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WHAT IS *CARPOLITHES ROSENKJAERI* HARTZ?

Co to jest *Carpolithes Rosenkjaeri* Hartz?

CONTENTS

INTRODUCTION

More then fifty years ago N. Hartz (1909) described a remarkable fossil fruit under the above-mentioned name, the true nature of which could not till now be established. It was found in Copenhagen or in the nearest vicinity of this city among a mixed flora, composed partly of fossils which originated from the Oligocene (Amber-Pine Beds) lying here as a dislocated intrusion inside pleistocenic material of glacial origin. The same fossil was later collected by other paleobotanists in different localities both in Europe and in Western Asia, sometimes *in situ* in the Tertiary and sometimes, like the classical find in Copenhagen, on secondary beds.

My interest in *Carpolithes Rosenkjaeri* arose from the fact that during palaeobotanical investigations carried out in Gliwice (Silesia) in the deposits of Tortonian age with abundant and well preserved fossils I came across remains of this fossil (Szafer 1960). Some new characteristics which I observed on it, led me to undertake the attempt to go one step further in finding for this problematic fossil its proper or at least probable place from the taxonomical point of view. It was clear that such an investigation could be carried out only if I could have at my disposal the classical fossil specimens, collected in Copenhagen. The Directors of the Museum for Mineralogy and Geology in Copenhagen very kindly granted my request and sent me the whole original material of Hartz, which consisted of 473 specimens. Together with my own collection from Gliwice Stare (212 specimens), and some others which though not so numerous were nevertheless of great value, I was able to proceed with my work. When my investigations were already advanced I received through the kindness of the Paläontologisches Institut der Universität Wien the last most interesting and important material consisting of about 200 specimens of *Carpolithes Rosenkjaeri,* described by Berger (1952) from the Pliocene of Vienna. Altogether I had at my disposal 941 specimens of these fossils, most of them well preserved.

1. THE LOCALITIES WITH FINDS OF *CARPOLITHES ROSENKJAERI*

At present we know 17 localities in Europe and in West Siberia with the fossil remains of *Carpolithes Rosenkjaeri.* Among them there are only about 11 localities whose geological age is quite certain, but we can accept as most probable that the oldest remains of the fossil in question come

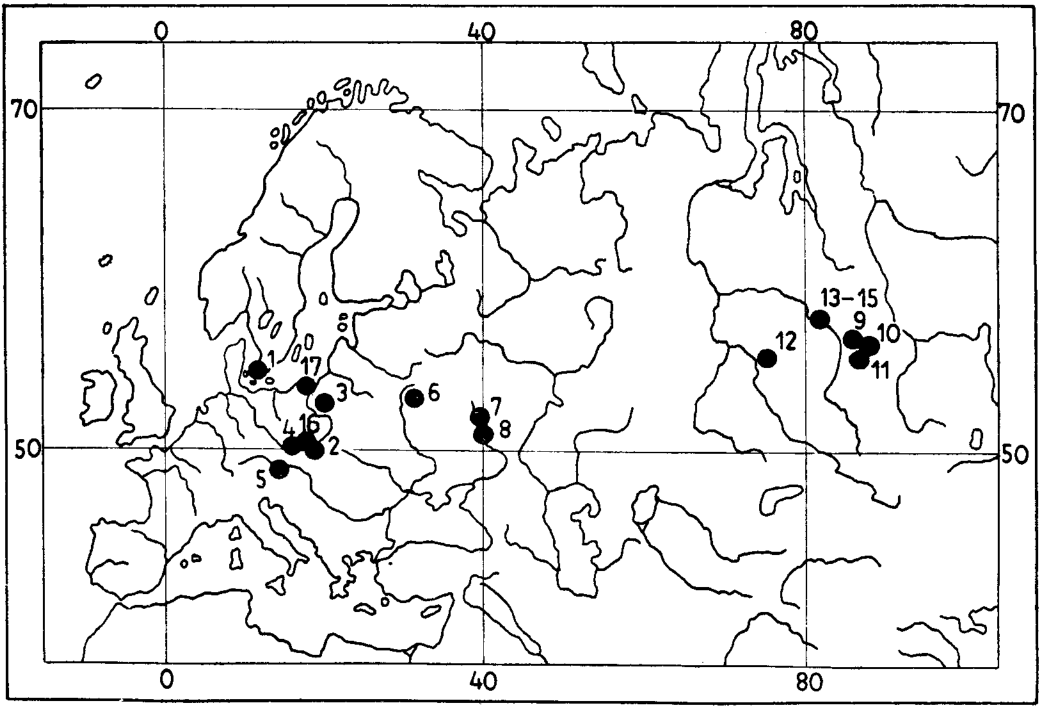

Fig. 1. Localities in Europe and West Siberia with fossil *Carpolithes Rosenkjaeri* Hartz

Miejscowości w Europie i Syberii Zachodniej, gdzie były znalezione owoce *Carpolithes Rosenkjaeri* Hartz

Table 1 — Tabela 1

LIST OF LOCALITIES IN EUROPE AND WEST SIBERIA, WHERE *CARPOLITHES ROSENKJAERI* WAS FOUND

Wykaz miejscowości w Europie i Zachodniej Syberii, gdzie znaleziono *Carpolithes Rosenkjaeri*

(+ Indicates only the presence of the fossils)
(+ Oznacza tylko stwierdzenie obecności)

Country Kraj	Name of locality Miejscowość	Approximate geological age Przybliżony wiek geologiczny	Name of investigator or collector Nazwisko badacza	Number of specimens Ilość okazów
Denmark	1. Copenhagen	Oligocene	N. Hartz 1909 (Rosenkjaer 1906)	473
Poland	2. Wieliczka	Middle Miocene	B. Namysłowski (1910)	5
	3. Rypin	Middle Miocene	M. Łańcucka-Środoniowa (1957)	51
	4. Stare Gliwice	Upper Miocene	W. Szafer (1961)	212
Austria	5. Brunn-Vösendorf near Vienna	Lower Pliocene	W. Berger (1952)	ca 200
Soviet Union (Europe)	6. Osowiec near Homel	Middle Miocene	P. N. Dorofeev (1960)	+
	7. Uryv near Voronezh	Pliocene	P. A. Nikitin and P. A. Dorofeev (1957)	30
	8. Ivnice near Voronezh	Pliocene	N. A. Nikitin and P. N. Dorofeev (1957)	6
Soviet Union (Siberia)	9. On the river Tim	Oligocene	P. N. Dorofeev (1961)	+
	10. On the river Velika Juksa (north of Tomsk)	Middle Miocene	P. N. Dorofeev (1955) (Gorbunow 1952)	+
	11. Tomsk	Miocene	P. A. Nikitin (1935)	+
	12. On the river Irtysh	Miocene?	P. A. Nikitin (1938)	+
	13. On the river Ob, Krivosheino	Miocene	P. A. Nikitin (1940)	+
	14. On the river Ob, II.	Miocene?	P. A. Nikitin (1940)	2
	15. On the river Ob, I (further north)	Miocene?	P. A. Nikitin (1940)	7
Poland (added in 1962)	16. Zabrze	Miocene?	L. Stuchlik (in litt.)	3
	17. Orłowo near Chłapowo	Lower Miocene	M. Łańcucka-Środoniowa (in litt.)	+

from Middle Oligocene, and the youngest from Lower Pliocene. This seems to be true in relation to their whole geographical distribution in the Tertiary (Dorofeev 1959). They are all cited on Table 1 without going into a more detailed description of every locality, which was for the present purpose unnecessary. The map (fig. 1) indicates the positions of points listed in Table 1.

2. SUPPOSED TAXONOMICAL POSITION OF THE FOSSIL

During a period of over 50 years *C. Rosenkjaeri* was only occasionally discussed as to its systematical affinity.

N. Hartz (1909) stated that: „...the systematic position of this carpolite is for the time being quite a mystery; I know nothing corresponding to it at the present day, nor have I found it described or figured in the literature accessible to me".

P. A. Nikitin (1935), and after him other authors from USSR where *C. R.* was found, added some new morphological and ecological remarks to its characteristics, but did not make any serious attempt to determine its systematical position. Nevertheless the remarks made by P. A. Nikitin (cited after his work concerning the fossil floras of the vicinity of Voronezh, edited by P. N. Dorofeev 1957) are interesting and worth-while mentioning here. He expressed the opinion that *C. R.* is similar to endocarps from the subfamily *Cornoideae,* especially from the Genus *Toricellia,* but at the same time he remarks on the absence in the last genus of the very conspicuous sculpture on the inside walls of the fruit chambers, which are essential for *C. R.* — Nikitin expressed the opinion that the old family of *Cornaceae* is probably the cradle of our fossil. He mentioned here *Carpolithes* sp. 4, described by Chandler (1925) from the Eocene of England, which shows a similar affinity with *C. R.* Both represent perhaps the same unknown group, lying near to the family of *Cornaceae.*

Most important for the establishment of the supposed affinity of *C. R.* with other *Carpolithes* fruit forms from Paleogene in Europe, are the remarks which were made by M. E. J. Chandler (1925). She received from Mr. Reid some *C. R.* specimens which were sent to him from Copenhagen by N. Hartz. Chandler stated that *Carpolithes* sp. 4 (l. c. Plate VIII, fig. 2a—b) described by herself from the Upper Eocene of Hordle, Hants, represented there by only a single specimen, is nearly related with *C. R.* because the morphological and other features of the two fossils are so similar that it „seems probably they may belong to the same family".

