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VARIABILITY OF THE RECENT AND FOSSIL FRUITS
OF THE GENUS *DULICHIMUM*

Zmienność współczesnych i kopalnych owoców rodzaju *Dulichium*

ABSTRACT

The subject of the present work was to investigate by means of the biometric method the morphology of the fruits of the genus *Dulichium*, i.e. of the recent species *D. spathaceum* Pers. and of the fruits of that species found in Poland in the fossil state. Moreover, the author tried to determine the relationships between the extinct species of *D. vespiforme* C. E. Reid, which is connected in Poland with the Pliocene, and the living *D. spathaceum*. In result of her studies the author has established that the morphological variability of the fruits of the recent *D. spathaceum* is small, while the fossil fruits of that species show a pronounced directional variability starting from the Tertiary, through the Pleistocene, up to the recent fruits. The fruits of the extinct species *D. vespiforme* form a distinct morphological type not comprised in the evolutionary sequence of the species *Dulichium* type *spathaceum*.

CONTENTS

Introduction	119
Aim and method of work	121
Variability of recent fruits	122
Fruits of <i>Dulichium</i> in the Polish fossil material	126
References	140
Streszczenie	141

INTRODUCTION

Dulichium is a monotypic genus at present. It belongs to the *Cyperaceae* family, order of *Cyperales*. Its only species living now, *D. spathaceum* Pers., grows in the Atlantic part of North America, from New

Foundland to Texas and Florida in the east, as well as in British Columbia and California in the west. It is a perennial plant with a cylindric stem up to 1 m high, upright, and leafed up to its top. The flowers, from 6 to 12 in number, are collected in spikes leaning out of the spathas. The perianth is composed of 6 to 9 pilose setas longer than the fruit and accreted with its base. The persistent style of the pistil is also much longer than the fruit. The base of the fruit is narrowed and pronouncedly distinct from the part containing the seed (Fernald 1950). In the present paper this base is called the fruit-base.

From the ecological point of view, *Dulichium spathaceum* is an aquatic-marshy species; it also grows near stagnant or slowly flowing waters. It requires an oceanic climate. In the Quaternary and Tertiary this species also grew in Europe and Asia. The fruits of *Dulichium spathaceum* are known from Quaternary and Tertiary European floras, namely from the Netherlands, Denmark, Germany, Poland and the U.S.S.R.

Professor Władysław Szafer (1930) was the first of the Polish palaeobotanists who found fossil fruits of *D. spathaceum* (in the interglacial peat at Samostrzelniki). In the course of work on the Polish Tertiary and Quaternary the list of such findings became longer. The fruit of *Dulichium* occurred there usually together with the fossil remains of marshy and aquatic plants of the genera of *Brasenia*, *Najas*, *Nuphar*, *Nymphaea*, *Potamogeton*, and *Aldrovanda*.

The other fossil species, *Dulichium vespiforme* Reid, not encountered in the contemporary flora, is connected in Europe above all with the Pliocene. The fruits of that species, much shorter and comparatively broader, were found in the fossil floras of the Netherlands, Germany, U. S. S. R., and Poland. The first reports about the finding of the Pliocene fruits of *Dulichium vespiforme* were submitted by C. and E. Reid in the years 1907/1908. In 1909 Stoller described the fruits of *Dulichium vespiforme* found beside those of *Dulichium spathaceum* in the peat of the oldest interglacial from Lauenburg and Friedrichshagen in Germany. In 1915 there appeared the extensive publication "The Pliocene Floras of the Dutch-Prussian Border" by C. and E. Reid in which besides *D. spathaceum* the authors described its two fossil varieties, i. e. *var. marginatum* with thinly margined fruits and *var. ellipticum*, as well as the fruits of *Dulichium vespiforme* with the triangular variety having its broadest part situated fairly low, and a third species, *D. urceolatum*, the fruits of which were larger in size, roundish, and passing suddenly in the style of pistil and fruit-base.

The description of the forms mentioned above is closed up by C. and E. Reid with a note that in the material studied there may be found all intermediate forms, from the roundish fruits of *D. urceolatum* to those reckoned among the *D. vespiforme* species, and from the *vespiforme* species through the comparatively short and broad extreme forms of

the fossil species of *D. spathaceum* to the narrow and much elongated fruits encountered in the specimens of that species living now. Kirchheimer (1957) was of the same opinion when he wrote that both the Tertiary and the Quaternary fruits of the genus *Dulichium* found in Europe showed a continuous variability and that in the past there existed only one species of the genus *Dulichium*, whose narrow and long forms of *D. spathaceum*, and short and broad ones of *D. vespiforme*, were connected by intermediate forms.

Dorofeev (1963) described a few findings of the fruit of *D. spathaceum* from the Pleistocene and Pliocene of the European part of the U. S. S. R., while from West Siberia he reported the occurrence of shorter and broader fruits determined by him as *D. vespiforme* Reid. The fruits were characteristic of the Pliocene, but also encountered, although more rarely, in the Miocene; in the Miocene of Siberia there appeared longer and comparatively narrower fruits which in their size and shape corresponded to the fossil variety of *D. spathaceum* var. *marginatum* Reid. Dorofeev raised this variety to the rank of a species and wrote that in West Siberia it was connected almost entirely with the Oligocene.

In Poland, the fruits of *D. vespiforme* were found for the first time by Professor W. Szafer (1947) in the Lower Pliocene flora from Krościenko on the Dunajec river (one drupel), and from the Upper Pliocene from Mizerna (1954) in more than 300 specimens.

In this place the present author wishes to thank most cordially Professor Janina Jentys-Szaferowa who encouraged her to undertake that work and offered advice during its performance. She also wishes to express her warm gratitude to all persons, and especially Doc. Dr. Maria Środoniowa, who submitted their material for elaboration.

AIM AND METHOD OF WORK

The aim of the present work was to study the morphology of the fruits of *Dulichium spathaceum*, both contemporary and those fossil ones which occur in Poland, and to determine the relationship between the extinct *D. vespiforme* and other fossil fruits of the genus *Dulichium*, and the contemporary species of *D. spathaceum*.

The fruits of the plants living now and used in the study were mainly derived from natural localities and collected by Prof. Szaferowa and Prof. Lúdi in the eastern part of North America and Canada. A part of the samples was formed of the carpologic collections of the Palaeobotanical Laboratory of the Botanical Institute of the Polish Academy of Sciences. The joint number of contemporary fruits subject to investigations was 347.

The samples of the fossil fruits of *D. spathaceum* from the Quaternary were composed of six floras from the Masovian and Eemian Interglacial. The Tertiary fruits of that species were connected with the period of the Upper Miocene. They were found in the floras from Chyżne, Sośnica, Komin and Czarny Dunajec.

The fruits identified as *Dulichium vespiforme* were derived from three Pliocene floras from Krościenko, Mizerna and Grywałd.

The morphology of the fruits of the genus *Dulichium* was elaborated biometrically. The results are represented graphically by means of the method described by Prof. J. Szaferowa (1959).

The fruits of *Dulichium* are of small size and therefore difficult for precise measuring. They were therefore drawn with the help of a magnifying photographic apparatus and next their silhouettes were measured. The specimens were drawn magnified eight times, and the same magnification was adopted in a specially prepared scale to allow the reading of measurements exact to 0.05 mm. At the beginning, the setas on the fruit were counted, but when measuring the fossil material the author saw that the setas had undergone partial or even total destruction and she gave up taking this character under consideration.

The morphology of the fruits was studied with respect to the characters as follows:

1. Length of fruit
2. Breadth of fruit
3. Length of fruit-base
4. Apical angle
5. Length/breadth of fruit
6. Position of broadest part in % of fruit length
7. Length of fruit/length of fruit-base

The method of measurement is represented in fig. 1.

