STUDIES ON THE VEGETATIONAL HISTORY OF PICEA OMORIKA PANC. ON THE GREAT HUNGARIAN PLAIN

by

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As it is well known, in this country only one spruce *(Picea)* species: the *Picea abies* exists. Its area is very limited (Western Hungary: Sopron, Kőszeg, the Vend region, Őrség) and even its indigeneity is debatable.

Palynological investigations have proved that previously, thus in the Weichselian (Würm) Glacial there had lived in Hungary two *Picea* species: *Picea abies* and *Picea omorika*. The fossil pollen grains of *Picea omorika* have been separated from those of *Picea abies* by a mathematical-statistical analysis of size frequencies.

In the course of palynological investigations of the Weichselian strata originating from the Great Hungarian Plain, in the layers supposed to be attached to the Brörup Interstadial the pollen grains of *Picea abies* and those of *Picea omorika* have been found (Fig. 1 – 3.). Observations connected with the composition of the flora found (J á r a i-K o m l ó d i 1966) indicate that during that Interstadial there prevailed wet, cool climate on the Plains (J á r a i-K o m l ó d i 1969). This climate suits well the ecological requirements of *Picea omorika*, too, and thus its occurence on the Plains might be accepted; moreover though it has not yet been proved, it could have lived also in the forests of the range of the Hungarian Central Mountains. It could have also occured in the Interglacials in this country, even in the Plains, too, and it seems likely to have survived from the Tertiary period on, though the pollen grains of *Picea omorika* have been demonstrated so far only from the Upper Pannon layers (Pliocene) in the Matra Mountain (N a g y 1958), and from Middle Miocene layers in Nógrád Mountain (S i m o n c s i c s 1969).

From the last (Eemian) Interglacial it has still been preserved to the warmest and longest-lasting Interstadial, the Brörup Interstadial where it has been found, while in the subarctic, dry, cold climate of the Pleniglacials it finally died out.