We will return later to the very valuable remarks concerning the *C. R.* and *Carpolithes* sp. 4. Here I will only cite the characteristics of *C. Rosenkjaeri* which were observed by Chandler. She states that: „1. the number of locules in *C. R.* varied from 1 to 3; 2. the locules communicate with the central vascular canal by apertures (marking the placentas) at about $^1/_3$ from the apex on the inner angle of the locule; 3. the locules of *C. R.* are lined with coarse papillae".

The cited characteristics found on the fruits of *C. Rosenkjaeri* by Chandler are of great importance, but unfortunately they were not known by later investigators of this fossil.

W. Berger (1952) who next described *C. R.* as a common fossil from the Pliocene of Vienna contributed nothing new to its description and expressed the opinion that these fossils are „unbestimmbar".

M. Łańcucka-Środoniowa (1956) expressed her opinion in a somewhat more precise form. She said: „It has not been determined yet even approximately to what systematic group it belongs".

F. Kirchheimer (1957) is inclined to hold *C. R.* as having an affinity with the genus *Cornus*. He writes: „Die Herkunft dieser Fossilien von zwei- oder dreifächerigen *Cornus*-Steinkernen bedarf der Prüfung". In this supposition he is very near to that of Nikitin (1936 and later).

The above are the rather sparse remarks about the supposed taxonomical position of *Carpolithes Rosenkjaeri* to be found in the literature. They show that till now no one suggestion has been made concerning the relationship of *C. R.* which could be accepted by the paleobotanists interested in this matter.

3. THE MORPHOLOGICAL CHARACTERISTICS

In the following description I use in the first place the observations which I made during my own investigations, undertaken on specimens from the following localities: Copenhagen, Gliwice Stare, Rypin, Wieliczka and Vienna. As to geological age this fossil material covers the time from Oligocene to Lower Pliocene.

a. Dimensions and form of fruits

The variability of length and breadth of *C. R.* is demonstrated in Table 2. It shows that the specimens of *C. R.* from the first three localities (Copenhagen, Rypin and Stare Gliwice) are in their dimensions (length and breadth) and their shape (ratio length: breadth) almost identical. They are almost spherical, 1.6—3.4 mm long and 1.6—3.1 mm broad.

Judging from the data cited by Russian investigators, the dimensions of *C. R.* from 10 localities in various parts of the Soviet Union territories are very similar.

On the other hand, the dimensions of the specimens of *C. R.* from the Pliocene of Vienna (Brunn-Vösendorf) are much smaller. According to Berger (1952, p. 109) they are spherical and 1.5—2.0 mm in diameter.

According to my measurements they are spherical, from 1.3—2.2 mm long (M±m = 1.67±0.03), and 1.3—2.2 mm broad (M±m = 1.64±0.02). *C. R.* from Vienna, having almost the same shape as the specimens from all other localities mentioned above, are in comparison with them distinctly smaller.

Table 2 — Tabela 2

LENGTH OF THE FRUITS IN mm

Długość owoców w mm

Locality Miejscowość	Geological age Wiek geologiczny	Number of specimens Ilość okazów	1,3	1,6	1,9	2,2	2,5	2.8	3,1	3,4	M ± m
1. Copenhagen	Upper Oligocene	100	—	3	21	51	22	3	—	—	2,20 ± 0,02
2. Rypin	Middle Miocene	15	—	3	2	9	1	—	—	—	2,06 ± 0,06
3. Stare Gliwice	Upper Miocene	95	—	6	12	30	26	18	2	1	2,35 ± 0,03
4. Vienna	Lower Pliocene	170	10	112	43	5	—	—	—	—	1,67 ± 0,03

Table 3 — Tabela 3

BREADTH OF THE FRUITS IN mm

Szerokość owoców w mm

Locality Miejscowość	Geological age Wiek geologiczny	Number of specimens Ilość okazów	1,3	1,6	1,9	2,2	2,5	2,8	3,1	3,4	M ± m
1. Copenhagen	Upper Oligocene	100	—	3	28	51	17	1	—	—	2,15 ± 0,02
2. Rypin	Middle Miocene	12	—	3	1	6	1	1	—	—	2,09 ± 0,10
3. Stare Gliwice	Upper Miocene	95	—	2	11	33	27	20	—	2	2,39 ± 0.03
4. Vienna	Lower Pliocene	170	21	108	38	3	—	—	—	—	1,64 ± 0,02

Table 4 — Tabela 4

RATIO LENGTH : BREADTH

Stosunek długości do szerokości

Locality Miejscowość	Geological age Wiek geologiczny	Number of specimens Ilość okazów	0,65	0,80	0,95	1,10	1,25	1,40	M ± m
1. Copenhagen	Upper Oligocene	100	—	7	48	35	9	1	1,02 ± 0,02
2. Rypin	Middle Miocene	12	—	2	6	3	—	1	0,99 ± 0,04
3. Stare Gliwice	Upper Miocene	95	3	13	41	33	5	—	0,99 ± 0,01
4. Vienna	Lower Pliocene	170	—	7	91	61	10	1	1,02 ± 0,01

b. The surface of the fruits

The surface of the fossil fruits is almost smooth or shows a variable amount of longitudinal furrows whose number is connected with the number of carpels. The horizontal folds which are so characteristic e. g. in the family of *Araliaceae* are here never developed. The fruits from Vienna very often have on their surface distinct tubercules (Plate II, fig. 6—9 and Plate IV, fig. 1 and 7).

At the depressed base of some fruits a very short pedicel is to be seen, which obviously separated the fruit from the stem by abscission. At the apex also there is as a rule a depression which communicates directly with the axial canal. Around the apex are visible traces of vascular bundles, which provided the sepals or lay at bordening edges of the carpels. Usually there are 8 such traces. There seem also to be traces belonging probably to the other floral appendages, but these are very indistinctly visible. Only in a few fruits could there be observed on the apex the remainder rest of a very short, knobby, and sessile style or stigma (Table II, fig. 9 and 10).

The above description of the morphological characteristics of the fruits of *C. R.* which could be observed on their surface indicates that the body of the fruit develops from the inferior ovary whose syncarpous carpels (pericarp) fuse with the hollowed receptacle (epicarp).

The number of carpels is variable and in most specimens could be easily counted owing to their margin lines being well marked. The most common number is 3 or 4. The cross-section of fruits reveals the fact that the number of locules does not always correspond to that of the carpels since the transversal walls originally existing between them can often not be developed. As a result we very often come across 4-carpeled fruits which have 3 or even 2 chambers. 1-chambered fruits were not observed.

The place and manner of dehiscence in the fruits of *C. R.* is very characteristic. As a rule there opens only one locule, which is fertile, the others, which are sterile, remaining closed. The line of dehiscence, which is independent from the vascular bundles, is regularly elipsoidal and is formed by bands of special parenchymatic cells loosely held together. Separation of the valves in the mature fruits occurs by the tearing apart of the tissues during changes in tension due to drying. The ecological significance of this process will be emphasized later.

Among the investigated fruits from all the localities there were often also found 4-chambered specimens with two fertile chambers opening in the same manner. In the material from Vienna I found one 4-chambered fruit with 3 fertile locules. Only once did I find in Gliwice a 3-chambered fruit with two fertile locules. I did not see any 3-chambered fruits in which all the locules opened by separate valves. Although the opening of values occurs along the lines of their dehiscence, near the base the tissues of the fruit wall remains entire and does not show dehiscence. For this reason the valves opened partially and they could be completely removed from the fruit only by the use of mechanical force.