VARIABILITY OF RECENT FRUITS

The fruits of *Dulichium spathaceum* are collected in spicules and these form spikes. The latter grow out of the nodes of leaves arranged alternately along almost the whole length of the shoot of plant. Considering this the author desired to learn whether there are any differences in the morphology of the fruits of one and the same plant depending on the position of the spike on stem. Therefore she chose for measurements the fruits from the spike situated right at the bottom of the shoot, next from the middle one, and lastly from the spike growing out at the apex of stem. It should be emphasized that the number of fruits taken for measurements was not the same in each of these spikes. The lower spike had only seven fruits, the middle one twenty-three, and the upper spike

Fig. 1. Measurement of the fruits of the genus *Dulichium*: a — a: length of fruit; b — b: breadth of fruit; c — c: length of fruit-base; d — d: distance between the broadest part and the fruit-base; α : apical angle

Ryc. 1. Sposób mierzenia owoców rodzaju *Dulichium*: a — a: długość owocu, b — b: szerokość owocu, c — c: długość stylika, d — d: odległość najszerszej części od nasady owocu, α : kąt wierzchołka

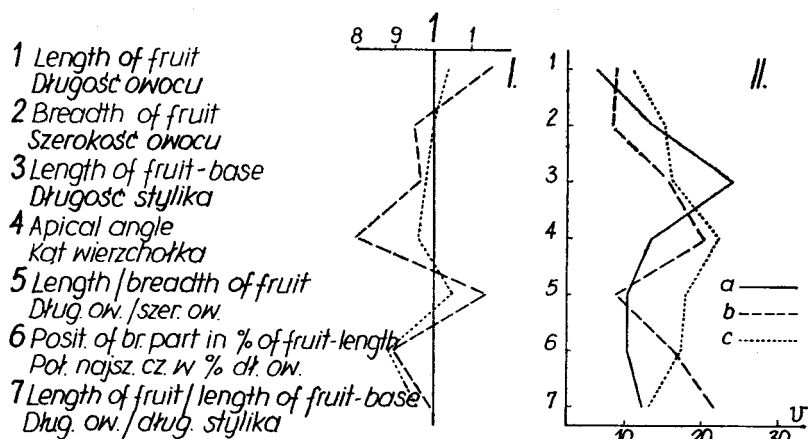
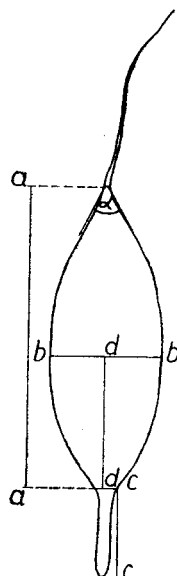


Fig. 2. I. Comparison of the arithmetic means of characters of fruits from the middle (b) and apical (c) spikes, with the arithmetic means of characters of fruits from the lower spike (a); II. Diagram of the coefficients of variability of the characters of fruits

Ryc. 2. I. Porównanie średnich arytmetycznych cech owoców z środkowego kłosa (b) oraz owoców z wierzchołkowego kłosa (c) do średnich arytmetycznych cech owoców z dolnego kłosa (a); II. Wykres współczynników zmienności cech owoców

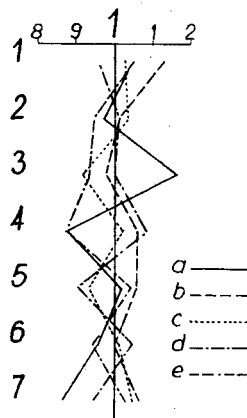
proved to be the most abundant and had as many as thirty-nine fruits. The fruits seemed to resemble one another very much, as regards both their size and shape, independent on the spike they were derived from. A detailed biometric analysis corroborated this observation to a certain

extent and showed rather small differences in the morphological characters of the fruits discussed. In fig. 2 the diagonal lines represent the ratio of the arithmetic means of characters of the fruits from the central and upper spikes and of those relevant to the spike situated lowest on the stem (straight line). Diagram II of that figure is a picture of the coefficients of variability, and their low values corroborate the rather small variability of the material within an individual plant. Thus, the conclusion may be drawn that to characterize the *Dulichium* population it was of lesser importance from which part of the plant the biometrically investigated fruits were derived.

In the next stage of her work the author studied the morphology of the fruits of the particular local populations. If the samples of the contemporary fruits were derived from the plants collected in the localities of the natural occurrence of *Dulichium spathaceum*, two fruits from the upper spike of every specimen were taken for measurements. In the cases when museum material was available there was no certainty whether the fruits had been collected from one individual plant or from a larger number of plants. This, however, should not arouse any doubts as to the representativeness of these samples, because while studying fossil material we also are not certain of the number of the individual plants from which the particular specimens are derived.

Fig. 3. Comparison of the arithmetic means of the characters of fruits from 5 local samples with the comprehensive sample of fruits of the contemporary *Dulichium spathaceum* Pers. (straight vertical line); a — Venice, b — Canada sample from a not determined locality, c — Montreal, d — Susquehanna, e — Lake Michigan

Ryc. 3. Porównanie średnich arytmetycznych cech owoców z 5 prób lokalnych do próby zbiorczej owoców współczesnego *Dulichium spathaceum* Pers. (linia prosta pionowa); a — Venice; b — Kanada (stanowisko bliżej nie określone); c — Montreal; d — Susquehanna; e — Lake Michigan



Roughly estimated, the fruits of the contemporary *Dulichium spathaceum* resembled one another closely, independent on the circumstance whether they were derived from natural localities or from the material cultivated in botanic gardens. Figure 3, in which 5 local samples are compared with the comprehensive sample of the contemporary *Dulichium spathaceum*, corroborates the observations quoted above and requires no detailed comments. It was only the fruit from Venice in Canada collected in a bird sanctuary which slightly differed in their morphology from the

remaining 4 samples by their much elongated fruit-base and sharper apical angle. Apart from that, the material seemed to be very even as regards the size and shape of fruits.

To show more clearly the distinctness of the fruits from Venice, this sample was chosen as a comparative unit (straight vertical line) in fig. 4. The fruits from four local samples (diagonal lines) form a close whole with respect to all characters. Deviations from the comparative unit run in accordance and in the same degree, and the small variability of the characters of size and shape are emphasized in diagram II of the coefficients of variability which is found in the same figure. Basing upon the facts observed and quoted above one might advance the supposition that the plants from Venice form a local biotype and have fruits with pointed tops and rather elongated fruit-bases. Nevertheless there is no doubt that these fruits belong to the *D. spathaceum* species.

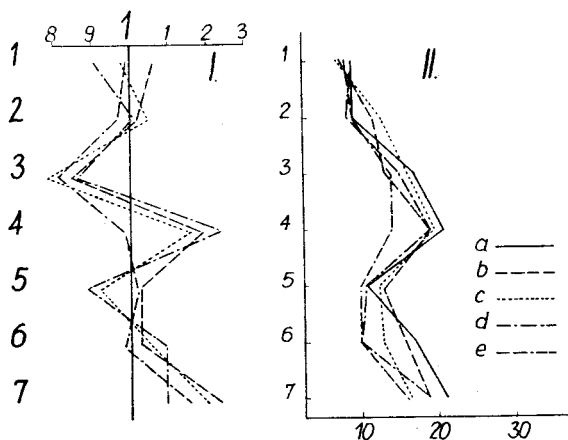


Fig. 4. I. Comparison of the arithmetic means of characters of the contemporary fruits of *D. spathaceum* in 4 local samples (b — Canada sample from a not determined locality, c — Montreal, d — Susquehanna, e — Lake Michigan) with the local sample from Venice — a (straight vertical line); II. Diagram of coefficients of the variability of characters of contemporary fruits of *D. spathaceum* in 5 local samples

Ryc. 4. I. Porównanie średnich arytmetycznych cech współczesnych owoców *D. spathaceum* z 4 prób lokalnych (b — Kanada, stanowisko bliżej nie określone, c — Montreal, d — Susquehanna, e — Lake Michigan) do próby lokalnej z Wenecji w Kanadzie — a (linia prosta pionowa); II. Wykres współczynników zmienności cech współczesnych owoców *D. spathaceum* z pięciu lokalnych prób

The establishment of an ability in *D. spathaceum* to form local populations with peculiar morphological characters proved to be important, because similar peculiarities of the local populations were also encountered in the fossil material.

FRUITS OF *DULICHIMUM* IN THE POLISH FOSSIL MATERIAL

The whole material of fruits, both contemporary and fossil, on which the investigations were based, is compared in Table 1. The material of the contemporary species has been given its name, *D. spathaceum* Pers. The author gave no specific names to the fruits from the three geologic periods, i. e. Pleistocene, Pliocene and Miocene, found in Poland, until they have been investigated biometrically. This material lacked uniformity as regards the number of specimens found in the particular fossil floras. However, in each of the geologic periods mentioned above samples were found which, owing to the fairly large number of specimens, were able to represent the local populations of their times. The interglacial

Table I
Tabela I

List of the material investigated
Zestawienie badanych materiałów

Age Wiek	Species Gatunek	Locality Stanowisko	Number of fruits Liczba owoców	Comprehensive sample Próba zbiorcza
Recent Dzisiejsze	<i>D. spathaceum</i>	Venice in Canada	100	347
"	"	Kanada*	50	
"	"	Montreal	100	
"	"	Susquehanna	65	
"	"	Lake Michigan	32	
Pleistocene Plejstocen	<i>Dulichium</i> sp.	Samostrzelniki	53	73
"	"	Józefów	12	
"	"	Rusinowo	3	
"	"	Żydowszczyzna	3	
"	"	Stanowice	1	
"	"	Główczyn	1	
Pliocene Pliocen	<i>Dulichium</i> sp.	Krościenko	1	452
"	"	Mizerna	167	
"	"	Grywałd	284	
Miocene Miocen	<i>Dulichium</i> sp.	Chyżne	1	309
"	"	Sośnica	1	
"	"	Konin	40	
"	"	Czarny Dunajec	267	

* Sample from a not determined locality
S stanowisko bliżej nie określone

sample from Samostrzelniki (53 fruits) and — to a lesser extent — that from Józefów (12) may be regarded as such. Two Pliocene samples, one from Mizerna (167) and the other from Grywałd (284), and two Miocene ones, from Czarny Dunajec (267) and Konin (40), were of prime importance. Having at her disposal such abundant local samples the author was able to characterize not only the size and shape of the *Dulichium* fruits occurring in the given period, but also their variability.