In our days *Picea omorika* (Serbian spruce) can be found only on very small relic sites in Europe. Previously, however, as known on the basis of fossil finds, it was much more frequent. Thus, in the Tertiary period it was generally widespread throughout Europe. Since *Picea abies* appeared only at the
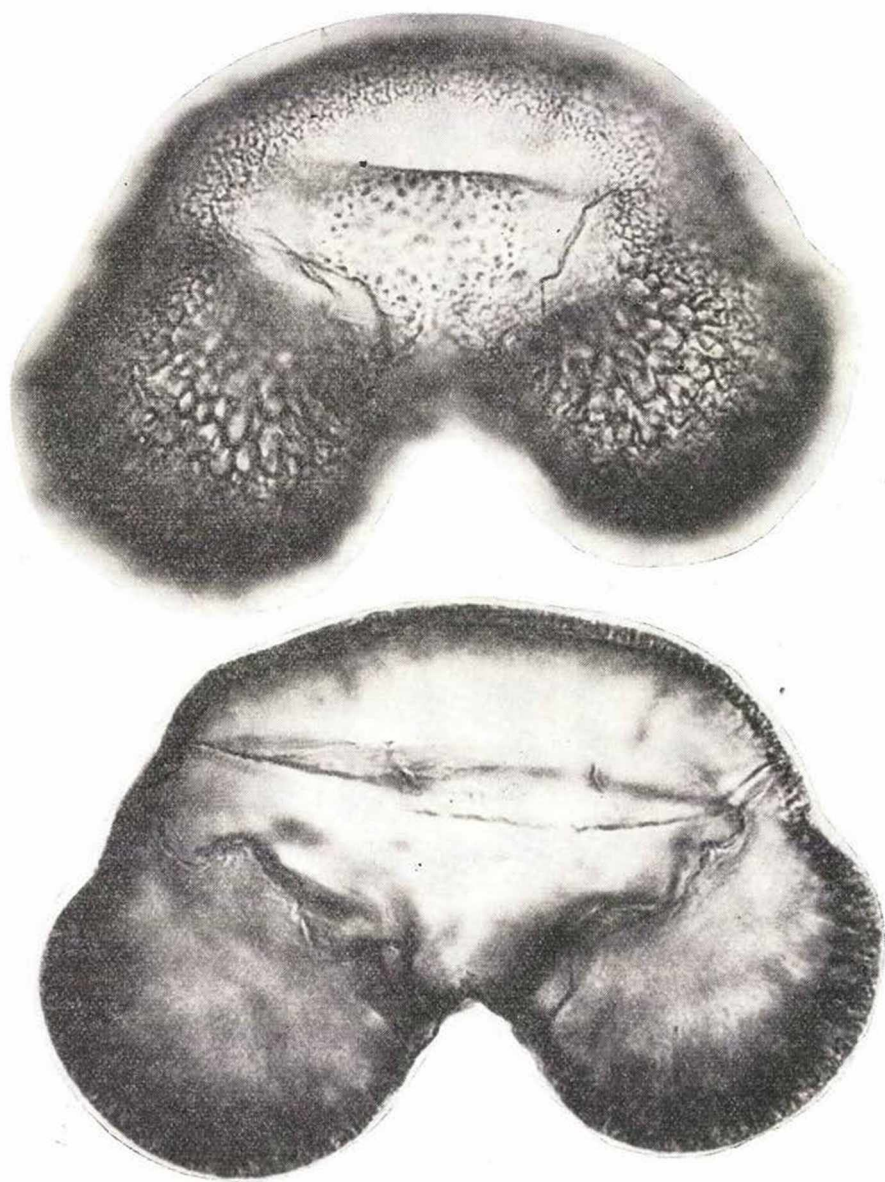
Fig. 1. Fossil grains of *Picea omorika* P a n c. Enlargement x1000
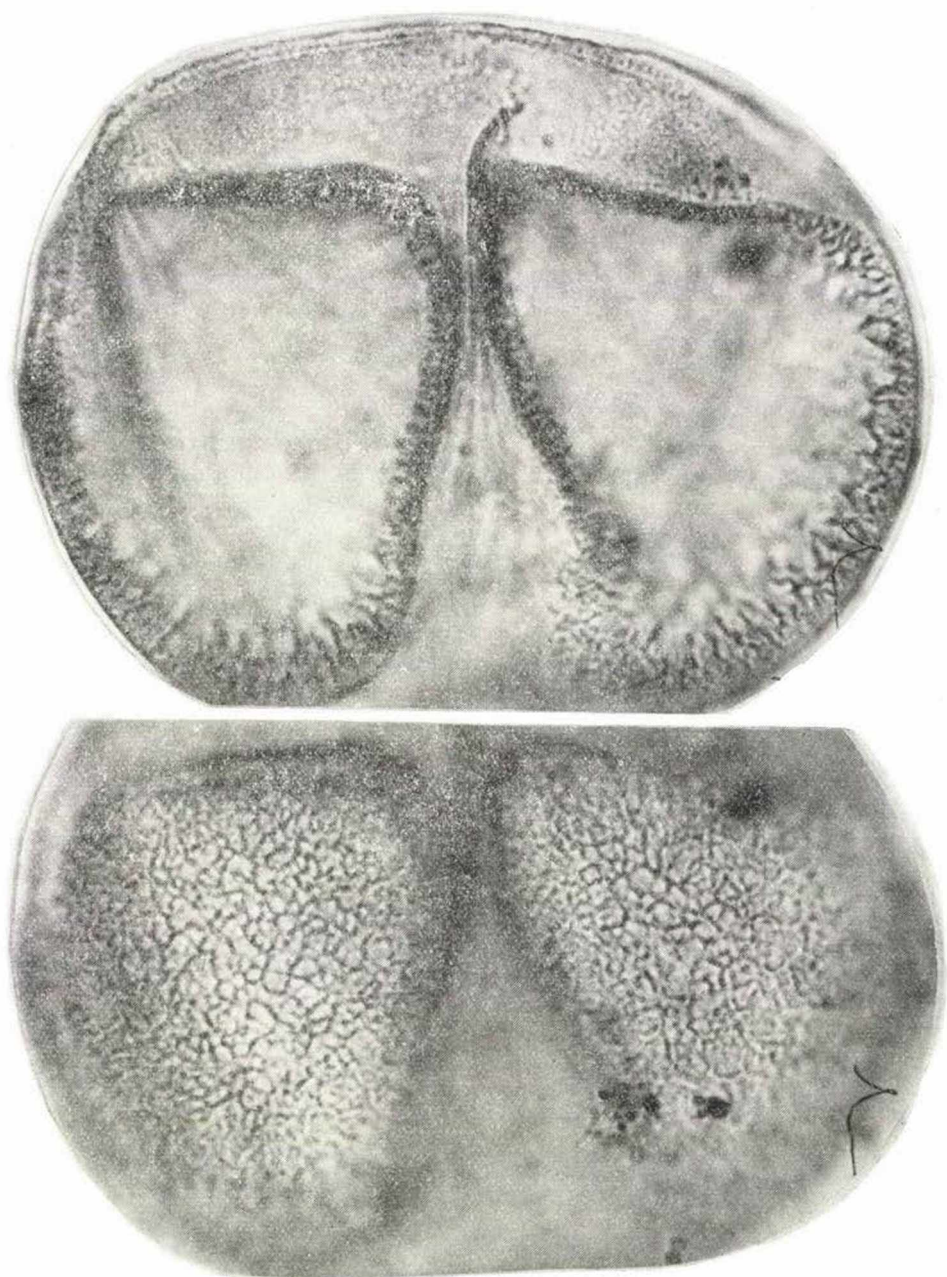
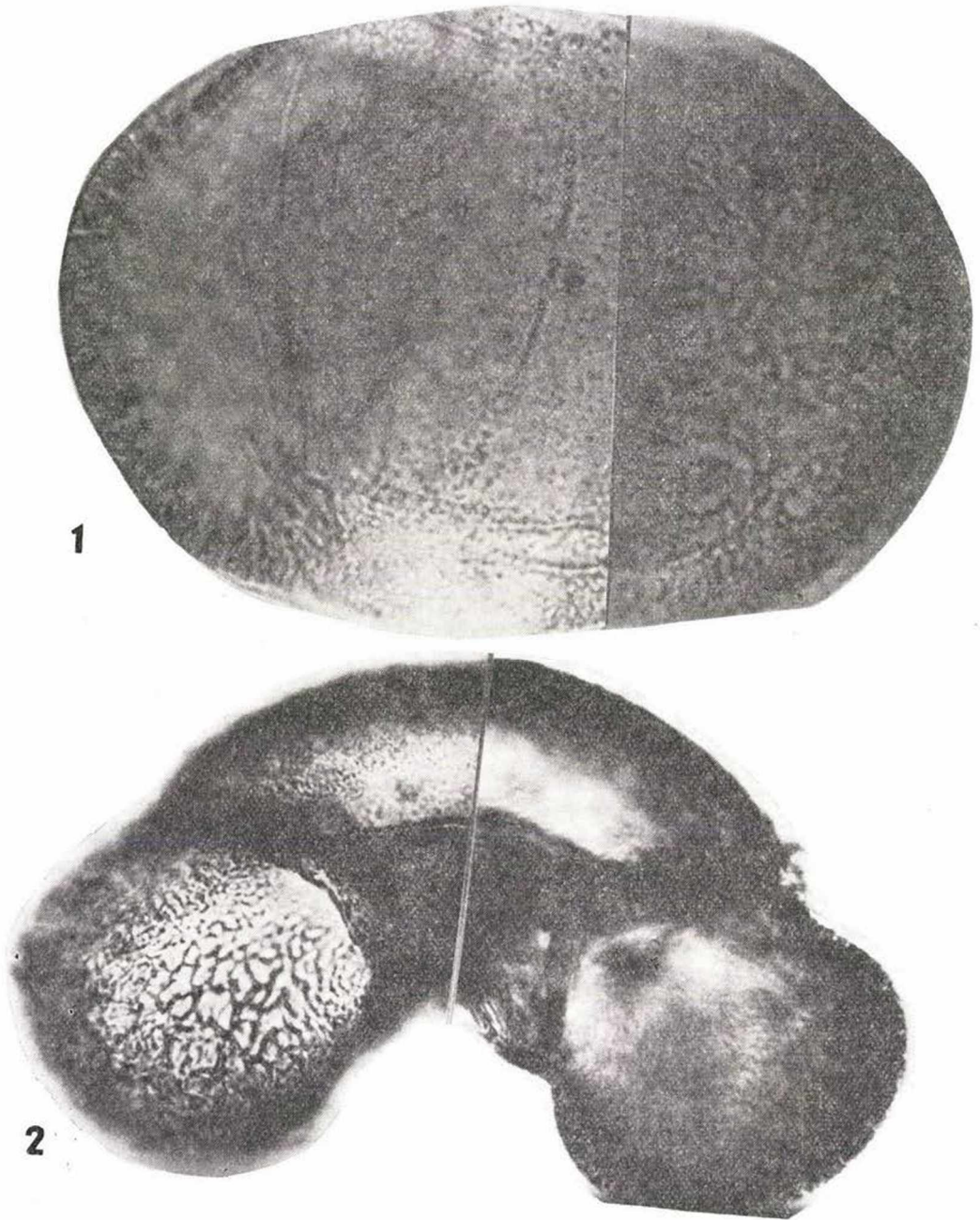Fig. 2. Fossil grains of *Picea abies* K a r s t. Enlargement x1000

