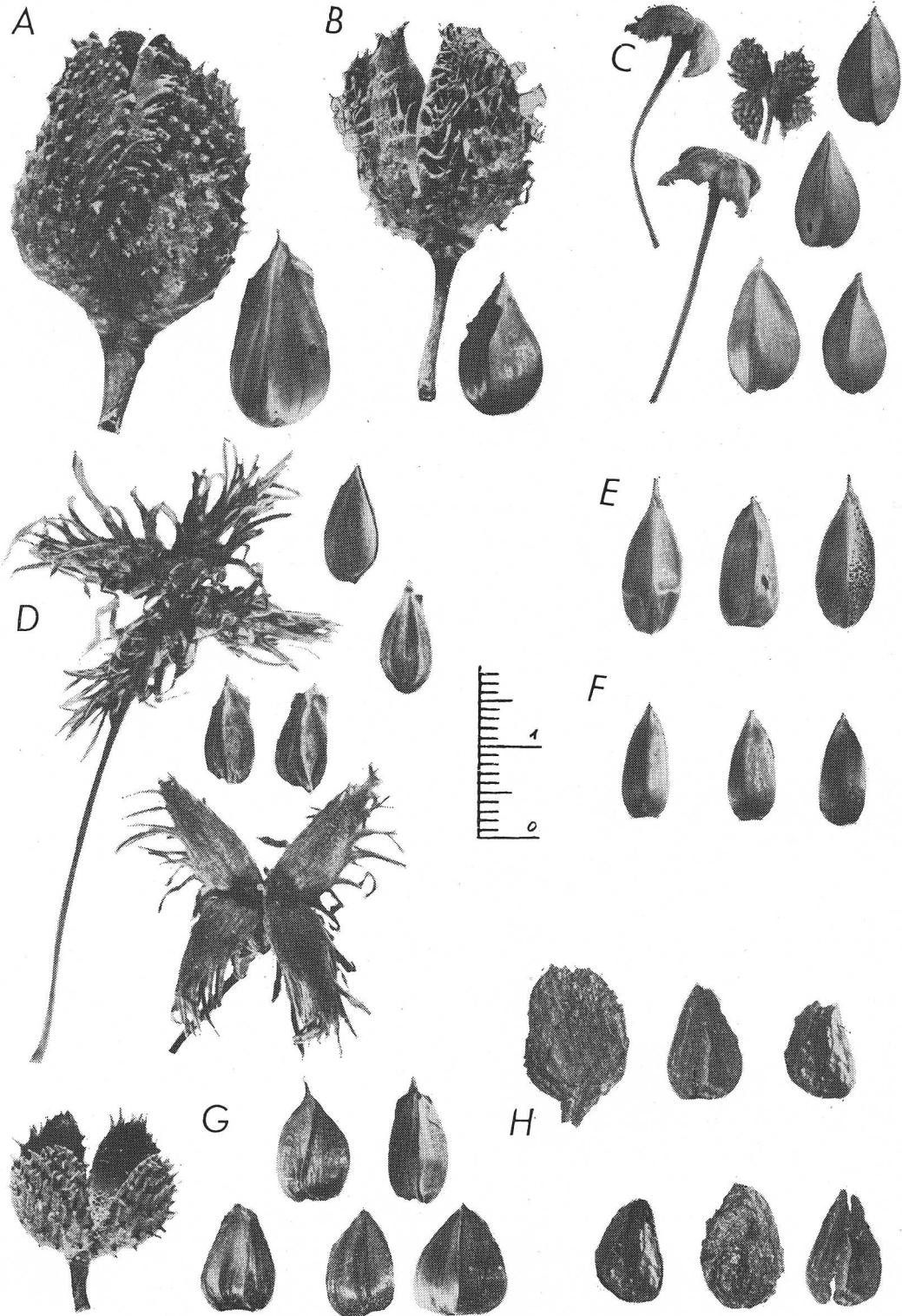


Plate II

Valves of cupules (left) and particular walls of the nuts (right)

- A — *F. sylvatica* L., recent
- B — *F. crenata* Blume, recent
- C — *F. japonica* Maxim., recent
- D — *F. engleriana* Seemen, recent
- E — *F. longipetiolata* Seemen, recent
- F — *F. lucida* Rehder, recent
- G — *F. grandifolia* Ehrh., recent
- H — *F. aff. grandifolia* Ehrh., Miocene (Koniówka)