While setting to work on a detailed analysis the author undertook three tasks: 1) to compile comprehensive samples for each of the geological periods mentioned above including all fruits even those occurring singly, 2) to compare the representative local samples with the comprehensive sample of each period and to determine the eventual differences; 3) to compare the comprehensive samples and determine the morphological differences among the *Dulichium* fruits from various geological periods in Poland.

The first task was executed by comparing the frequency series distribution for the seven characters considered for each of the 3 geological

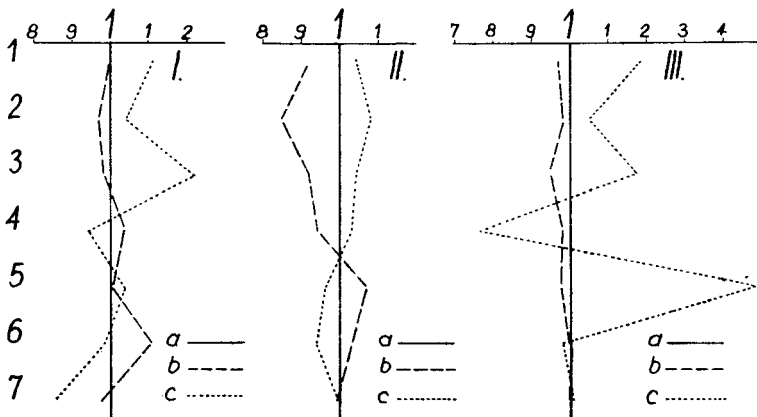


Fig. 5. Comparison of the arithmetic means of characters of size and shape of the fossil fruits of the genus *Dulichium* in the particular geological periods. I. a — Pleistocene comprehensive sample (straight vertical line); b — local sample from Samostrzelniki; c — local sample from Józefów; II. a — Pliocene comprehensive sample (straight vertical line); b — local sample from Mizerna; c — local sample from Grywałd; III. a — Miocene comprehensive sample (straight vertical line); b — local sample from Czarny Dunajec, c — local sample from Konin

Ryc. 5. Porównanie średnich arytmetycznych cech wielkości i kształtu kopalnych owoców rodzaju *Dulichium* w poszczególnych okresach geologicznych. I. a — próba zbiorcza z plejstocenu (linia prosta pionowa), b — próba lokalna z Samostrzelnik, c — próba lokalna z Józefowa; II. a — próba zbiorcza z pliocenu (linia prosta pionowa), b — próba lokalna z Mizernernej, c — próba lokalna z Grywałdu; III. a — próba zbiorcza z miocenu (linia prosta pionowa), b — próba lokalna z Czarnego Dunajca, c — próba lokalna z Konina

Table 2
Tabela 2

Numbers representing the fruit characters of comprehensive samples
Liczby charakterystyczne cech owoców prób zbiorczych

1. Length of fruit
Długość owocu

Age — Wiek	Min. — Max.	M±m	σ	V
Recent Dzisiejsze	2.1—3.3	2.64±0.01	0.24	9.09
Pleistocene Plejstocen	1.8—2.7	2.31±0.03	0.24	10.38
Pliocene Pliocen	1.2—2.1	1.66±0.01	0.20	12.04
Miocene Miocen	1.5—3.3	2.20±0.01	0.29	13.18

3. Length of fruit-base
Długość stylka

Age — Wiek	Min. — Max.	M±m	σ	V
Recent Dzisiejsze	0.50—1.10	0.69±0.01	0.13	18.84
Pleistocene Plejstocen	0.40—0.90	0.61±0.01	0.13	32.50
Pliocene Pliocen	0.20—0.75	0.41±0.01	0.09	21.97
Miocene Miocen	0.30—0.80	0.47±0.01	0.08	17.02

2. Breadth of fruit
Szerokość owocu

Age — Wiek	Min. — Max.	M±m	σ	V
Recent Dzisiejsze	0.5—1.0	0.69±0.01	0.11	15.94
Pleistocene Plejstocen	0.5—0.9	0.69±0.01	0.08	11.59
Pliocene Pliocen	0.6—1.2	0.87±0.01	0.16	18.39
Miocene Miocen	0.5—1.1	0.80±0.01	0.11	13.75

4. Apical angle
Kąt wierzchołka

Age — Wiek	Min. — Max.	M±m	σ	V
Recent Dzisiejsze	25—80	44.60±0.50	9.40	21.07
Pleistocene Plejstocen	35—70	51.95±1.20	10.30	19.82
Pliocene Pliocen	40—105	68.50±0.55	11.85	17.29
Miocene Miocen	25—95	61.70±0.39	6.90	11.18

5. Length/breadth of fruit
Długość/szerokość owocu

Age — Wiek	Min. — Max.	M ± m	σ	V
Recent Dzisiejsze	2.7—5.7	3.76 ± 0.02	0.49	13.03
Pleistocene Plejstocen	2.4—4.5	3.23 ± 0.04	0.42	13.00
Pliocene Pliocen	1.2—2.7	1.90 ± 0.01	0.28	15.26
Miocene Miocen	2.1—3.9	2.74 ± 0.02	0.39	14.23

6. Position of broadest part in % of fruit-length
Polożenie najszerszej części w % długości owocu

Age — Wiek	Min. — Max.	M ± m	σ	V
Recent Dzisiejsze	25—60	42.50 ± 0.32	6.10	14.35
Pleistocene Plejstocen	30—60	43.95 ± 0.77	6.60	15.01
Pliocene Pliocen	25—55	42.30 ± 0.24	5.25	12.41
Miocene Miocen	25—75	43.75 ± 0.40	7.10	16.22

7. Length of fruit/length of fruit-base
Długość owocu/długość stylka

Age — Wiek	Min. — Max.	M ± m	σ	V
Recent Dzisiejsze	2.5—6.0	3.92 ± 0.04	0.82	20.91
Pleistocene Plejstocen	2.5—6.0	3.92 ± 0.09	0.78	19.84
Pliocene Pliocen	2.5—8.0	4.18 ± 0.05	1.10	26.31
Miocene Miocen	3.0—7.5	4.72 ± 0.04	0.87	18.00

periods, comprising all the fruits found in the given period and calculating the characteristic numbers of each character. This is expressed in Table 2.

The second task consisted in a comparison of the local populations with the comprehensive sample within each of the 3 geological periods, similar to the comparison of the local samples of the contemporary *Dulichium spathaceum* with the sample covering its wider range (see fig. 3). This comparison is submitted in fig. 5. In each of the three diagrams drawn in it the comprehensive sample characteristic of the given period served as the comparative unit represented in the form of a straight line, and the two diagonal lines represent the local samples. We see there that in the particular characters the mean values of the local samples were higher or lower than in the comprehensive sample, but these deviations were not great, which means that in each case we had to deal with the samples of fruits slightly differing in size and shape.

The comparison described above does not prove that there were no morphological differences among the *Dulichium* fruits encountered in the particular geological periods which might suggest that in the past there existed more forms or species within the *Dulichium* genus than are met with in the contemporary flora. We shall find an answer if we take the comprehensive sample of the recent *Dulichium spathaceum* as a comparative unit with which we compare the arithmetic means of the three fossil comprehensive samples. An illustration of this is the diagram in fig. 6.

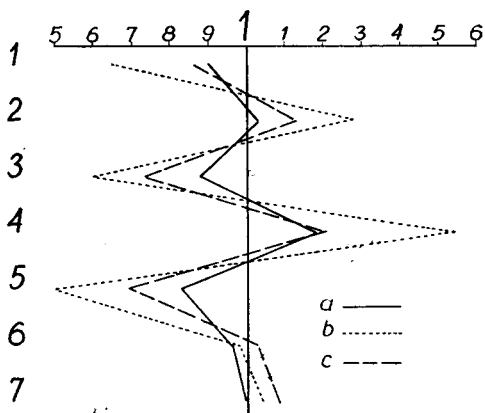


Fig. 6. Size and shape lines of the fossil fruits of the genus *Dulichium*: a — Pleistocene comprehensive sample; b — Pliocene comprehensive sample; c — Miocene comprehensive sample. The comprehensive sample of fruits of the recent *Dulichium spathaceum* served as the comparative unit (straight vertical line)

Ryc. 6. Linie wielkości i kształtu kopalnych owoców rodzaju *Dulichium*: a — próba zbiorcza z plejstocenu, b — próba zbiorcza z pliocenu, c — próba zbiorcza z miocenu. Jednostką porównawczą (linia prosta pionowa) jest tu próba zbiorcza owoców dziś żyjącego *Dulichium spathaceum*

A detailed analysis of that diagram indicates that the Quaternary fruits of the genus *Dulichium* (continuous diagonal line) differed from the contemporary ones in a very characteristic manner. They were on the average shorter (character 1) at an almost similar breadth (2), which pronouncedly changed their shape expressed in the length/breadth ratio (character 5). Besides, their apical angles (4) were wider. Thus, they were on the average shorter, comparatively broader, and not so pointed as the recent fruits. The same changes are seen on the broken diagonal line which in that diagram represents the comprehensive sample from the Polish Miocene, but these have appeared in a much greater degree. Those fruits were still shorter, comparatively broader, and more bluntly ended than the Quaternary fruits.