4. THE ANATOMICAL STRUCTURE

The anatomical characteristics which could be observed on the fruits of *C. R.* both on cross- and on longitudinal-sections are very similar but not identical in specimens derived from different localities and of different geological age.

a. The epicarp is very often almost washed off during the transportation of fruits by water. Nearly always, however, some remains of its tissues can be found which are parenchymateous and in their outer layers loosely arranged with prominent intercellular spaces, in the inner parts being rather thicker and more compact, closely merging with the pericarp. Only in a few cases and only in some places on the surface could one thin external epidermis be observed on the specimens from Gliwice. Plate I, fig. 8—12 shows the different stages of the washing off of the parenchymateous epicarp. On the longitudinal sections one can observe (Plate IV, fig. 1, 3, 4, 7) the connection of the tissues of the epicarp with the parenchymatical parts of the apex of the fruit located around the central canal in the axis.

b. The pericarp is anatomically differentiated into exocarp, mesocarp and endocarp. In the specimens from Copenhagen the exocarp is on its surface smooth and merged with the thin parenchymatic epicarp, in those from Gliwice its surface is uneven, and gradually transitive in the parenchymatic epicarp, and in the specimens from Vienna it is uneven, almost tuberculate, and more gradually transitive in the thick parenchymatic epicarp. Analogical differences could be observed in relation to the thickness of the hard pericarp which consist of almost isodiametric sclerenchyma with very thick cell walls which are arranged in more or less regular layers. The number of these layers differs in specimens from various localities, this being shown in the following table:

	Number of sclerenchyma cell-layers in pericarp										
	6	7	8	9	10	11	12	13	14	15	16
Copenhagen					—	—	—	+	—	—	—
Gliwice		—	—	+	—	—					
Vienna	—	—	—	+	—	—					

The variability of the above characteristic was only approximatively established.

The lumina of sclerenchymateous and lignified cells of the pericarp in the specimens from Copenhagen are very small, those from Gliwice are somewhat larger, and in the specimens from Vienna they are comparatively very large. The endocarp consists only of one layer of epidermis, whose cells in the sterile locules are very small and arranged evenly; in the fertile ones, on the other hand, the epidermis consists of cells which are very oddly pearlshaped, very hard and persistent, partly arranged in rows. This very striking feature will be described later in more detail.

On the basis of the above given description it could be seen, that the anatomical structure of the fruits of *C. R.* from different localities is not quite identical. In the specimens from Copenhagen (Oligocene) the pericarp has comparatively very thick walls, which are covered rather sparsely by parenchymatic epicarp. Therefore *C. R.* from the Oligocene were heavy and still imperfectly adapted to transportation by water unlike *C. R.* from the Pliocene, which were much smaller, lighter, and provided with more effectively operative spongiose and thick epicarp, well adapted for drifting by water.

The specimens of *C. R.* from the Miocene of Gliwice occupy a medial position between the two mentioned.

c. The vascular system of fruits of *C. R.* — as far as it was possible to investigate it — is composed of two separate groups of vascular tissues. The external one, situated in the epicarp (?), is composed of 6 (in the 3-carpelled fruits) or 8 (in 4-carpelled) main bundles, which supply the floral appendices (calyx, corolla etc.). The second group of bundles lies in the central part of the axis and consists apparently of axillar bundles corresponding to the ventral bundles of adjacent carpels intimately fused.

In the fossil fruits bundles are very rarely to be found and they are only partially preserved. They could not therefore be properly investigated (Plate IV). It is probable that in the centrum of the axis there was present always a cavity in the form of a canal, such as we find in some contemporary fruits of the genus *Halorrhagis.*

We can observe that the vascular bundles situated in the axial part of *C. R.* are similar to the analogically situated vascular bundles in the family of *Halorrhagaceae* or *Onagraceae.* Unfortunately I found it impossible to carry out properly the necessary comparisons, which would be of great importance from the taxonomical point of view. Perhaps other investigators of *C. R.* will be more fortunate. *Especially* would be interesting to know whether there was present inside the axillar bundles in *C. R.* interxylemary phloem, which is peculiar to various genera in the family of *Onagraceae.* I saw only very small fragments from the vessels which unfortunately did not give me a sufficient basis for establishing their anatomical peculiarities (comp. Metcarfe and Chalk 1950).

d. The type of placentation in *C. R.* is most remarkable. Ovule traces are derived from the bundles accumulated in the central axis of the fruit, strictly speaking from the placental branches of the axial bundles. The only trace is a single strong bundle that leads to the base of the ovule, passing it as far as the chalazal region. On the placenta in the seed-chamber there are only few or even one ovule which develops into the seed.

The placenta developed in all 3—4-chambered fruits is represented by a local robust enlargement of the area lying on the ventral margin of the carpel, usually mostly in the upper part of the locule (at a distance of about $^1/_3$ from its apex). The tissues of the placenta are here collarlike, and surrounded by the appendix of the sclerenchymatical tissue of the carpel (Plate IV, fig. 7 and 8).

The placenta of this type could be developed approximately at the same height inside each locule, not only in the fertile seedchamber but also in the locules which remain sterile (Plate III, fig. 1 and 2). The described placenta is similar to those found in some genera of the *Onagraceae.*

It is interesting that in the sterile fruitchambers deep inside the funicular canal there is present a typical tissue of cork (phellem), which due to suberization is excellently preserved (Plate IV, fig. 5 and 6). The cells constituting phellem are radially arranged, uniform in shape (polygonal), empty, and lacking intercellular spaces. The occurrence of the cork tissue in the region of the placentas of sterile seedchambers is obviously connected with the separation and closing of the chambers from the central axis. The analogical phellem, which formed the abscission tissue, separating in the ripe seed the hilum from the funicular canal, must have been present in the fertile fruitchamber. Unfortunately I did not find in the seedchamber well preserved remnants of such tissue, because after the abscission of the seed it easily undergoes destruction. At this place as a rule only one aperture can be seen.

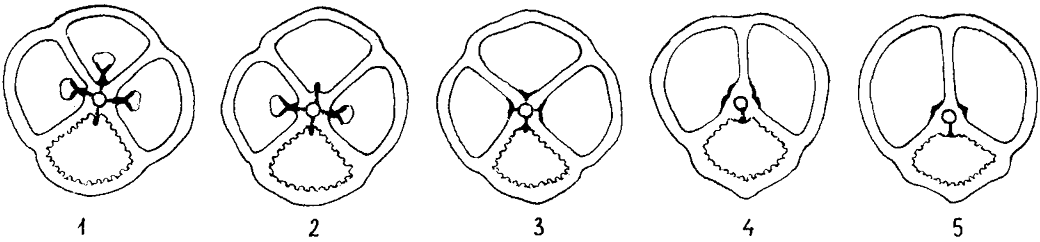

Fig. 2. The probable evolutionary line of reduction of axial placentas in the fruits of *Carpolithes Rosenkjaeri* Hartz
Przypuszczalna linia ewolucyjna redukcji łożysk osiowych w owocach *Carpolithes Rosenkjaeri* Hartz

Instead of the above described placentas surrounded by the wall-appendix, there are often developed in the fruitchambers of *C. R.* only funnelled hollows, which form canals where the vascular bundle passes from the fruit axis to the ovulum. This form of placenta is obviously a reduced one, and originated from the normal, above described type by the depression of the collarlike appendix of the wall which characterises the normally built placenta. From the point of view of evolution the depressed form of placentation described above leads gradually to the disappearance of the placentas in the sterile fruitchambers. Very often in the fossil fruits, especially from Gliwice and from Vienna, specimens could be found either without any sign of the former presence of the placenta, or with the smallest trace of it in the form of a very small aperture. The best developed normal placenta in all chambers is to be found in the Copenhagen specimens, but I found them also in the specimens from Gliwice and Vienna. I am therefore unable to construct one clear evolutional line of the metamorphosis of the placenta in *C. R.*, although some observations (not, however, statistically proved) seem to confirm the existence of such a way of evolution (Fig. 2). It is worth mentioning that the apertures situated very near the apex in the seedchamber (almost apical) are always simply hollow, often funnelled. This kind of subapical placentation is somewhat similar to the apical placentation of single as a rule ovules in the seedchamber of the genus *Holorrhagis*. In addition the body of the pericarp in *C. R.* is provided in the apical region, independent from the valve, with the bands of parenchymatic cells (Plate IV, fig. 2) in a similar manner as is so typical for *Halorrhagis*.

In the material from Copenhagen I found one very curious specimen which had in the fruitchamber, besides the placenta of normal type, immediately under it, traces of serial undeveloped ovules, very similar to those which are to be found in the genus *Jussieueae*. On the other hand I found one specimen of fruit from Copenhagen which had the normal type of placenta surrounded by a collar of sclerenchymatic tissue; this placenta, however, was not placed vertically to the axis (as is the rule), but lay obliquely in the relation to the axis, so that its base lay near the base of the fruitchamber.

Taking into consideration all the facts mentioned above concerning the placentation of the fruits of *C. R.*, we may state that:

1. The placentation of *C. R.* in its normal form is very similar to that of some genera of the family of *Onagraceae*.
2. Besides this type of placentation there sometimes occur in *C. R.* simple placentas, lying in funnelled hollows; when this kind of placenta lies in the seedchamber subapically there is a similarity between the placentation in *C. R.* and the apical placentation of *Halorrhagis*.
3. There were also observed (only in one specimen from Copenhagen) besides the placenta of normal type traces of marginal placentation, not unlike the serial placentation in the genus *Jussieua*.
4. The striking diversity of placentation in *C. R.* seems to be the most important phenomenon from the point of view of the taxonomical position of these fossils.

e. Inside of the fruitchamber in the fossil fruits with opened valve we never find any organical remnants. Such remains could be looked for in unopened, not quite ripe fruits. In all cases which we have observed more closely we have found only a whitish and thin film-like membrane adhering more or less tightly to the wall of the fruitchamber. We see it quite distinctly on Plate V, fig. 4 and Plate VI, fig. 4, 5a and 5b. It consists obviously of dried slime which in cross-sections hangs loose from the wall of the seedchamber. The internal sculpture of this slime membrane is a negative replica of the papillous epidermis of the seedchamber described above. No remnants of the testa of the seed, resp. seeds, could be found.