Fig. 3. 1. Fossil grain of *Picea abies* K a r s t. 2. Fossil grain of *Picea omorika* P a n c.
Enlargement x1000

end of the Tertiary period, it might be supposed that previously it had been substituted by *Picea omorika* (A n d r e á n s z k y 1954). On the basis of its fossil remains, however, it can be well traced back and we can conclude that *Picea omorika* was in the Pleistocene, e.g. even in the Last Glacial, much more widespread in Europe.

The first fossil finds of Serbian spruce have been found by W e b e r in 1898, in Germany (Erzgebirge, Lüneburg). He has pointed out the similarity of the macroscopic remains to the species *Picea omorika*. He supposed these macrofossils to be an already extinct species and he referred the fossil finds to *Picea omoricoides*. At the same time W e b e r mentioned also that the *Picea* pollens found in the Lüneburg layers were strikingly small but he did not yet identify them (W e b e r 1898, M ü l l e r and W e b e r 1904). In 1927 F i r b a s identified two kinds of *Picea* pollens from the Eemian (Riss— Würm) Interglacial layers of the Inn Valley, ranging the small type pollen grains to the *Picea omoricoides* (F i r b a s 1927). Later, he found it in the Lüneburg turf where W e b e r's *Picea omoricoides* macrofossils originated from (F i r b a s and F i r b a s 1936). In C e r n j a v s k i's paper which deals with the recent pollen grains of trees in the Yugoslavian forests the separation and the identification of two kinds of *Picea* pollens were carried out on the basis of size frequency analysis (C e r n j a v s k i 1935). Later on B e r t s c h, too, published the drawing and the description of the pollen grains of *Picea omorika*. There were also other efforts to separate the two species (B e r t s c h 1942, E r d t m a n 1943, N a g y 1958) but size frequency analysis has proved to be the most reliable method.

After having identified both the macroscopic and microscopic remains of *Picea omoricoides* it was found in numerous Quaternary layers of Europe. Thus, it is known from Denmark, the Netherlands, Poland, Germany, Switzerland, Yugoslavia and Italy (A n d e r s e n 1961; Z a g w i j n 1961; D y a-k o w s k a 1952; B r e m 1953; S o b o l e w s k a 1956; S r o d o n 1957; S o b o l e w s k a, S t a r k e l and S r o d o n 1964; S t a r k and O v e r-b e c k 1932; R e i c h 1953; A v e r d i e c k 1962; L ü d i 1953; S e r c e l j 1965; L o n a 1959; P a g a n e l l i and S o l a z z i 1962).

Of the findings mentioned it has been known since 1961 from Brörup Interstadial (Z a g w i j n 1961; A n d e r s e n 1961; A v e r d i e c k 1962; S o b o l e w s k a, S t a r k e l and S r o d o n 1964). To these can be added our *Picea omoricoides* findings on the Great Hungarian Plain (Kiskunfélegyháza, Timár).

Accordingly, *Picea omorika* existed in several places of Europe even 50 000 — 60 000 years ago, and yet nowadays only a very limited occurence is known in Yugoslavia, in the region of the river Drina, and in a few smaller relic stands.

Its presence, the form of its occurence, the phytosociological relations, and the ecological investigations connected with them allow to draw certain conclusions regarding the ecological requirements and history of this species.

As to the most important environmental factors for *Picea omorika*, humidity and diffuse light might be stressed. Presently it occurs is everywhere on the northern slopes of the mountains where, except a few days in the middle of summer, there prevails diffuse (lateral) light (F u k a r e k 1957). Other

authors also stress its requirement for diffuse light (T r é g u b o v 1934; K a r o l y i 1921). It seems to be indifferent to the chemical and physical properties of the soil while the moisture of the soil is an important factor. The microclimate at its present places of occurence is marked by a higher relative air-humidity, and by a more oceanic character connected with the higher soil moisture as a local factor.

Undoubtedly, as it has been established by several earlier authors, and also recently, *Picea omorika* is a Tertiary relic (W e t t s t e i n 1890; K o s a n i n 1924; F u k a r e k 1957; C o l i c and G i g o w 1958). Moreover it has been stated on the basis of ecological, phytosociological, and palynological investigations that not only *Picea omorika* but the once existing Tertiary (Pliocene) forest should have been survived at one place of its occurences in the Mount Tara being on the right side of the river Drina. These stands of forest can be considered − regarding their occurence, flora composition, and origin − the remains of the so-called Turgaic flora (Č o l i ć and G i g o v 1958).

The real ecological requirement of *Picea omorika* might have been a warm, humid, subtropic climate but diffuse light supply must have been also needed. Its spreading in the Tertiary period and its very interesting "pyramidal" shape indicate its climate claim mentioned above; according to some authors this morphological feature is manifested as its adaptation to the light conditions of the subtropical climate (K a r o l y i 1921; T r é g u b o v 1934).

The climate getting worse at the end of the Tertiary period, reaching the maximum deterioration during the glacial epochs of the Pleistocene, caused *Picea omorika* partly to die out partly to be forced to live on refugium territories. In the course of interglacials and interstadials with warm, humid or even cool and humid climate the Serbian spruce spread again and again, but, always to a less degree. On the contrary, its North American and East Asian equivalents, *Picea sitchensis* and *Picea ajanensis* (W e t t s t e i n 1890) occur even today on larger areas. This might be explained by the fact that their escaping from unsuitable circumstances and their spreading again were not hindered by geographical factors.

An essential factor in its being diminished might be the appearance of *Picea abies* at the end of the Tertiary period. The climatic requirements of this young, vigorous species took advantage over *Picea omorika* in Pleistocene.

It is well known that *Picea abies* is a frostresistant species; it bears well the cold continental winters, moreover, it is necessary that the average winter temperature should be below $+1C°$. It requires a pause of vegetation period of at least 4 months but it needs humidity. The ecological requirements of the two species might be briefly characterized as follow: *Picea abies* requires the cold, wet climate and endures well also the continental winters, while *Picea omorika* requires a warmer, humid climate, though its conspicuous property is cold resistance.