The dotted diagonal line in fig. 6 is most striking, as it shows the same deviations as the two former lines but in a much greater degree. If that line represented the fruits older than the Miocene, one might assume that this was the primeval type of fruits of the genus *Dulichium*, very short, and slightly narrower than the former (characters 1, 2, 5) and with a broad apical angle. From that primeval type there might have developed, by way of evolution, the longer and more acutely pointed Miocene type, from which the Pleistocene type might have evolved, and from the last mentioned, due to further directional changes, there might have originated the fruits of the contemporary species *Dulichium spathaceum*, comparatively narrow and much elongated, the acute apex of which passes gradually in the woody style of the pistil. However, short and broad fruits have been found in Poland not in the deposits older than the Miocene but in much younger ones, i. e. in the Lower, and even in the Upper Pliocene. These were the fruits from Mizerna, which were determined by W. Szafer as *Dulichium vespiforme* and established by him to be identical with the fruits described by C. and E. Reid in 1915 from Pliocene deposits. According to Szafer their variability concerns on the one hand the roundish forms called by C. and E. Reid *D. urceolatum*, and on the other hand the forms approaching *D. spathaceum* var. *elipticum* C. E. Reid. Most of them, however, occurred at Mizerna in the form of the typical *D. vespiforme* Reid. Prof. Szafer wrote: "However, while besides the extinct species (*D. vespiforme* Reid and *D. urceolatum* Reid) there occurs at Reuver and Swalmen the recent species of that genus, i. e. *D. spathaceum*, which now lives in America, I have not found any typical specimens in the rich material from Mizerna, which might have been reckoned to the latter species, well known to me from the younger interglacials".

The number of fruits found at Mizerna exceeded 300 specimens. Unfortunately, there are only 167 specimens in the Museum of the Palaeobotany Department of the Institute of Botany of the Polish Academy of Sciences, because having finished his studies on Mizerna, Prof. Szafer

left only a part of his collection to the Museum of the Institute of Botany and sent the rest to other palaeobotanic museums in Poland and abroad. However, the sample deposited in Cracow is abundant enough to form the basis of a study on the shape and variability of the fruits of the local population from Mizerna. The value of the Mizerna sample was enhanced by the finding of 284 fruits at Grywałd in the Lower Pliocene, which doubtlessly belonged to the same species, though they showed the peculiarities characteristic of a separate local sample. Therefore the Pliocene fruits will be discussed in detail, not excepting the only specimen found by Szafer in the Lower Pliocene of Krościenko.

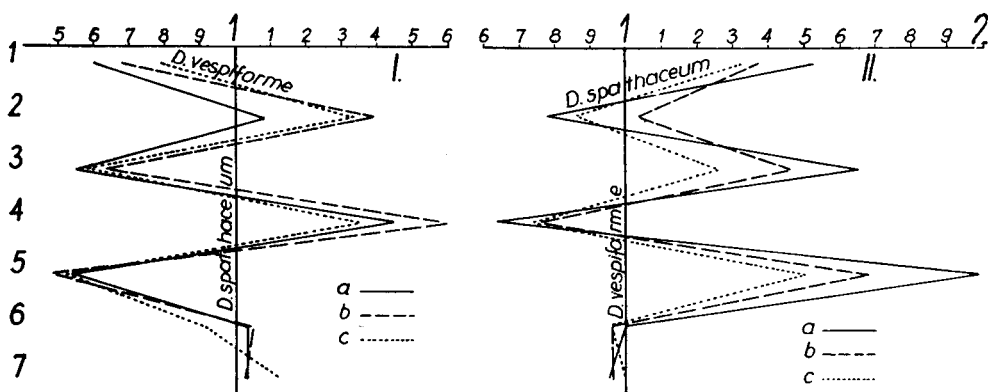


Fig. 7. I. Size and shape lines of fruits of *D. vespiforme* of 3 local samples from: a — Mizerna, b — Grywałd, c — Krościenko compared with the comprehensive sample of the contemporary *D. spathaceum* (straight vertical line); II. Size and shape lines of fruits of the comprehensive samples of *D. spathaceum* compared with the comprehensive sample of the Pliocene species of *D. vespiforme* (straight vertical line); a — contemporary fruits, b — Pleistocene fruits, c — Miocene fruits

Ryc. 7. I. Linie wielkości i kształtu owoców *D. vespiforme* z 3 prób lokalnych: a — z Mizernej, b — z Grywałdu, c — z Krościenka, w porównaniu z próbą zbiorczą dziś żyjącego *D. spathaceum* (linia prosta pionowa); II. Linie wielkości i kształtu owoców prób zbiorczych *D. spathaceum* w porównaniu z próbą zbiorczą plioceńskiego gatunku *D. vespiforme* (linia prosta pionowa): a — owoce dzisiejsze, b — owoce plejstocenske, c — owoce mioceńskie

The results of measurements of the Pliocene fruits are represented graphically in figs. 7 and 8. We see in diagram I fig. 7 that both the arithmetic means of the local samples from Mizerna and Grywałd and the particular values of the only fruit from Krościenko (diagonal lines) deviate in all characters in a very similar way from the comprehensive sample of the contemporary *Dulichium spathaceum* (straight line). Thus, if compared with the *D. spathaceum* sample these fruits represent a separate morphological type, whose characters were typical of the fossil species of *D. vespiforme* Reid. On the contrary, if the comprehensive

sample of the contemporary *D. spathaceum* and those from the Pleistocene and Miocene (diagonal lines) are compared with the general sample of *D. vespiforme* (straight vertical line) it is evident that all the diagonal lines run almost parallel and deviate in a similar way from the comparative unit represented in the form of a straight line. This is a proof that there are good reasons for giving them a separate specific name of *D. vespiforme*. In comparison with them, the fruits from the Miocene, Pleistocene and those of the recent plants of the genus *Dulichium* form a separate type which may be given a common name of the *Dulichium spathaceum* type.

In this aspect, the Pliocene fruits would not form an immediate link between the Miocene and the Pleistocene, but an evolutionary side-line, the fate of which so far remains unknown to us.

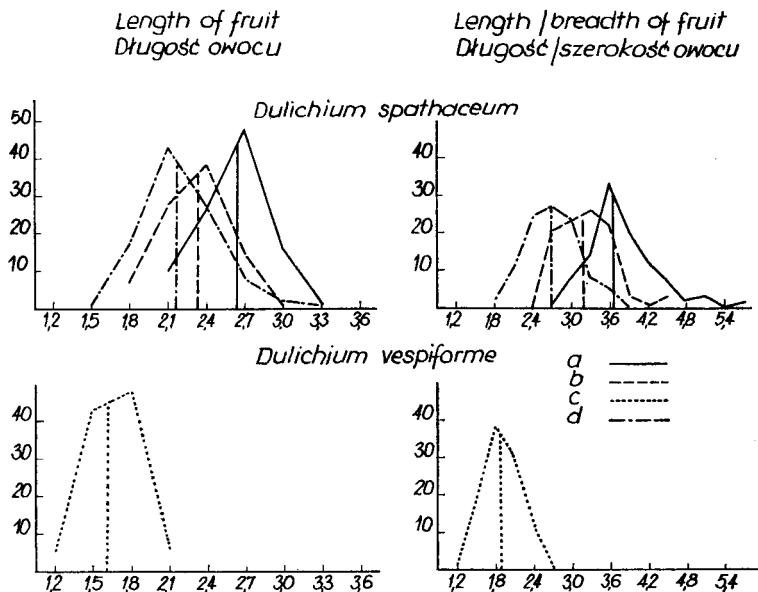


Fig. 8. Polygons of frequency of two characters of fruits of the comprehensive samples of the genus *Dulichium* in the particular geological periods: a — recent, b — Pleistocene, c — Pliocene, d — Miocene

Ryc. 8. Wieloboki frekwencji dwu cech owoców prób zbiorczych rodzaju *Dulichium* w poszczególnych okresach geologicznych: a — współczesne, b — plejstocen, c — pliocen, d — miocen

The distinction of Pliocene fruits as a separate form different from the rest of the fossil fruits and from the recent ones is evident in fig. 8 where the whole scale of variability of the samples investigated is represented with respect to the two most important characters, i. e. length and length/breadth ratio. It can be seen there that these values

are not only smaller for the Pliocene fruits than for the remaining ones, but that their scale of variability is narrow. The frequency drawn there in the particular classes gives a picture approaching "Gauss's curve" which proves that we have to deal here with a homogenous morphological form, and not with a mixture of two or more forms. This corroborates the specific distinctness of the specimens of the genus *Dulichium* which grew in Poland in the Pliocene.