Having described the morphological and anatomical characteristics of the fruits of *C. R.* it would be logical now to answer the question whether fossil fruits from all localities and therefore of different geological age, could be considered as belonging to one and the same taxonomical unit.

However, it seems more appropriate to take this problem into consideration later, after making an attempt to connect the principal features peculiar to *C. R.* with their functions.

5. ECOLOGICAL PECULIARITIES OF FRUITS

The fruits of *C. R.*, taken from all the localities, have very similar characteristics in their fundamental morphological and anatomical structure, but ecologically they were much more differentiated. It is true that the aim and the function for which they were designed was always the same, i. e. to secure the distribution and the sowing of the seeds, but the degree of adaptation and perfection of the mechanisms which were designed to act for this purpose, were not uniformly effective.

From the ecological point of view the following two processes are the most important:

1. the change of the functions in the ovary chambers,
2. the gradual improvement of the efficiency of the mechanisms for the distribution of fruits and for the abandonment of the seedchamber by the ripe seed.

If we look at the change of functions in the fruitchambers our starting point is the assumption that the theoretically possible primitive ancestral type of fruit possessed all fruitchambers built alike. Far reaching but logical and therefore possible would be the assumption that in these primitive fruits all the chambers were fertile and produced on their axial placentas probably many ovules which developed normally into seeds. Therefore all locules were seedchambers. The means by which these probably dry fruit (*drupa*) opened is not easy to suggest. Taking into consideration the fact that all fossil fruits of *C. R.* opened their seedchambers by the valves produced in the outer chamber walls, we may suppose that the *C. R.* ancestor opened all its seedchambers analogically. The state of balance and equality of all the fruitchambers could remain in the fruit only so long as the ecological conditions remained the same. In any case we can assume that the ancestral type of *C. R.* was probably a land plant dispersing its seeds by means unknown. It is probable that already at this stadium the ancestral form lived near water which took over the transportation of the seeds.

Stahl, to whom we owe many very interesting observations, brought into the ecology of plants among others one new notion, which he called „Konverse Anpassung", and which was later developed by Neger (1913). When an organism is in the state of „konverse Anpassungszustand" then „nützt er irgend einen Factor aus seiner Umgebung zu seinem Vorteil aus", in order to gain from it as much advantage as possible. In this way hydrochory originated and specialised as the most effective adaptation of fruits to be distributed by water. When short periods of strong torrential rains alternate with long periods of dryness the rainy periods are connected with the transportation by water of fruits and seeds; at the beginning of the dry season the abandonment of the seeds from the seedchambers takes place as the result of the drying out of the fruits in the process of xerochasy (Neger 1913). The Tertiary and especially the Miocene were the geological periods in which the climate in Europe was characterised by an alternate succession of wet and dry seasonal changes. Not long ago I devoted more attention to this very striking feature of miocenic climate in Central Europe and I find it unnecessary to repeat it here (Szafer 1961).

During the Tertiary, and especially during the Miocene, the climate of Central Europe was influenced by the great transgressions and regressions of the Parathetys-seas, which created for the *C. R.* very advantageous conditions for the conquest of a maximum area. The torrential rains which flooded large regions along the river valleys and across spacious lowlands transported the fruits of *C. R.* which later, at the moment of drying out, were deposited on the ground and germinated.

Transport by running water of the fruits of *C. R.* was more effective with the fruits from Miocene and Pliocene, and less effective with the fruits from Oligocene. This increasing ability to drift along running water was induced by the improvement of the morphological and anatomical characteristics, already mentioned above. Here arises the question, which form of fruit of the fossil *C. R.* may be considered as the most perfect in assuring the longest lasting transport by water. From this point of view the most privileged fruits were probably those which were best balanced when drifted by water. The 4-chambered fruits were in this respect rather less perfect in comparison with the 3-chambered ones, which possessed two floating airchambers and one relatively smaller seedchamber situated in a flowing state below them. This chamber, with a heavy seed (or seeds) inside and with comparatively thick walls, gave certainly

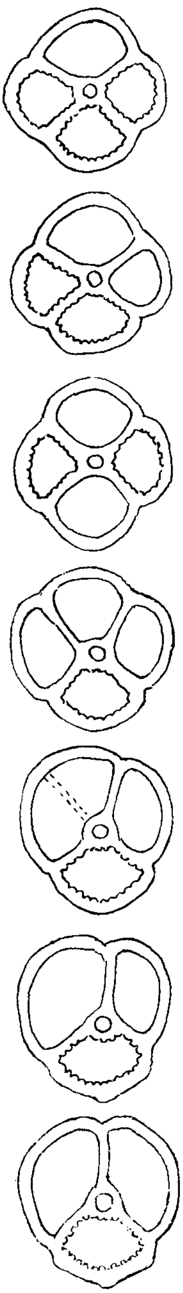

Fig. 3. Successive forms of the fruits of *Carpolithes Rosenkjaeri* Hartz showing their increasing adaptation to the hydrochory
Szereg owoców *Carpolithes Rosenkjaeri* Hartz, wykazujący ich wzrastające przystosowanie do hydrochorii

a heavy ballast, which enabled the fruit to keep its balance while floating in the water. Such 3-chambered fruits of *C. R.* were to be found very often, especially in the Miocene of Gliwice. Fig. 3 shows some forms of the fruits of *C. R.* leading from 4-chambered and badly balanced fruits, to 3-chambered ones with an increasing ability to be well adapted to floating in moving water.

The second question which we must try to answer is the way in which the seed or seeds emerged from the seedchamber. This chamber (and only this one) is valvate, and was partially opened during the desiccation of the fruits which were deposited upon the earth after their drifting in the water. The opening of the valve was a simple mechanical process of xerochasy induced by the drying out of the fruit and especially the seedchamber.

Judging by the analogical processes which could be observed in many contemporaneous plants which show xerochasy of their fruits (Ulbrich 1928), we may assume that the function of the half-opened valve in the drying out of the fruits of *C. R.* was rather passive. We must therefore look for an active factor which would be responsible for the emergence of the seed (seeds) from its chamber. It would seem that in this case not one but at least two factors were in concerted action. Firstly increased the pressure of the seed (seeds) against the wall and against the valve, due to the swelling of the cover of slime which at the beginning of the opening of the fruitchamber imbibed water. Secondly it was the fact that as a result of the drying out of the fruits there were formed in the middle parts of the chambers horizontal swellings, which pressed strongly on the seed (seeds). The pressure of these swellings was increased by the fact that the valve at the base was closely connected with the seedchamber and created there a strong point of resistance, so that the seed (seeds) could glide only towards the end of the half-opened valve.

Similar phenomena are known in many groups of plants. Ulbrich (l. c.) stated that xerochasy is very often accompanied by „Tangentialquellungen der Gewebe der Kapselwandung die eine Längskrümmung erfährt, bei welcher die Krümmungsgewebe parallel, die Krümmungsachse senkrecht zur Längsrichtung der Frucht liegt" (Comp. also Weberbauer 1898).

Loose seeds of *C. R.* have not so far been found in the fossil state or they have not yet been recognized as belonging to this fossil.

6. THE RELATION OF C. R. TO THE GENUS *TORICELLIA* DC.

As regards the possible affinity of *C. R.* with the contemporary living genera of Dicotyledonous plants of similar morphological properties, the supposition has been expressed that there is a possible affinity of *C. R.*

with the genus *Toricellia* DC. We will now concentrate our attention on this subject.

P. A. Nikitin (1935) was the first to draw attention to the probability of this taxonomic relationship. He was joined in this cpinion by P. N. Dorofeev (1957). According to them *C. R.* shows a resemblance to the subfamily *Cornoideae* and especially to the genus *Toricellia.* While advancing this hypothesis the two Russian scientists emphasized that *Toricellia* shows two characteristics by which it differs pronouncedly from *C. R.*, i. e. the lack of the longitudinal channel in the axis of the fruit, usually 3-chambered, and the sculpture of the inner wall of the seed chamber which runs transversally.

Kirchheimer (1938) also reported the genus *Toricellia* as being related to *C. R.* among the genera living at present without, however, considering this presumption to be of any great importance, as can be seen from the fact that in his fundamental work of 1957 he never returned to this idea and did not even mention the name *Toricellia.* He restricted himself to the short statement already quoted.