In the course of the Pleistocene the *Picea abies* was one of the characteristic trees of Europe's greatest part. It spread mostly during the rather cool, rainy periods of the Interglacials and Interstadials. In the dry, subarctic glacial and stadial climate it got reduced to refugium areas. At that time the Syberian spruce, *Picea obovata*, having occupied even the former sites of *Picea abies*, spread much more to the West than its present area (S r o d o n 1957; S r o-

d o n 1967). On the basis of palynological results it can be supposed that *Picea abies* had 3 main refugium centres during the Weichselian Glacial: one in the East-Southeastern Alps, the other in the East-Southeastern Carpathians, while the third in East-Europe around the Volga and the Ural (P o p 1929; Pop 1942 F i r b a s 1949; B e r t s c h 1953). F i r b a s assumed — mainly on the basis of the investigations of M o t t l (M o t t l 1938) — that there existed a *Picea abies* refugium also in the Hungarian Central Mountains (F i r - b a s 1949). This, however, has not been proved palynologically and is somewhat contradicted by the Nagymohos pollen-investigation, too (Z ó l y o m i 1931). S z a f e r supposed the existance of another refugium south-west from the Tatra Mountain (S z a f e r 1935).

On the basis of palynological investigations the spreading of *Picea abies* in the Post-glacial can be well traced from these 3 refugia. The main direction of the migration was from east to west. Thus, it had spread from the Carpathians through the Tatra till the Erzgebirge, from the South-Eastern Alps to the Schwarzwald, and from the region of the Volga — Ural to the Nyemen in the direction of the Lower — Vistula (B e r t s c h 1953). The climate of the Brörup Interstadial suited the spreading of *Picea* on the Hungarian Great Plain, too. In the extremely subarctic climate of the Weichselian Glacial maximum (Pleniglacial B) it disappeared, and there has not been to date such climate on the Plains that it could have migrated again. In the interstadials of Late Glacial, especially in the Alleröd Interstadial, the climate would not possibly exclude the occurenc of *Picea* on the Great Hungarian Plain. The shortness of the suitable intervals and the climate of Dryas stadials, however, might have prevented its migration from the refugium territories to this country, especially to the Plains.

Thus, while *Picea abies* had refugium in the Alps and in the Carpathians, these mountains could not have given refuge to *Picea omorika* during the glacials due to the low snow-line and to the continental cold climate.

Only the more southern mountains of the Balcan Peninsula could grant refuge of *Picea omorika* as it happened in the case of so many plant species. But even here it could only survive where there prevailed shadow and long-lasting humidity. Even in our days one of the conditions of its occurence is the winter soil-moisture.

The phenomenon why after the passing away of the ice-ages *Picea omorika* has not spread again may be explained by a sudden increase of the temperature and because there was not enough humidity; it can be interpreted also with the quick spreading of recent pioneer and thermophilous trees for which the climate of Post-glacial is very favourable. Thus, these trees could hinder the immigration of spruce by their competence.

In any case, it has to be taken into account that from the present requirements of a relic plant being restricted to a very small relictum area, it is rather difficult to conclude the ecological conditions which had been required by this species during its widely distribution. The environmental conditions in the Tertiary period with a warm, humid, balanced climate were surely optimal for *Picea omorika*. From the fact, however, that remains of Serbian spruce were found in the layers which originated from the intervals with cool and humid climate it can be assumed that *Picea omorika* got more or less adapted

to the decrease of temperature in the course of the Pleistocene and thus the cool and humid climate became also suitable for it. On the other hand, and in the same way, its occurence on present soils is certainly not indication of its original soil requirements. The Serbian spruce can be found both in chalky and in silicate soil. Thus it seems very likely that a more important factor for it is to live in areas where the competition with other trees is less. Of course, the assumption cannot be excluded that *Picea omorika* has originally a very wide ecological amplitude regarding soil rquirements with the exception of its claim for soil humidity.

It is to be expected that further fossil remains of *Picea omorika* will be found in several different places of Europe. By the help of sufficient finds the history of *Picea omorika* is likely to be detected in more detail.

The pollen grains of *Picea omorika* which originated from the Weichselian layers of the Hungarian Great Plain were identified and separated from *Picea abies* by the application of mathematical statistical analysis.

The description of the method applied and the results are as follows:

As a preliminary remark, it should be noticed that the present way of analysis reflects a novel attempt of complex evaluation. Statistical features of our material are systematically exploited; thus going far beyond analyses of graphs by eye. As to a detailed description of the principles involved we refer to the work of K e n d a l l and S t u a r t (1962); for function tables and brief explanations see e.g. "Biometriai Értelmező Szótár" (1966).

Table I.

Mean sizes of airsack length of spruce pollen grains (in μ).