Having established that in the fossil material there may be distinguished at least two species within the genus *Dulichium*, which are characterized by a different shape of the fruits forming populations connected with places and time determined, consideration had to be focussed on the problem whether and to what extent these results agree with those obtained by other authors who encountered *Dulichium* fruits in their fossil material. This was rather difficult. First of all, in the palaeobotanical literature the exact number of specimens upon which the determination of their systematic position has been based is quoted only exceptionally. Szafer's papers formed an exception in this respect, because he tried to base his studies on as abundant material as possible, and even if he did not submit it to measurements he quoted the number of specimens reckoned to the given fossil taxon. With other authors no such data were encountered besides a general information that the specimens were numerous or few. Moreover, if measurements were performed, their method was not described in detail, which often made them uncomparable. To make her material and the data drawn from the papers of other authors uniform the present author adopted one of the two ways. If the given author submitted the size of fruits, she introduced corrections, e. g. to make the length of fruit correspond to that accepted by her as the length of fruit (fig. 1), or she measured the length and breadth of the *Dulichium* fruits on their photographs published in the papers by other authors and compared them with her measurements. In this way she obtained the length/breadth ratio, a character very important to the shape of fruit and absolutely comparable with the results of the present paper. The comparison of the results of investigations is submitted in fig. 9, in which the papers of three authors are considered who described, measured or photographed the fossil fruits of that genus, i. e. C. and E. Reid, Stoller, and Dorofeev.

Fig. 9 represents the scale of variability of the populations studied by the present author with respect to three characters of great importance to the fruits of the genus *Dulichium*, i. e. length, breadth, and their mutual ratio, which decide upon the shape of the fruits found in the given geological periods. On each of the thick horizontal lines uniting the extreme values for the Polish populations under investigation there has been marked the position of the arithmetic mean. In the column to the right there is the number of the variants of which the population studied

Variability of fruits of genus *Dulichium* Zmienność owoców rodzaju *Dulichium*

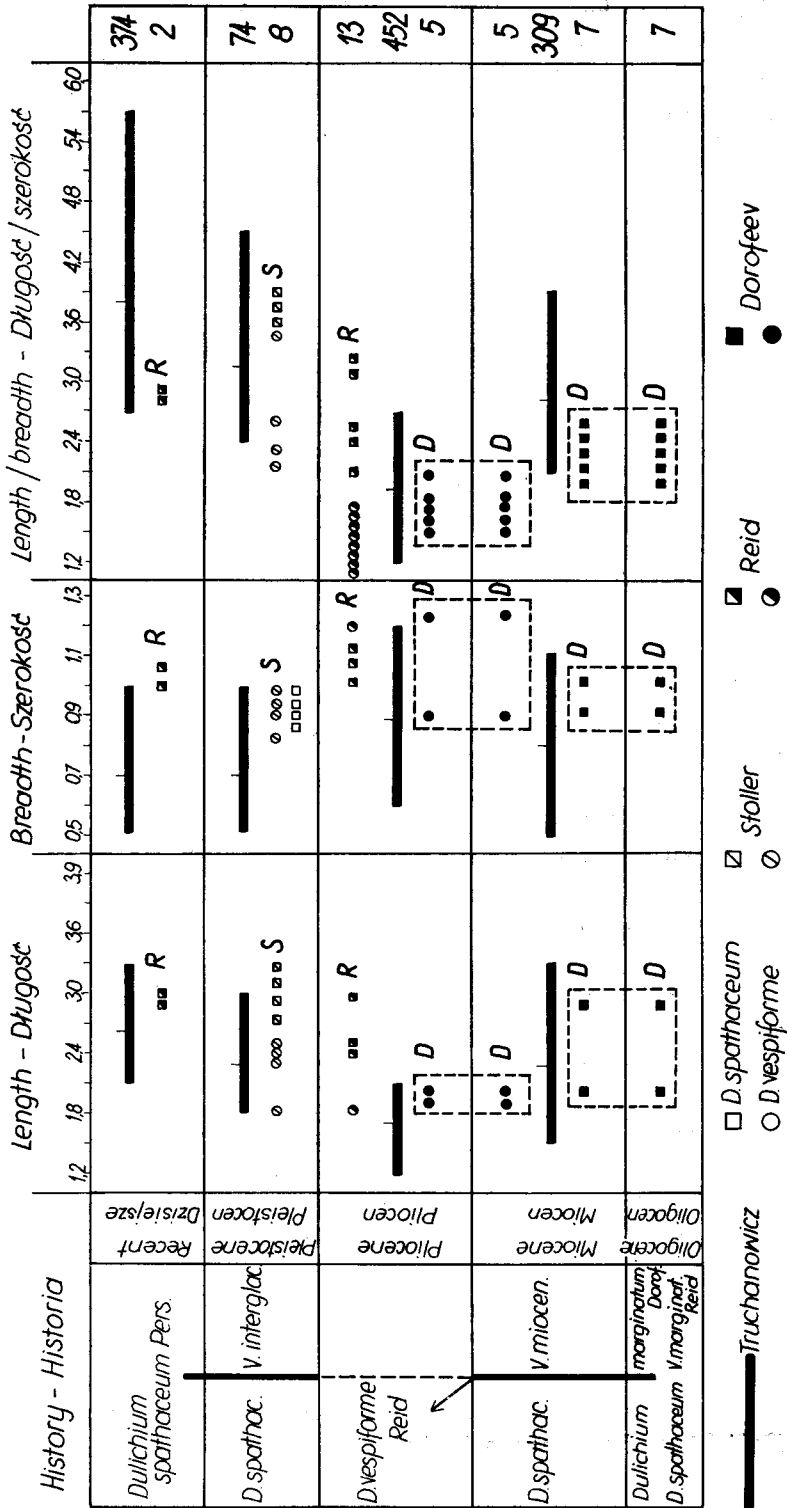


Fig. 9. Variability of the fruits of the genus *Dulichium* determined on the basis of the material investigated

Ryc. 9. Zmienność owoców rodzaju *Dulichium* określona na podstawie zbadanego materiału

was composed. In each case it includes all the *Dulichium* fruits found in the given geologic period, and thus it corresponds to the so called "comprehensive samples". In that diagram, the specimens found and identified by the authors mentioned above as *Dulichium spathaceum* were marked by means of squares, and *D. vespiforme* as circles, with the letters S, R or D added to mark the names of the authors by their first letters. The corresponding numbers in the last column comprise the amounts of fruits which could be taken under consideration on the basis of the data submitted in the papers by Stoller, C. and E. Reid and Dorofeev. They do not correspond to the numbers of fruits which formed the basis of their determinations, because none of these authors mentioned these numbers.

The first question to which the present author tried to give an answer by fig. 9 was, whether the fruits found by Stoller in what he called the second interglacial, or probably the Riss-Würm Interglacial, may be reckoned among the Pliocene species *Dulichium vespiforme* C. E. Reid. To this purpose, four fruits identified by Stoller as *Dulichium vespiforme* and four identified as *D. spathaceum* were introduced in that diagram. We see that as regards their length and breadth all the eight fruits are comprised in the scale of variability of the material derived from the Polish interglacials and, eventually, of the recent specimens measured by the present author. However, the third column includes only two fruits identified by Stoller as *D. vespiforme*, and two are outside that scale and represent a morphological type encountered by the present author in the Polish Pliocene as an extreme deviation of the forms found there. Thus, the important problem remains still open, whether the *vespiforme* species had survived two glaciations and lived in Europe in the period of the second glaciation. It should only be emphasized that Stoller's eight interglacial fruits do not form two distinct groups but show a continuous variability in the characters investigated.

The Pliocene material of C. and E. Reid proves to be different. It is composed of two samples. One of them is formed of the fruits found in the Upper Pliocene of Tegelen, the other includes the material from Reuver. According to C. and E. Reid's opinion, the fruits from Tegelen, younger than those from Reuver, were slightly larger and comparatively narrower, and it was with these that Stoller compared his material. They, too, formed the basis for C. and E. Reid's description of *D. vespiforme*. The fruits from Reuver, the age of which was determined as the Middle Pliocene, seemed different to C. and E. Reid, they were shorter and comparatively broader. Thus, according to their opinion, they did not meet with a typical *D. vespiforme* but with its varieties or altogether different species. Unfortunately, C. and E. Reid do not report how many *Dulichium* fruits were included in these floras, and it is only the

photographs submitted by them in Plate IV which form the only basis of investigations.