Owing to the kindness of Dr. Wilczek, associate-professor from Brussels, I had at my disposal the fruits of *Toricellia tiliaefolia* Oliv. from the Himalayas and was able to examine in detail their morphological and anatomical structure. Having carried out these investigation I arrived at the conclusion that the genus *Toricellia* DC. now represented in the flora of our globe by 3 species does not belong to the family *Cornaceae* but bears the characteristics of the family *Araliaceae* (Plate V, fig. 5).

It should be emphasized that the views on the systematic position of the genus *Toricellia* DC. have undergone a change.

A. P. De Candolle (1828—1830) was the first to describe the genus *Toricellia* and he attributed it to the family *Araliaceae.* Endlicher (1840) followed him. It was only 27 years later that G. Bentham and J. D. Hooker (1867) included the genus *Toricellia* in the family *Cornaceae.* They were followed first by Baillon (1887) and then by the authors of Index Kewensis (II, 1895).

The transposition of the genus *Toricellia* from the family *Araliaceae* to that of *Cornaceae* was accompanied by the characteristic remark of the authors of Genera Plantorum (Vol. I London 1867, p. 952) who called it „genus valde anomalum". Thirty years later, Harms (1898) left the genus *Toricellia* in the subfamily *Cornoideae* but stated that „*Toricellia* hat einige Merkmale ähnlich wie *Araliaceae*". Other taxonomists (Schindler 1905, Wettstein 1935 and Engler-Diels 1936) either omitted the genus *Toricellia* altogether in their reviews or left it among *Cornaceae* (subfamily *Cornoideae*), and so did Wangerin (1906) who, however, emphasized that this genus „aus den Ramen der übrigen Gattungen sowohl in morphologischer wie in anatomischer Beziehung ziemlich weit herausfällt; da es aber nicht möglich ist dieser Gattung einen besseren

Platz im System anzuweisen, so belasse ich sie als Tribus *Torricelieae*[1] bei den *Cornoideae,* weil sie mit letzteren immerhin in einigen Merkmalen zusammentrifft und daher eine genetische Verknüpfung mit diesen die wahrscheinlichste ist'.

I do not intend to develop here a more detailed consideration of the systematic position of the genus *Toricellia* DC. because this is not the aim of my paper. Considering: 1. the lack of the central channel in the axis of the fruit, 2. the horizontal (transversal) course of the silky threads lining the inner wall of the endocarp, 3. the transversal folds of the outer wall of the pericarp, these three characteristics being altogether absent in the fruits of *Carpolithes Rosenkjaeri* and peculiar to some genera of the family *Araliaceae,* we arrive at the conclusion that the genus *Toricellia* DC. belongs to the family *Araliaceae* in accordance with the statement of its discoverer, and that the fossil *Carpolithes Rosenkjaeri* has nothing in common with it.

Obviously, the statement quoted above which, in my opinion, is quite justified from the point of view of palaeobotany, does not decide the systematic position of the genus *Toricellia.* This problem must take into account not only the few morphological and anatomical characteristics of the fruits mentioned here, but also numerous other characteristics. Of these, the most important are those of the structure and development of the ovulum, the manner in which it is attached to the placenta and hung in the chamber, the structure of the integumenta and of the testa of the seed, and also the details of structure of the fruit itself. These characteristics, which are of essential importance for the establishment of the systematic position of the genus *Toricellia,* were not studied thoroughly enough.

Our final statement is that the genus *Toricellia DC.* belongs to the family *Araliaceae* and does not show any essential characteristics by which it would approach *Carpolithes Rosenkjaeri.*

7. *CARPOLITHES ROSENKJAERI* HARTZ IN COMPARISON WITH *CARPOLITHES* SP. 4 CHANDLER (1925)

Before we proceed with the consideration of the question of the taxonomical value of *C. R.*, we must include in the circle of our interest one more fossil which was found in the Upper Eocene of England (Hordle, Hants) and described by Chandler (1925) as *Carpolithes* sp. 4.

This interesting fruit, unfortunately known only in one single specimen, was characterised by Chandler as follows:

„*Carpolithes* sp. 4. Plate VIII, fig. 2a—b. — Endocarp sub-spherical with a central canal, somewhat pointed at the base, with a shallow depression at the apex; locules 4, each opening by a valve which remains

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[1] The generic name is spelled by De Candolle with one „r", i. e. *Toricellia* (after the name of the well-known prominent physicist).

attached at the base; external surface ornamented with fine pits, walls thick, internal surface with tiny irregular tubercles. One specimen. Length 3.25 mm; breadth 3.5 mm.

Seeds attached to basal placentas, solitary. The fossil bears a resemblance to *Carpolithes Rosenkjaeri* Hartz, from the Amber-Pine Beds of Denmark. It is larger than this species, which measures 1.6 to 3 mm in diameter, but the shape is similar, and both have thick woody walls and the same method of germination. The number of locules in *C. Rosenkjaeri* varies from 1 to 3; whether a similar variation occurs in the Hordle species cannot be stated on account of lack of material. Thanks to the fact that I had access to a fine series of Amber-Pine Bed fossils sent to Mr. Reid by Dr. Hartz, it has been possible to make a study of the Danish species. In it the locules communicate with the central vascular canal by apertures (marking the placentas) at about ¹/₃ from the apex on the inner angle of the locule, while in the Hordle species the placentas are at the base of the locules. The locules of *C. Rosenkjaeri* are lined with coarse papillae, whereas in the Hordle endocarp they are finely tuberculate. The two species are not identical therefore, but the form and essential structures are so similar that it seems probable they may belong to the same family".

This exact description of the two fossils cited above, could lead to the conclusion that *Carpolithes* sp. 4 from the Eocene of England was probably a more or less direct ancestor of *C. R.*

Recently Chandler (1961) found a second fruit of *Carpolithes* sp. 4 which made it possible to correct certain details in the former description (1926). In the amended description Chandler emphasized that: 1. the fruit is without a central canal, 2. the locule has a lining of convex cells with finely digitate walls, 3. the solitary seeds with the testa adhering closely to the locule wall were probably pendulous, 4. the testa shows transversely aligned cells which give rise to transverse striae.

In consequence of these properties found by Chandler for the eocenic fruits of *Carpolithes* sp. 4 she revised her determination and now refers this fossil as *Cornus quadrilocularis* Chandler n. sp. Further remarks on the relationship of the fossil will follow.

In the face of the above cited facts we are obliged to accept that *Carpolithes* sp. 4 Chandler (1926) = *Cornus quadrilocularis* Chandler 1961, does not remain in any taxonomic connection with *Carpolithes Rosenkjaeri* Hartz.

8. THE TAXONOMICAL POSITION OF *CARPOLITHES ROSENKJAERI* HARTZ

On account of the peculiar morphological, anatomical, and ecological characteristics of *C. R.* this fossil fruit is apparently distinctly different from all fruits known today and owing to this fact its taxonomical position is very difficult to establish. The authors who were interested in this question expressed very different opinions in this matter as I explained in Chapter 2.

After my own investigations, which I carried out especially in the family of *Halorrhagidaceae* and partly also in some genera of *Onagraceae,* I came to the conclusion that *C. R.* is indeed related in some characteristics with both of these families. Nevertheless the fossils from the Tertiary known under the name of *C. R.* are in reality a set of forms very similar in their principal characteristics and belong to the only one taxonomic unit inside the order of *Myrtiflorae.*

a. *Halorrhagidaceae* is the family of the order of *Myrtales (Myrtiflorae)* which is in many characteristics very near to the *C. R.* forms complex. In the monographic description of this family which was worked out by Schindler more than half a century ago (1905), we naturally do not find many taxa which were discovered later. A serious disadvantage of this excellent work is the neglect of the ecological side in the description and causal explanation of many characteristics. My own studies, made on the fruits of 27 species of *Halorrhagis,* have convinced me that among the enormous diversity of their morphological, anatomical, and ecological characteristics only the following characteristics could be mentioned as separating the genus *Halorrhagis* from the complex of forms of *C. R.*

1. The styles in *Halorrhagis* are short or elongate, usually corresponding in number to the amount of carpels (usually 4); they are free, but in some species they are merged together into one. In *C. R.* the style is not usually preserved, but where it exists we find it in the form of a short and simple one (comp. Table II, fig. 10). I must add that in many specimens, especially those from Copenhagen, there could be observed on the apex of the fruits 3 or 4 very badly preserved remnants of small appendices, which could correspond with the 3 or 4 free styles common in the fruits of *Halorrhagis.*

2. The ovules (1 in every chamber) are, according to Schindler, in all genera of *Halorrhagidaceae* „ab apice loculi pendula, anatropa in tegumentis 2 plerumque discretis raro coalitis". The ovula in *C. R.* are not placed apically in the chambers, but they could be subapical, connected with funneled apertures. This kind of placentation could be compared with the placentation of *Halorrhagidaceae.* Nevertheless it would be very risky to consider the placentation of recent *Halorrhagis* as really near to that found in *C. R.*

3. Germination in the family of *Halorrhagidaceae* is very peculiar, since the fruits of all genera germinate through an apical aperture which is closed either by thin or by soft tissue. In *C. R.,* on the contrary, the emergence of the seeds takes place by a valve which develops in the wall

of the fertile fruitchamber. These two peculiar forms of germination (or opening) of the fruit are the most important differences between the family *Halorrhagidaceae* and the group of *C. R.* forms.