		Picea omorika		Picea abies
Recent	1.	53,1	14.	67,2
	2.	53,1	15.	65,3
	3.	50,8		
	4.	42,8		
Fossil	5.	50,0	16.	68,6
	6.	54,5	17.	66,7
	7.	52,0	18.	67,2
	8.	47,0	19.	67,2
	9.	52,0	20.	69,7
	10.	50,0	21.	68,0
	11.	53,0	22.	66,0
	12.	53,0	23.	77,0
	13.	46,0	24.	71,0
			25.	68,5
			26.	69,9
			27.	70,0
			28.	68,0
			29.	64,1
			30.	61,0

1 – 5, 14, 16 – 21: Firbas 1927; 6: Firbas and Firbas 1935; 7: Stark and Overbeck 1932; 8, 15, 22: Reich 1953; 9 – 10, 23 – 24: Lüdi 1953; 11 – 13, 25 – 30: Andersen 1961.
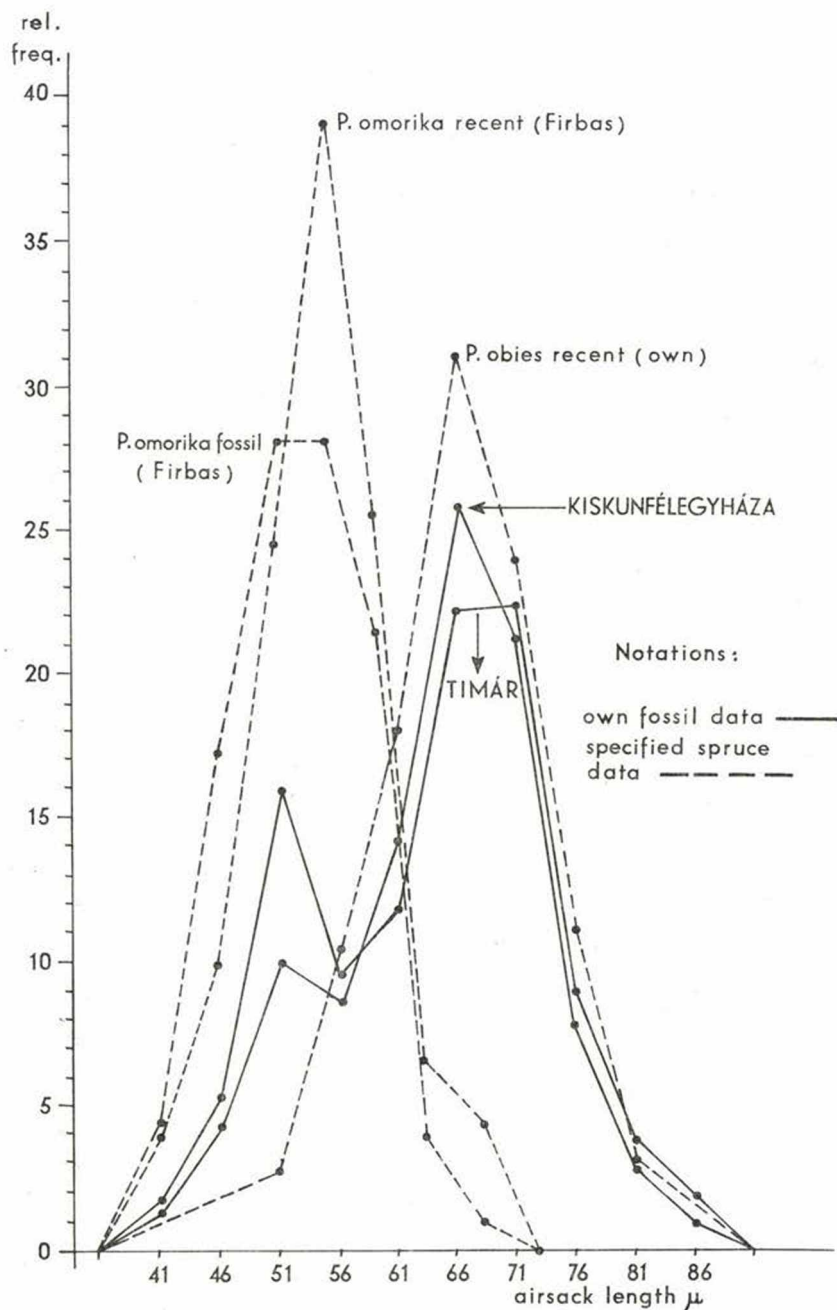
Fig. 4. Frequency distributions of own fossil findings illustrated by pure *P. omorika* and *P. abies* airsack length distributions. Relative frequencies are expressed in percentages of the whole related to midclass values ±2.5

The mathematical investigations into how far our fossil airsack length data fit a mixture of separate observations on the two spruce species were performed as follows. First the two series of pollen grains found in Kiskun-félegyháza and Timár were analyzed independently. As theoretical mean airsack lengths of *Picea omorika* and *Picea abies* the arithmetic mean of fossil and recent literary averages was taken based on 13 *P. omorika* and 17 *P. abies* series of measurements, respectively (Table 1.). For justification confront the spread of the latter and Figure 4.