C. and E. Reid's fruits marked in the column of the length/breadth ratio are strictly comparable with the present author's data, because that character was calculated on the basis of the measurement executed by her on the photographs published in C. and E. Reid's paper dating back to the year 1915. In the upper row there are five fruits from Tegelen, i. e. typical of the *vespiforme* species (nos. 8 to 12); however, the present author is inclined to reckon the narrowest one (no. 12) to the *spathaceum* species. Further circles illustrate the fruits from Reuver which were identified by C. and E. Reid as quite a different species or the variety of the *vespiforme* species. In the same column 5 Pliocene fruits from Reuver were marked with squares and identified as *D. spathaceum* or its varieties *marginatum* and *elipticum*. In that character there was no continuous variability between the fruits resembling *D. vespiforme* and the fruits reckoned to *D. spathaceum* species, but it would have occurred if all the Pliocene fruits of C. and E. Reid were united in one sample, i. e. the fruits from Reuver were joined with 5 fruits from Tegelen.

No such mixed populations composed of at least two species were encountered in the Polish Pliocene material. Although in fig. 9 the fruits from the Upper Pliocene (Mizerna) and those from the Lower Pliocene (Grywałd) were joined in one sample, they were all short and relatively broad and belonged to the population of one form, which was discussed above. The present author wishes to add that among these fruits there were encountered all the morphological forms described by C. and E. Reid as *D. vespiforme* or its varieties, as is seen on the photographs in Plate III.

The circles and squares marked in the "Length" and "Breadth" columns are based on the single values submitted by C. and E. Reid in their descriptions.

The absence of the fruits of the *spathaceum* type in the Polish Pliocene material may only be explained by the fact that the numerous fruits found there belonged to plants having different ecological requirements than those bearing fruits of the *spathaceum* type. However, there is a chance of finding that type of fruits in the Polish Pliocene but in other floras which, may be, grew in a different environment. This furnishes ground for the supposition that the fruits photographed by the present author in Plate III, which are so different and characteristic, should be acknowledged as belonging to a different species than the narrower and rather elongated fruits of the *D. spathaceum* type.

The acceptance of the Polish Pliocene fruits of the genus *Dulichium*, and thus also of the fruits found by C. and E. Reid at Reuver as belonging to a species other than the recent *D. spathaceum* was more-

over supported by the data reported by Dorofeev in his description of his investigations in the fossil floras in West Siberia. Dorofeev's data are more precise than those quoted by C. and E. Reid because he submitted the length and breadth scale of the fruits described, while C. and E. Reid gave only one dimension for the length and one for the breadth, without even accepting the possibility of deviations in the variability, which is so characteristic of each population. This scale of variability has been introduced in fig. 9. The lack of precise data in Dorofeev's paper makes that we fail to distinguish pronouncedly the Pliocene fruits from the Miocene ones, and it is only from the text that we learn that the fruits reckoned by Dorofeev to the *vespiforme* species were numerous in the Pliocene and less so in the Miocene, but in spite of that it was possible there to distinguish them pronouncedly from another form called *D. marginatum* by the author who regards it as identical with the Pliocene *D. spathaceum* var. *marginatum* C. E. Reid.

The abundant and exclusive occurrence of the *vespiforme* type in West Siberia in the Pliocene, the quantitative reduction of its fruits in the Miocene, and its total disappearance in the Oligocene are regarded by the present author as a support of her supposition that *D. vespiforme* was some side-line of the genus *Dulichium* which lived already in the Miocene but found suitable conditions only in the Pliocene. In the Oligocene of West Siberia the *spathaceum* type occurs as the only form of the genus *Dulichium*. Dorofeev did not find any fruits of the *vespiforme* type in the Oligocene.

The data submitted in column 3, fig. 9 relating to Dorofeev's material are precise because, much like those given by C. and E. Reid, they were determined on the basis of the photographs published by that author in his paper in 1963; these are 5 fruits of the *vespiforme* and 7 of the *spathaceum* types. The variability of that character forms a continuous line in the Miocene, nevertheless these two types on the photographs in Dorofeev's Plate differ pronouncedly by their shape, the elipsoidal fruits of the *spathaceum* type from the reversely ovoid ones of the *vespiforme* type.

As these two types of fruits occurred in the Pliocene, Miocene and Oligocene, the same values were marked twice also in fig. 9, in the Pliocene and Miocene for *D. vespiforme*, and in the Miocene and Oligocene for the type called *D. marginatum* by Dorofeev who wrote that that type was identical with the Pliocene *D. spathaceum* var. *marginatum* C. E. Reid and regarded the characteristic margination of the fruits in his Oligocene material as a dominating character.

The importance of the margination of the fruits of the genus *Dulichium* as a character distinguishing the species was critically discussed by Kirchheimer who drew attention to the fact that the same phe-

nomenon also is encountered in some fruits of the plants living now. The present author is of the same opinion. She, too, met with a more or less distinctly marked marginations in the fruits of all the populations investigated. Of course Dorofeev's opinion cannot be questioned when he writes that this was the most important character of the Oligocene fruits. It can only be pointed out that on the photographs of the fruits submitted in his paper and identified by him as *D. marginatum* Dorof. this margination is not visible. On the other hand, the present author was struck by the great similarity of the photographs Nos. 17—23 in Dorofeev's Plate XIII, the photographs of the Miocene *spathaceum* type submitted in Plate IV of the present paper, and the photograph No. 7 in Plate III in the book by C. and E. Reid, and therefore, basing upon these photographs, she would be inclined to acknowledge the similarity of the fruits of the Miocene population from Poland and the fruits of *D. spathaceum* var. *ellipticum* of C. and E. Reid.

Basing upon these considerations the present author tried to draw the genealogical tree of the genus *Dulichium*. These considerations, represented on the left hand side of fig. 9, in the column "History", are of course provisional. She has collected in them what she was able to notice in the Polish populations investigated by her and learn from the rather fragmentary data reported by other authors.

Two things are striking in that figure. One concerns the fairly large differences in the length of the fruits, lesser differences in their breadth, and very pronounced differences in their shape, marked in the third column. The other striking thing is the gradual decrease of the mean length of the fruits of the *spathaceum* type, starting with the contemporary through the Pleistocene to the Miocene population. In this chain Polish Pliocene material is lacking, and this gap is not filled by the values reported by C. and E. Reid for the few fruits. On the other hand, if we include in this series the scale of variability submitted by Dorofeev for the Oligocene fruits, then the fruits would probably be still shorter on the average; his scale is very small because, apparently, he had few specimens and it should be extended towards both maximum and minimum, if he had at his disposal as numerous Oligocene fruits as the present author had in her material from the Polish Miocene. This points to a pronounced directional evolution from the fruits of the *D. spathaceum* type from the Oligocene to the fruits of the plants living now, which goes towards an elongation of the fruits, as their geological age becomes younger. Short, ovoid fruits of the *vespiforme* type are not comprised in that developmental series, much like the Pliocene seeds of the genus *Menyanthes* (*M. carpatica*) were not comprised in the former papers of the present author (1953, 1964, 1967), but formed a side-line which died out and did not survive to the Pleistocene.

To summarise in brief the results of the studies on the morphological variability of the fruits of the genus *Dulichium* the conclusions may be drawn as follows:

1. The fruits of the recent *Dulichium spathaceum* Pers. form a morphologically uniform material. Nevertheless, there was observed in that species the ability to form biotypes, i. e. fruits with characters peculiar of the given population.

2. In each of the geological periods investigated there occurred the fruits which closely resembled one another with respect to their morphology. It has been proved that the local samples from the particular geological period did not deviate much from the comprehensive sample composed of all the fruits found in that period.

3. The fossil fruits of *Dulichium* of the *spathaceum* type show a pronounced directional variability beginning with the Tertiary, through the Pleistocene, to the fruits of the plants living now. This evolution is manifested in a gradual elongation and a relative narrowing of the fruits.

4. The extinct Pliocene species of *Dulichium vespiforme* C. E. Reid showing short and egg-shaped fruits forms a distinct morphological type not comprised in the evolutionary series of the species of *Dulichium* of the *spathaceum* type. The history of that fossil species still remains unexplained. If the localities of *D. vespiforme* from the periods older than the Pliocene or from the Quaternary were found in Poland, its provenance and history might be elucidated. We may hope, too, that in future Pliocene floras will be found in Poland which will include the fruits of *Dulichium* of the *spathaceum* type and thus the gap in the evolutionary sequence of that species will be filled.

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STRESZCZENIE

ZMIENNOŚĆ WSPÓŁCZESNYCH I KOPALNYCH OWOCÓW RODZAJU *DULICHIMUM*

Dulichium jest dziś rodzajem monotypowym. Należy on do rodziny *Cyperaceae* rzędu *Cyperales*. Jedyny jego żyjący gatunek *D. spathaceum* Pers. rośnie w atlantyckiej części Ameryki Północnej. W czwartorzędzie i trzeciorzędzie gatunek ten rósł również na terenach Europy i Azji, owoce jego bowiem spotykane są we florach kopalnych Holandii, Danii, Niemiec, Polski i ZSRR. Drugi gatunek, *D. vespiforme* C. E. Reid, nie występujący we florze współczesnej, jest związany w Europie głównie z pliocenem.