All other differences which could be found between the fruits of *Halorrhagis* and *C. R.* are of only small importance, as they are mostly connected with the manifold ecological functions performed by the fruits of *Halorrhagis.*

Among many species of the genus *Halorrhagis* that I investigated I found that *Halorrhagis prostrata* Forst. from New Caledonia, which is very closely adapted to transportation by water is also in its anatomical characteristics perhaps most like *C. R.* (Plate V, fig. 6 and 7). Equally adapted to transportation by water in *H. prostrata* are both the pericarp and the epicarp, the later especially in its median tissues (mesocarp).

The geographical distribution of the family of *Halorrhagidaceae* is not sub-antarctic, as is often supposed, but it is almost cosmopolitan. On the other hand it is true that Australia and the nearly situated islands are now the main centre of life of the genus *Holorrhagis.* Cookson (1954) is of the opinion, based upon the fossil pollen evidence, that among many of the families the *Haloragaceae* (like *Casuarinaceae* and *Proteaceae*) were widespread in southern Australia already in the lower Tertiary. Crocker (1959) considers that „in the Tertiary many genera have had in Australia only one limited habitat-diversity, and therefore many genera and species were then very widely distributed. During the pleistocenic changes of climate, many taxa underwent alternate constrictions (in glacials) and expansions (in interglacials). Therefore one may accept that the Quaternary left a profound impression upon the Australian flora and that the climatic changes in Pleistocene „were probably responsible for much species complexity and have led to the development of the current plant communities". If this supposition of Crocker is correct and if it applies to *Halorrhagis,* then we could accept as probable that this genus is of tertiary origin, but this enormous specific differentiation occurred in Australia later under the influence of the changeable climate of Pleistocene, and that this process from the point of view of evolution is at the present time still in action.

As a result of the above remarks we may conclude that between *Halorrhagis* and *C. R.* there exist some striking similarities, but any direct mutual relationship between them is hardly acceptable.

Lastly I will here recall the interesting fact that Reid and Chandler (1933) described from the London Clay (Eocene) a new genus and species *Haloragicarya quadrilocularis* n. sp. which was a 4-loculed fruit, in length 3.5 mm, with elongate sausage-shaped locules passing at the apex into filiform canals. If this last characteristic is an actual fact (the authors themselves somewhat doubt its correctness) we would have the proof that the *Halorrhagis*-type as a taxonomical unit was present in Europe already at least in Eocene, and could have had at that time connections with the ancestral forms of *C. R.*

b. *Onagraceae* is the second family of the order *Myrtiflorae,* which must be taken into consideration as possibly being related with the *C. R.* complex. This family is indubitably the nearest one to the family of *Halorrhagidaceae.* Eichler (1878) was of the opinion that „der Blütenbau der *Halorrhagideae* stimmt vollständig mit dem der Onagraceen überein". Of similar opinion was Schindler (1905) and many other investigators whose names I will not quote here. From our point of view of special interest are the following characteristics, which are present both in the fruits of *C. R.* and in the more primitive genera, especially of the subfamilies of *Jussieueae* and also *Gaureae* (Raimann 1898, Broekens 1924):

1. The fruits in both groups are usually 4-carpelled and 4-chambered with a tendency to reduce this number;
2. The seeds in *C. R.* were present only in the seedchambers similarly as in the subfamily of *Gaureae;*
3. *C. R.*, like the adapted water genera of *Jussieueae*, have in the central axis around their fascular bundles a well developed cork tissue (periderm) in the form of a sheath. From this tissue in *C. R.* the cork-tissue grows into the funnelled axil placentas. It is well developed also in the sterile fruitchambers (Plate IV, fig. 7 and 8);
4. The fruits in *C. R.* and in many genera of *Onagraceae* were opened by valves, which as a rule remain at their base connected with the fruit-wall.

As the conclusion of the above comparison carried out on forms of *C. R.* with the families of *Halorrhagidaceae* and *Onagraceae*, we may state that *C. R.* shows close connections with both of them. On the other hand we must state that the fruits of *C. R.* are distinguished by at least the two following important groups of characteristics: firstly by the peculiar anatomical structure and the opening of the seedchamber and by the kind of placentation, and secondly by the extreme adaptive ecological properties, connected with the peculiar climate of Tertiary in Europe.

Now arises the question: are the characteristics which we have found in *C. R.* from all the localities sufficiently similar as to form the basis of an argument that all our fossils could be assigned as one taxon? Considering that all fossil fruits described under the name of *Carpolithes Rosenkjaeri* Hartz independently of their geological age are fundamentally of the same morphological and anatomical properties and that their ecological characteristics are the result of analogical evolutionary processes of adaptation, we can be sure that all forms of *C. R.* belong to the same taxonomic unit.

The next question is of what rank is this unit? If we accept that *C. R.* take an intermediate position between the families *Halorrhagidaceae* and *Onagraceae*, it would be proper to value its rank as a new family. But in my opinion *C. R.* is more closely connected with the *Onagraceae* than with *Halorrhagidaceae*. From this standpoint more proper is to establish the rank of *C. R.* inside the family of *Onagraceae* as a new subfamily or a new genus.

The above indicated possibilities must be considered not only from the point of view of the formal system of recent plants, but they must be also considered as a special palaeobotanical problem. The question is this: is it right to place a taxon of a fossil plant, which lived about 40 million years ago and has been extinct at least two million years, among the now living taxa? The answer in my opinion is that it could be done only in relation to the taxa of very high rank (orders, families, or subfamilies), but in relation to taxa of minor ranks (genera or subgenera and species) such a proceeding would be wrong. Also from the logical point of view it is impermissible to locate an extinct taxon beside more or less similar now living taxa, unless the taxon known as a fossil only could be considered as a joining unit between two taxa now living. In the case of *C. R.* we are unable to indicate either within *Halorrhagidaceae* or *Onagraceae* two genera for which *C. R.* could be considered as being intermediary.

After long consideration I came to the conclusion that all fossil forms of fruits of *C. R.* type taken together belong to the family of *Onagraceae*, to its extinct subfamily which I propose to name: *Parajussieueae* nov. subfam.

I have chosen this name for two reasons: first in order to indicate the affinity of this taxon with the subfamily *Jussieueae* as the most primitive of all subfamilies of *Onagraceae*, and second by the suffix *para* to support the assumption that our fossil taxon cannot be considered as immediately preceding the *Jussieueae*, but that these two subfamilies have developed simultaneously on a parallel line along different ways of adapting their fruits to dissemination.

It is hardly possible to accept that the contemporary representatives of the subfamily *Jussieueae* are descended directly from our fossil subfamily. As a member of the very old family of *Onagraceae* our new taxon should be placed first in the line of 9 subfamilies, just before the subfamily of *Jussieueae*. *Parajussieueae* is the most primitive of them all and by means of this subfamily the *Onagraceae* are very closely connected with the family of *Halorrhagidaceae*.

The family of *Onagraceae (Oenotheraceae)* is a very old taxon which is common in temperate and subtropical regions (rare in the tropics), containing today 38 genera and about 500 species, generally with tetramerous flowers. They are perennial herbs, a few only being annuals (e. g.

Epilobium, Clarkia, Godetia) or biennials (e. g. *Oenothera biennis*). Mostly herbaceous, they may sometimes be shrubby or even arborescent (e. g. *Fuchsia*). The subfamily *Jussieueae,* contains three genera (*Jussieua, Oocarpon* and *Ludwigia*) which are herbaceous or shrubby marsh or water plants, widely distributed, also in the tropics of both worlds.

The family of *Halorrhagidaceae (Haloragaceae)* is smaller but widely distributed throughout the world and is very closely related to *Onagraceae.* The plants are herbs which are often aquatic with very remarkable differences of habitat more or less associated with the varied mode of their life. This family contains 7 genera and about 160 species and finds its chief centre in Australasia. Largest and richest in forms is the genus *Halorrhagis* (more than 60 species) which is australasiatic and antarctic, with a few species passing into South-eastern Asia and South America (Chile, Juan Fernadez).

I have purposely cited the above information (Rendle 1956) about the two families which we consider to be closely related to the subfamily of *Parajussieueae* because they give us the proof that both are in every respect so richly differenciated that they are able to live in almost any conditions and are capable of occupying almost any habitat. The adaptive characteristics of all vegetative organs in the families of *Onagraceae* and *Halorrhagidaceae* are so numerous and variable that they possess only limited value from the taxonomical point of view. This fact leaves us with the generative organs as being the most useful for taxonomy and at the same time emphasises the taxonomical usefulness of the fruits.