These values turned out to be $m_1 = 50.8\mu$ for *Picea omorika* and $m_2 = 67.3\mu$ for *Picea abies*, respectively. There seems to be no indication that fossil findings should be distinguished as far as mean airsack length is concerned. Thus the first relative frequency estimates of *P. omorika* and *P. abies* for a presumable compound distribution of these two are given by equations of the type

$$\bar{x} = pm_1 + (1-p)m_2 \tag{1}$$

$$\text{by which } p = \frac{m_2 - \bar{x}}{m_2 - m_1}$$

Here $\bar{x}$ stands for the arithmetical mean of the mixed population under examination, p denotes the relative frequency estimate for the occurence of *P. omorika* and hereby $1-p$ that of *P. abies*. Hence the above could be used as initial estimates for the following procedure. The variance of a compound distribution of two components being

$$\sigma^2 = p\delta_1^2 + (1-p)\delta_2^2 + p(1-p)(\mu_2 - \mu_1)^2$$

theoretically, the respective empirical equation is

$$s^2 = ps_1^2 + (1-p)s_2^2 + p(1-p)(m_2 - m_1)^2 \tag{2}$$

$$\text{whence } s_1^2 = \frac{s^2 - (1-p)s_2^2 - p(1-p)(m_2 - m_1)^2}{p}$$

For s_2^2 the value yielded by the author's observations on recent *P. abies* could be taken applying Sheppard's correction formula for grouped data

$$s^2(\text{corr.}) = s^2(\text{comp.}) - \frac{h^2}{12}$$

i.e., subtracting $\frac{5^2}{12}$ for the class width $h = 5\mu$. Hence the only remaining unknown s_1^2 (an indirect estimate for the *P. omorika* variance) was expressed. Now, the probability distribution of the airsack length of spruce pollen grain is known to follow roughly the Gaussian normal law. Substituting the "standardised" values $\frac{x - m_1}{s_1}$ for *P. omorika* into the standard normal distribution

function $\Phi(t)$ and taking similarly $\Phi\left(\dfrac{x-m_2}{s_2}\right)$ for $P.$ *abies*, theoretical frequencies

$$\hat{f} = \varDelta\left[p\Phi\left(\frac{x-m_1}{s_1}\right) + (1-p)\Phi\left(\frac{x-m_2}{s_2}\right)\right] \tag{3}$$

can be calculated. The symbol $\varDelta$ indicates that differences of the computed values of the expression in brackets are taken between neighbouring class limits (in our case 43,5 to 88,5 in steps of 5) and it is understood that an initial $\Phi = 0$ and a final $\Phi = 1$ is taken for completion of forming $\varDelta$. Fitting the measurements obtained to such theoretical frequencies there exists a p—value yielding the *best* fit. By that the p—value is meant for which the sum of squared deviations between frequencies f actually found and $\hat{f}$: those calculated according equation (3) is minimum

$$\Sigma(f-\hat{f})^2 = \min \tag{4}$$

The left-hand side of (4) is a quadratic function of p and so the minimum looked for is given by the site of the horizontal tangent to a parabola describing it. The value of p pertaining to the zero-slope tangent is determined by differentiating expression (4) for p on which it depends in the way given by (3). One gets as condition for the extreme value

$$\Sigma\left\{(f-\hat{f})\varDelta\left[\Phi\left(\frac{x-m_1}{s_1}\right) - \Phi\left(\frac{x-m_2}{s_2}\right)\right]\right\} = 0 \tag{5}$$

Denote $\qquad \Phi_1 = \Phi\left(\dfrac{x-m_1}{s_1}\right)$ and $\Phi_2 = \Phi\left(\dfrac{x-m_2}{s_2}\right)$;

then $\qquad p = \dfrac{\Sigma f + (\varDelta\Phi_1 - \varDelta\Phi_2) - \Sigma(\varDelta\Phi_1 - \varDelta\Phi_2)\varDelta\Phi_2}{\Sigma(\varDelta\Phi_1 - \varDelta\Phi_2)^2}$

Hence the best fitting p can be reckoned from a simple linear equation.