Celem niniejszej pracy było zbadanie morfologii zarówno owoców *D. spathaceum* dziś żyjącego, jak też owoców występujących w Polsce w stanie kopalnym. Drugim ważnym zadaniem było określenie stosunku wymarłego *D. vespiforme* oraz innych owoców kopalnych rodzaju *Dulichium* do dziś żyjącego gatunku *D. spathaceum*.

Morfologię owoców opracowano biometrycznie, biorąc pod uwagę 7 następujących cech:

1. długość owocu,
2. szerokość owocu,
3. długość stylika,
4. kąt wierzchołka,
5. stosunek długości do szerokości owocu,
6. położenie najszerszej części w % długości owocu,
7. stosunek długości owocu do długości stylika.

Sposób mierzenia owoców przedstawia ryc. 1, a materiał jakim rozporządzano w trakcie badań zestawiono w tabeli 1. Tabela 2 zawiera wyniki pomiarów w postaci liczb charakterystycznych cech owoców prób zbiorczych. Materiał ilustracyjny stanowią tablice fotograficzne I—IV. Analizę biometryczną przedstawiono w sposób graficzny, posługując się metodą opisaną przez prof. J. J e n t y s - S z a f e r o w ą.

Wstępne obserwacje morfologii owoców dotyczyły określenia ich zmienności u dziś żyjącego gatunku *D. spathaceum* w obrębie jednego osobnika. Dokładna analiza biometryczna wykazała nieduże różnice w cechach morfologicznych owoców oraz małą ich zmienność niezależnie od tego z jakiej części pędu rośliny pochodziły. Przedstawione to zostało na wykresach I i II ryc. 2. Również owoce prób lokalnych były do siebie bardzo podobne i wykazywały małą zmienność w swych cechach. Nie mniej zaobserwowano, że gatunek ten ma zdolność tworzenia biotopów lokalnych, jak np. próba lokalna z Venice w Kanadzie, co obrazują ryciny 3 i 4. W wyniku opracowania materiału kopalnego ustosunkowano populacje lokalne do prób zbiorczych w obrębie każdego z trzech badanych okresów geologicznych. Stosunek ten przedstawiony został na ryc. 5, która dowodzi, że w obrębie poszczególnych okresów występowały owoce morfologicznie bardzo zbliżone do siebie. Istniało jednak wtedy więcej form lub gatunków rodzaju *Dulichium* niż spotyka się w dzisiejszej flrze. Odpowiedź na to zagadnienie daje porównanie 3 prób zbiorczych reprezentujących średnie arytmetyczne cech owoców z 3 okresów geologicznych do jednostki porównawczej, która obejmuje populację owoców dziś żyjącego *D. spathaceum*. Dokładna analiza ryc. 6 pozwala na stwierdzenie, że owoce plejstoceny były przeciętnie krótsze, stosunkowo szersze i nie tak ostro zakończone jak dzisiejsze; jeszcze krótsze, szersze i tępo zakończone na wierzchołku były owoce próby zbiorczej z polskiego miocenu. Populacja z pliocenu wykazuje te same odchylenia od jednostki porównawczej, co dwie poprzednie próby, ale w nierównie silniejszym stopniu. Analiza cech owoców z pliocenu przedstawiona jest na ryc. 7, na podstawie której można twierdzić, że owce plioceny tworzą odrębny typ morfologiczny, którego cechy są charakterystyczne dla kopalnego gatunku *D. vespiforme* C. E. Reid. Odrębność gatunkową *D. vespiforme* podkreśla jeszcze ryc. 8, na której wyrysowano całą skalę zmienności badanych prób w dwu najważniejszych cechach: długości owoców oraz stosunku długości do szerokości owoców. Stwierdzenie, że w materiale kopalnym można wyróżnić co najmniej dwa gatunki rodzaju *Dulichium*, skłoniło autorkę do konfrontacji własnych obserwacji z wynikami badań innych autorów. Wyrazem tego jest ryc. 9, na której przedstawiono zmienność trzech najważniejszych cech owoców całych populacji, a także i pojedynczych okazów. I w tym przypadku potwierdza się wyraźna zmienność kierunkowa owoców kopalnych *Dulichium* typu *spathaceum*. Ewolucja ta wyraża się w stopniowym wydłużaniu się i stosunkowym zwię-

żaniu się od owoców trzeciorzędowych poprzez czwartorzędowe do owoców dziś żyjących roślin. Wymarły gatunek plioceński *D. vespiforme*, posiadający krótkie o jajowatym kształcie owoce, przedstawia odrębny typ morfologiczny i nie mieści się w szeregu ewolucyjnym gatunku *Dulichium spathaceum*. Znalezienie na terenie Polski stanowisk *D. vespiforme* w okresach starszych od pliocenu względnie w czwartorzędzie rzuciłoby światło na jego pochodzenie i historię. Spodziewać się także należy, że znajdą się w przyszłości w Polsce flory plioceńskie, zawierające owoce *Dulichium* typu *spathaceum* i w ten sposób zapełni się luka w szeregu ewolucyjnym tego gatunku.

Instytut Botaniki Polskiej Akademii Nauk w Krakowie
Zakład Zmienności Roślin

Plate I

Fruits of the recent *Dulichium spathaceum* Pers., \times ca. 12

Tablica I

Owoce współczesnego *Dulichium spathaceum* Pers., \times ok. 12

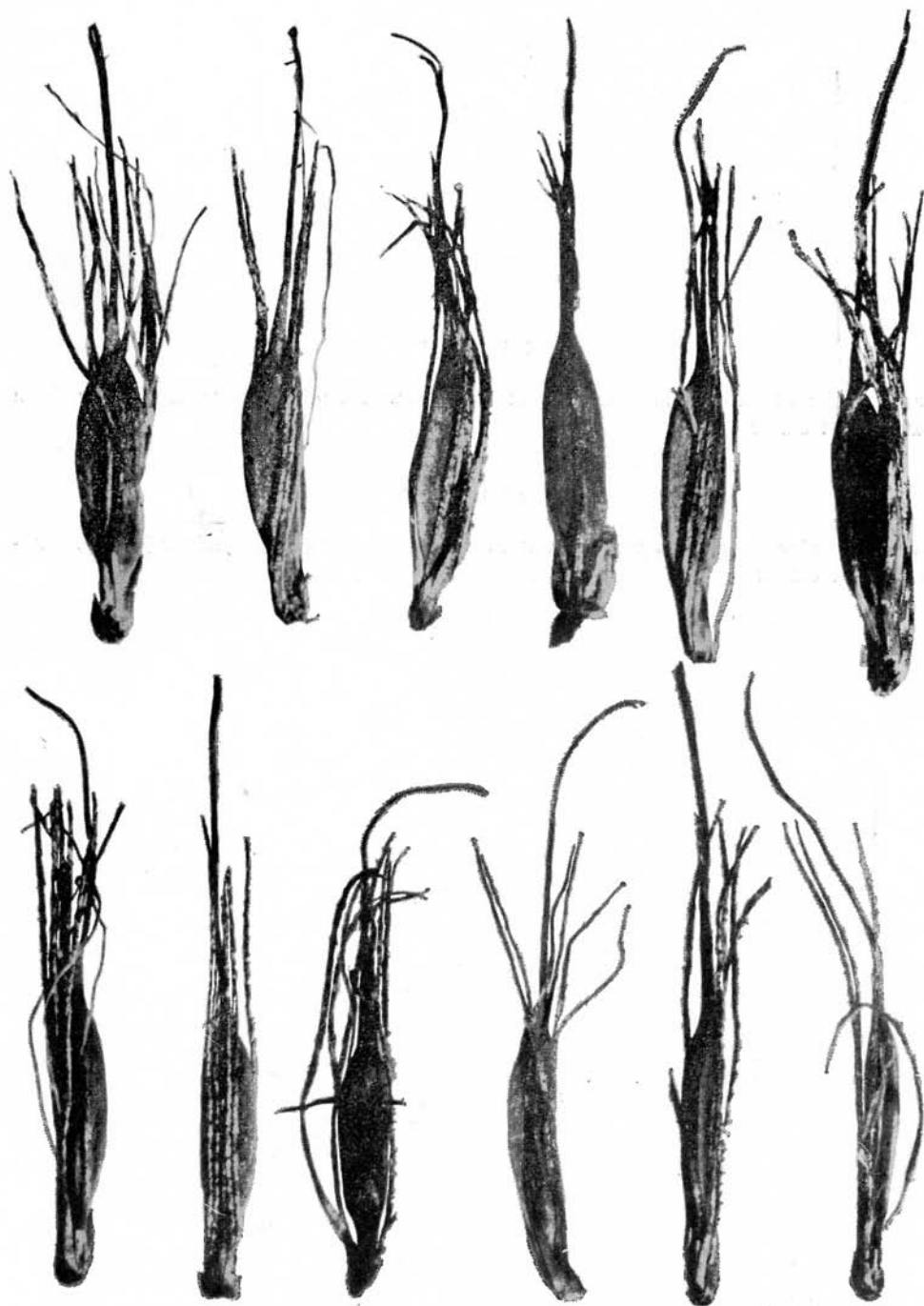


Plate II

Fossil fruits of *Dulichium spathaceum* Pers. found in the interglacial flora from Józefów, \times ca. 12