Even in the classification of contemporary taxa of *Onagraceae* the most important characteristics are those concerning the fruits and seeds. This circumstance makes it easier for us to carry out the classification in the subfamily *Parajussieueae.* With our present knowledge of the circle of forms which we have decided to take as members of this subfamily the classification could be as follows:

Family: Onagraceae

Subfamily: *Parajussieueae* nov. subfam.

The 4 (2—5)-chambered fruits are drupes opening their seedchambers (as a rule 1 in every fruit but sometimes 2, or 3) loculicidally by one valve, which in the basal part remains connected with the fruitwall. The seedchamber is lined with coarse papillae and covered with a slime membrane, the sterile chambers are similarly, but more finely tuberculate or almost smooth. All locules communicate with the central vascular canal by protruding apertures or by funnelled hollows marking the placentas, usually about $^1/_3$ from the apex of the locule, but sometimes nearly at the apex.

The seeds, which develop only in the seedchambers, probably filled them, but are not yet known in their other properties.

They were plants of unknown vegetative structure and duration of life, but it may be true that their habitat was connected with marshy or watery conditions, and that the water (perhaps not only fresh water but also brackish- and salt-waters) was necessary for the transportation of fruits and indirectly it was also important for their germination.

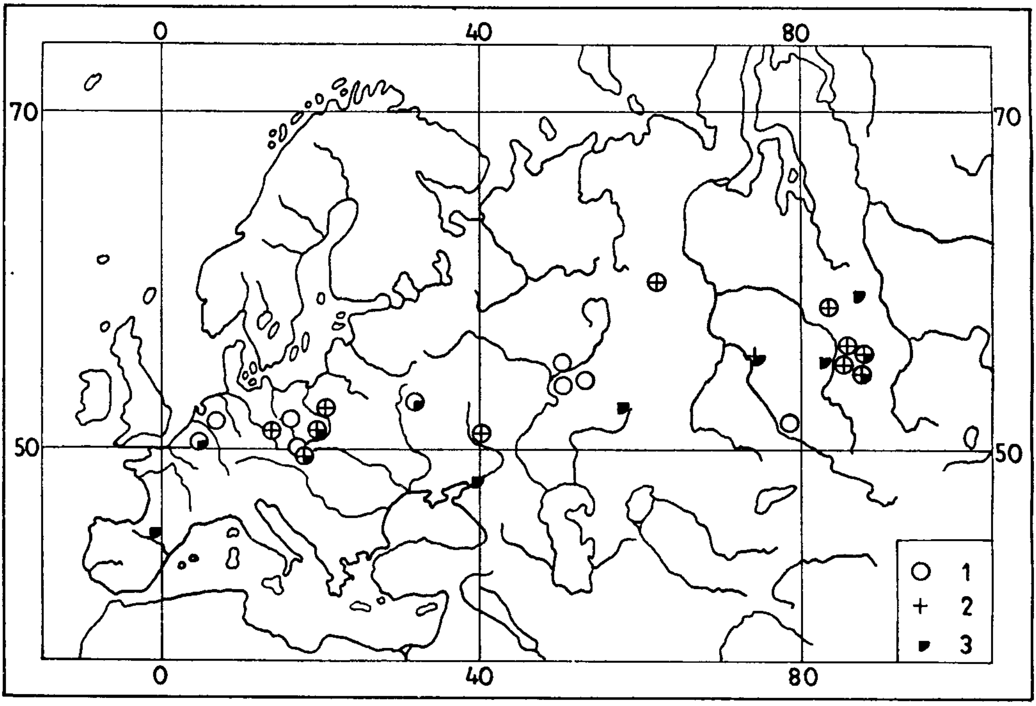

Fig. 4. Distribution of 3 genera of water plants in the Younger Tertiary: 1 — *Decodon*; 2 — *Diclidocarya*; 3 — *Proserpinaca*

Rozmieszczenie trzech rodzajów roślin wodnych w młodszym trzeciorzędzie: 1 — *Decodon*; 2 — *Diclidocarya*; 3 — *Proserpinaca*

The assumption that members of the subfamily *Parajussieueae* were water- or marshplants is supported by the fact that the maps of geographical ranges of some water plants in younger Tertiary (chiefly Miocene) were very similar (fig. 4). It complies especially with the geographical ranges of: ***Decodon, Diclidocarya, Proserpinaca,*** and *Azolla* (Kryshtofovich 1957 and others).

The subfamily of *Parajussieueae*, now completely extinct, probably appeared first in Europe in Eocene, reached there its maximum geographical range in Miocene and died out in Lower Pliocene.

The nearest kindred is the recent subfamily *Jussieueae*, which differed distinctly in having capsuled fruits, usually with many seeds in their chambers which opened both by loculicide and by septicide valves, or by other means not comparable with those present in the subfamily *Parajussieueae*. In some adaptive ecological characteristics, especially connected with water-habitat, the two subfamilies are similar.

My proposal as to the classification of the subfamily *Protojussieueae* is the following:

Genus: *Hartziella* nov. gen.
(*Carpolithes Rosenkjaeri* Hartz *s. lato)*

This taxon known so far from 17 localities in both West, Central, and Eastern Europe and in West Siberia has been described in detail above. Since among the very rich and variable fruits we could distinguish somewhat three different types of fruits, we have decided to take them here as three species:

1. *H. Rosenkjaeri* n. comb.
(*Carpolithes Rosenkjaeri* Hartz, *s. str.)*

The specific characteristics of this taxon are: the relatively thin layer of aerenchyma on the surface (epicarp) of the fruits and the very variable placentation, which in some specimens remind us of the placentation in the genus *Jussieuea*. The 4- or 3-chambered fruits have sometimes not 1 but 2 (or even 3) fertile locules. The sclerenchyma in the pericarp consists of about 12 cell-layers.

Known from the Oligocene of Copenhagen (Hartz 1905), it is possible that *H. Rosenkjaeri s. str.* is connected by intermediary forms with *H. miocaenica*.

2. *H. miocaenica* n. sp.
(= *Carpolithes Rosenkjaeri* auct. div.)

Very similar to the proceeding taxon, but usually with 3- (4) chambered fruits and mostly with only 1 (2) fertile locules. The seedchamber is smaller than the sterile floating ones and there are about 9 sclerenchymatic cell--layers in the pericarp. Obviously very well adapted to hydrochory and xerochasy.

This species was very common in Miocene along the shores of the Parathetys-Sea in Poland, and in similar living conditions in USSR as far as West-Siberia, where its geological age could be determined as most probably Miocene, but possibly also as Oligocene and Lower Pliocene.

3. *H. vindobonensis* nov. sp.
(= *Carpolithes Rosenkjaeri* Berger 1952)

The fruits are much smaller than in other taxa of the subfamily (comp. the Plates 2—4) and there is a tuberculate pericarp. The pericarp consists of about 7 layers of sclerenchyma, whose lumina are about twice as large as in other species. On the surface of the seeds there are very often more or less deep hollows of different dimensions, whose origin could not be established. It is possible that they are traces of the activity of insects.

The position of the aperture in the seedchamber is here mostly (?) subapical. Connected with this characteristic is the fact that the valve opened often only in its upper part. Among 30 ripe fruits which I investigated, 15 (50%) opened above half the length of the seedchamber, in 5 specimens in the upper part of it, and in 10 specimens only the base of the valve was situated near the lower part of the fruit.

Till now it is known from one locality only: from the Congerienlayers of Lower Pliocene in Vienna (Berger 1952).

This taxon is much different from the two described above, and it is clear that it could not be connected with them directly. It has, however, the same main characteristics and therefore it was left in the genus *Hartziella.*

9. SOME REMARKS ABOUT THE EVOLUTION OF THE GENUS *HARTZIELLA*

There are various opinions concerning the affinity and the possible ways of evolution of the order *Myrtales (Lythrales)*, and especially of the family of *Onagraceae*. It would be not advisable to discuss here these very complicated problems. I will therefore restrict myself here to the following short remarks:

1. The family of *Onagraceae* probably had in old Tertiary or even in Cretaceous period common ancestors with the family of *Halorrhagidaceae.*
2. The subfamily of *Parajussieueae* was probably represented in Europe in Paleocene only by one mesophytic and subtropical genus. In Oligocene this genus evolved into the genus *Hartziella* by gradual adaptation of the fruits to hydrochory and by producing mechanisms in the xerochastic dispersal of seeds.
3. The specialisation of these adaptive characteristics advanced during the Miocene and was induced by the peculiar climate in Europe along the shores of the Parathetys-seas, which favoured hydrochoric plants with xerochastic dissemination. During this geological period the adaptive characteristics of the fruits of *Hartziella* became very specialised and were therefore unable to adapt themselves to new and quite different life conditions at the end of Tertiary.
4. *Hartziella vindobonensis,* which was the last representative of the subfamily *Parajussieueae,* with small fruits and with obviously diminished ability to open their seedchambers, seems to offer us an example of so-called senescence of a taxon which was unable to adapt itself to new climatic conditions.