Both the p-values corresponding to (1) and (5) and the rough estimates used to control them and obtained by confronting the two "truncated bells" of the frequency distributions with the locally minimal saddle classes omitted, yielded about $10-16$ per cent for Kiskunfélegyháza and $25-29$ per cent in the case of Timár. Thus 13 and 27 per cent were considered reasonable estimates for these collections, respectively. This made it possible, however, to arrive at a least squares solution for a single s_1^2 of $P.$ *omorika* viz. that value of s^2 which gave the least sum over the two communities of squared deviations between the actual values of s_1^2 and those substituting 0,13 and 0,27 into their expressions in (2). In fact, this solution equals the weighted mean of the s_1^2-values for the two findings as expressed below (2) with the relative $P.$ *omorika* frequencies as weights. The completion of the whole procedure was then a simple rounding off. This is to say that in this stage the original $s_2 = 6,52$ and the above attained $s_1 = 3,46$ furthermore the frequency percentages, could already by a slight modification produce a rather sufficient graphical fit
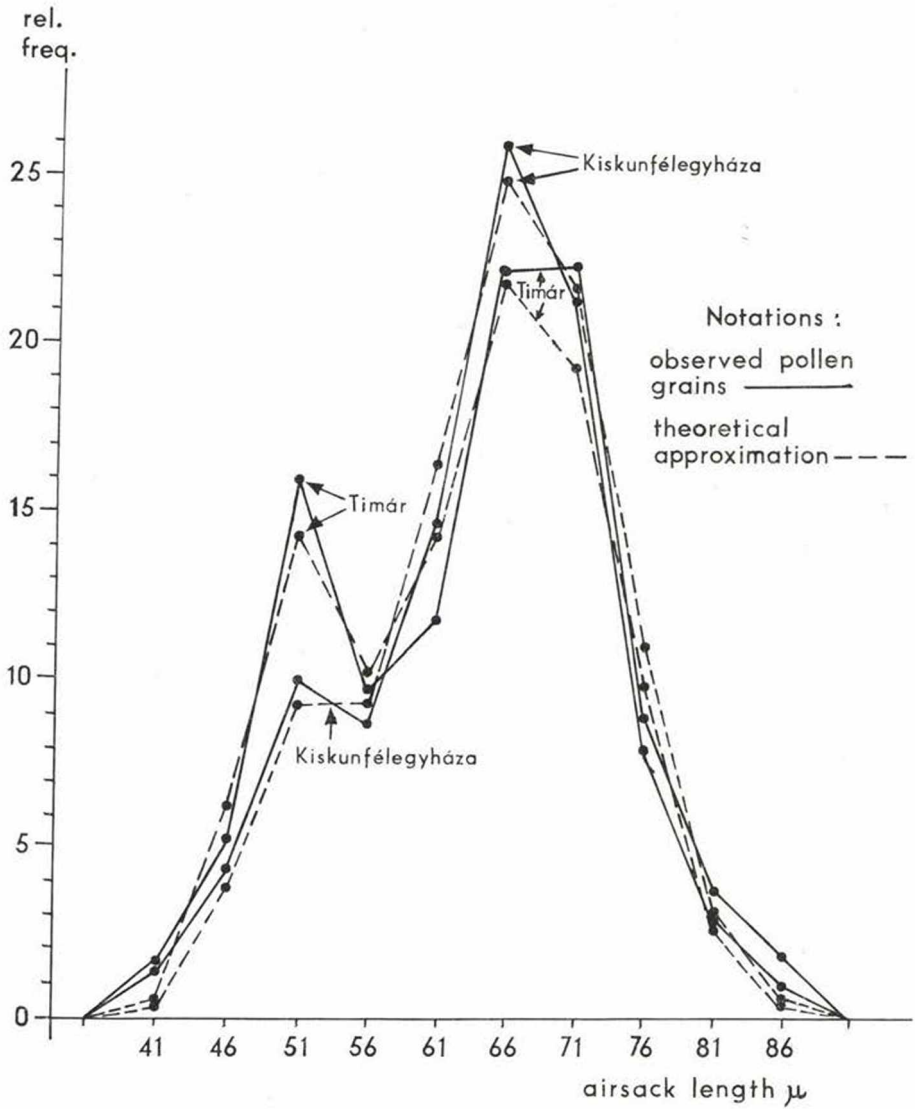
Fig. 5. Frequency distributions of own fossil findings and group frequencies yielded by the theoretical Gaussian mixture approach with the parameters in Table 2. Relative frequencies as in Figure 1

and at the same time unique estimates of the distribution parameters of the two species, too (Table 2). The author believes that the values are accurate enough to satisfy the requirements of describing a material like hers. It was not intended to claim a precision which has not been achieved; with 3,46 and 6,52 σ-values even a narrower fit could be attained. Finally, the corresponding actual and "theoretical" size group frequencies are plotted and confronted in Figure 5. It is natural that the grouping based upon theoretical frequencies done for sake of uniformity does not show as narrow a fit as the mixture of original bell-shaped curves would. For instance it is easy to see that the main peaks correspoding practically to *P. abies* density functions would have the approximate coordinates (67, 26) and (67, 23).

Table II.

Mathematical-statistical results of own fossil spruce pollen grains

Species / Community	P. omorika			P. abies		
	frequency %	mean value μ	standard deviation μ	frequency %	mean value μ	standard deviation μ
Kiskunfélegyháza	15	50,8	3,5	85	67,3	6,5
Timár	25			75		

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