Tablica II

Owoce kopalne *Dulichium spathaceum* Pers. znalezione w interglacjalnej florze z Józefowa, \times ok. 12

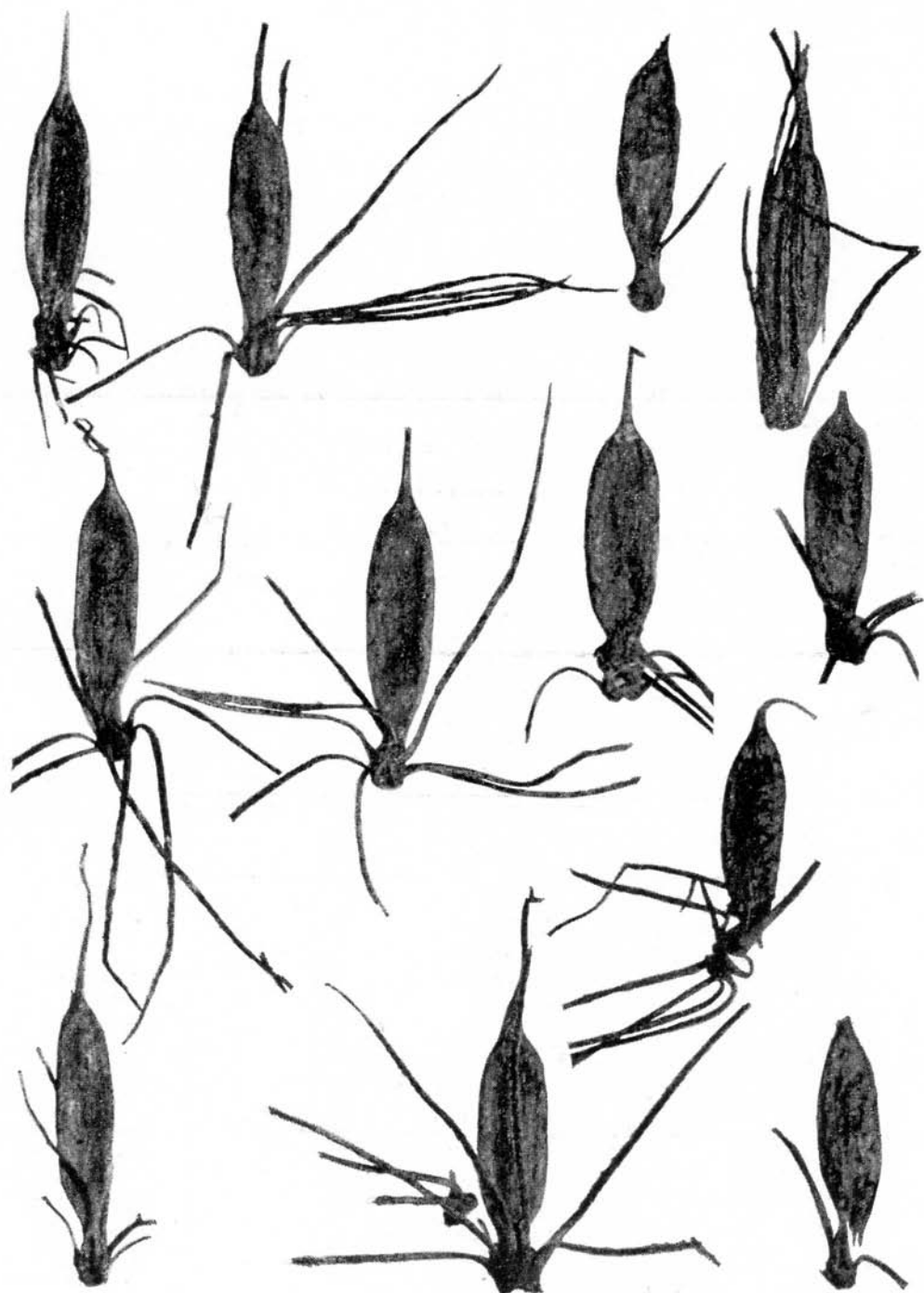


Plate III

Fruits of *Dulichium vespiforme* C. E. Reid from the Pliocene floras from Mizerna and Grywałd, \times ca. 12

Tablica III

Owoce *Dulichium vespiforme* C. E. Reid z plioceńskich flor z Mizerny i Grywałdu, \times ok. 12

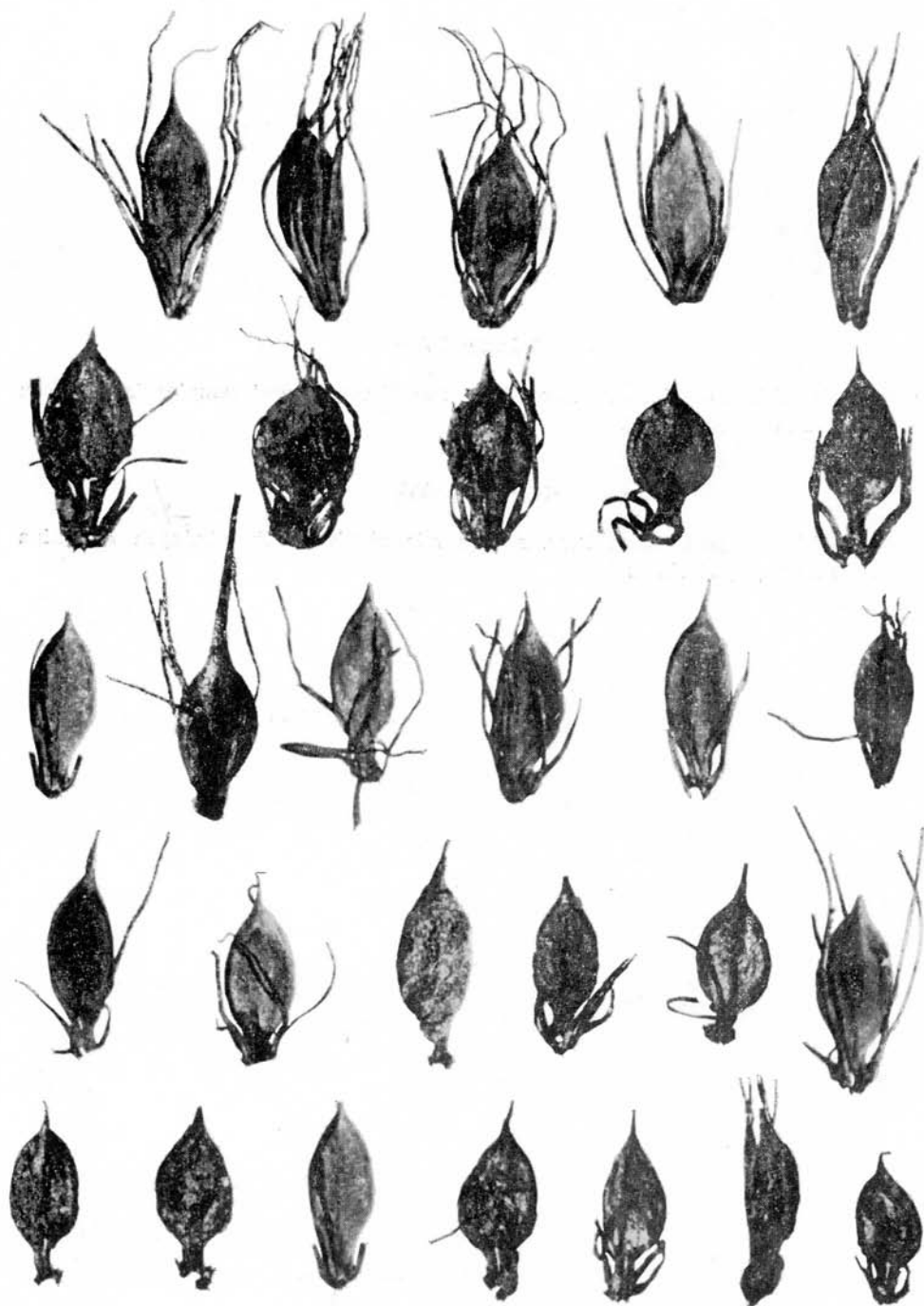


Plate IV

Fruits of *Dulichium spathaceum* Pers. from two Miocene local samples from Konin and Czarny Dunajec, \times ca. 12

Tablica IV

Owoce *Dulichium spathaceum* Pers. z dwu miocenijskich prób lokalnych z Konina i Czarnego Dunajca, \times ok. 12