If we accept that the above indicated process of evolution lasted ca 30—40 million years, and proceeded basically along one line and in one direction only, we would be able both to understand more clearly the causes of evolutionary processes and to distinguish their stages. The causes which were in action are connected chiefly with the changes of climate. After first the tropical and later the subtropical climate in Europe during the Paleocene and Eocene which was wet and warm without greater seasonal or regional differences, there followed in Oligocene climatic changes which were regionally very much differentiated. These changes were directed in Europe mainly by the orogenesis of the mountains of alpine type and by the changes in the localisation of seas. At the end of the Oligocene these two processes were already very far advanced and exercised a stimulative influence on plants which then changed many of their characteristics. This was the time of origin in Europe of many new taxa, of the rank of subfamilies and genera.

Among many others there developed at this time also the genus *Hartziella*, which as *H. Rosenkjaeri* was a very polymorphic taxon, representing obviously a vital and changeable complex of populations. We can accept as probable that its hypotetical tropical ancestor from Eocene lived in West Europe and from this evolved *Hartziella*. In Oligocene the geographical range of *Hartziella* was yet limited, and the populations of *H. Rosenkjaeri* could not therefore be great. This stands obviously in striking disproportion to the variability of this taxon in Oligocene, which was then rather rapid.

The next stadium in the evolution of the genus *Hartziella* was reached in Miocene. The transgressions of the Parathetys-seas covered at this time great territories of plains extending in the North of Carpathian- and Sudeten Mountains and further towards the North-East in the Russian plains. At this time the genus *Hartziella* obtained new territories for its expansion from West to East mostly along the North shores of the Parathetys sea, whose axis reached a length of about 6000 kilometres. The warm temperate (or subtropical) climate became then drier and drier with heavy torrential rains which influenced the spacious plains expanding along the seashores. These particular conditions created very favourable conditions for the hydrochoric fruits of *Hartziella* to occupy very large new territories. Consequently the *Hartziella* populations considerably enlarged their size in Miocene, but the rate of variability in this taxon became rather small. During this period the already existing morphological, anatomical, and ecological characteristics, which we have observed in *Hartziella miocaenica,* reached perfection.

The subfamily of *Parajussieueae* reached the final stage of evolution in Europe in Lower Pliocene through the *Hartziella vindobonensis,* whose possible senescence I have already described.

Whether the above indicated stages of evolution of the subfamily *Parajussieueae* agree with the process which took place in reality is a question which I will leave here unanswered. In any case there is a striking similarity between the above described stages of supposed evolution and the analogical stages of the evolution of animals emphasized by Simpson (1951, 1953), Heberer (1955) and others.

10. SUMMARY

In summing up the results of the research on the fruits of *Carpolithes Rosenkjaeri* Hartz, I have come to the following conclusions:

1. The affinity of *C. R.* with the genus *Toricellia* DC. does not exist.
2. The morphological characteristics and the anatomical structure of the investigated *C. R.* from all localities are basically the same.
3. The ecological peculiarities of *C. R.* are closely connected with the hydrochory of its fruits and with the xerochastic manner of the emergence of the seeds from the seedchamber.
4. It is accepted that the taxonomical position of the subfamily *Parajussieueae* within the family of *Onagraceae* is similar to the position of the subfamily of *Jussieueae*, but at the same time the new described subfamily is more primitive because it occupies in some characteristics an intermediate position between the families of *Onagraceae* and *Halorrhagidaceae.*
5. The evolutionary changes within the subfamily of *Parajussieueae* were strictly connected with the changes in climate during the Tertiary period in Europe.

Remark: After having sent the present paper to the printers I happened to come across an article by W. P. Nikitin on the climate and plant problems in Siberia in the epoch of the *Hipparion's* fauna (W. P. Nikitin: „K voprosu o klimatie i rastielnosti Sibiri v epochu Hippariona" in the book „Doklady Paleobotanitschnei Konferentsii", Tomsk 1962), including a list of the tertiary plants from a locality near Pavlodar on the river Irtish in West Siberia. Among other plants, the name of *„Hartzia Rosenkjaeri* Nikitin" is quoted presumably representing *Carpolithes Rosenkjaeri* Hartz.

According to the information imparted in a letter by P. I. Dorofeev from Leningrad, who kindly answered my question on this purpose, the name of the genus *„Hartzia"* to design *Carpolithes Rosenkjaeri* Hartz was introduced by P. A. Nikitin in a hitherto unpublished treatise on the aquitane flora in Tomsk. It is not known, whether P. A. Nikitin using the name *„Hartzia"* gave its description or diagnosis. According to the relation of P. I. Dorofeev, P. A. Nikitin's pupils (W. P. Nikitin and G. A. Bałujewa) use this name, but no Russian scientist determined the family to which *„Hartzia"* belongs. They accept the possibility of its relationship with the family *Cornaceae* or *Tiliaceae.*

In this situation, P. A. Nikitin's genus *„Hartzia"* [*Hartzia Rosenkjaeri* (Hartz) P. A. Nikitin] doubtlessly concerns *Carpolithes Rosenkjaeri* Hartz, but its meaning is rather symbolical (*nomen nudum).* In our conception it should be placed as a synonym of *Hartziella Rosenkjaeri* [= *Hartzia Rosenkjaeri* (Hartz) P. A. Nikitin *in litt.*].

The name „*Hartzia*" cannot be used in any case for *Carpolithes Rosenkjaeri*, because it was already applied by Harris (1935) in the description of a plant from the group *Ginkgophyta* found in the Rhaetic beds in East Greenland. (Comp. Index of Generic Names of fossil Plants, 1820—1950, Geological Survey Bull. 1013, Washington, 1955).

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STRESZCZENIE

W roku 1909 N. Hartz opisał osobliwe owoce kopalne z oligocenu w Kopenhadze, o nieznanym pokrewieństwie systematycznym, które nazwał *Carpolithes Rosenkjaeri* n. sp. Później *C. R.* został znaleziony w 16 innych miejscowościach w Europie oraz w zachodniej Syberii, których wykaz znajduje się na str. 5, zaś mapka ich rozmieszczenia na str. 4.

Opierając się zarówno na materiale owoców kopalnych z Kopenhagi (473 okazów), jak i na materiałach z Polski (razem 270 okazów) oraz na analogicznych owocach z pliocenu okolic Wiednia (ok. 200 okazów), autor zbadał ich właściwości morfologiczne i anatomiczne, celem udzielenia odpowiedzi na pytanie, jakie stanowisko w systemie naturalnym zajmuje zagadkowy *C. R.* Badania takie umożliwił dobry stan zachowania owocków — niezależnie od wieku osadów sięgających od oligocenu po górny pliocen.

Wyniki własnych badań autora poprzedzone zostały przedstawieniem zapatrywań innych paleobotaników, którzy wypowiedzieli swe przypuszczenia co do możliwego pokrewieństwa *C. R.* z dziś żyjącymi jednostkami taksonomicznymi. Odkrywca owocków *C. R.* Hartz (1909) wyraził zapatrywanie, że nie może wskazać żadnej takiej grupy roślin współcześnie żyjącej, do której by można włączyć *C. R.* Radzieccy paleobotanicy Nikitin i Dorofiejew (1935 i 1955—1960), dopatrywali się w cechach właściwych *C. R.* pewnego podobieństwa do podrodziny *Cornoideae*, w szczególności do rodzaju *Toricellia* DC. Podobne przypuszczenia o możliwości pokrewieństwa *C. R.* z rodziną *Cornaceae* wypowiedzieli: Chandler (1925), Berger (1952) i Kirchheimer (1957).

Przechodząc do wyników własnych badań (rozdział 3) autor zajął się następującymi cechami *C. R.*: 1^0 wymiarami i kształtem owocków (por. tabela 2—4 na str. 8 i 9), 2^0 skulpturą ich powierzchni, 3^0 budową anatomiczną epikarpu i perykarpu ze szczególnym uwzględnieniem budujących je tkanek, zwłaszcza wiązek sitowo-naczyniowych, położeniem i budową łożyska w komorach słupka i budową nasienia. Badania te wykazały, że istnieje szereg ważnych cech morfologicznych i anatomicznych, które albo nie były dotychczas zupełnie zauważone u *C. R.*, albo też były znane tylko bardzo niedokładnie.

W osobnym rozdziale (5) wykazał autor, że opisane przez niego cechy morfologiczno-anatomiczne, charakterystyczne dla kopalnych owoców *C. R.*, mają charakter cech przystosowawczych, pozostających w związku z rozsiewaniem owoców przez wodę (hydrochoria) oraz z wydobywaniem się nasion z komór nasiennych w drodze tzw. kserochazji, tzn. usuwania nasion z owocu na początku okresu suszy, przy użyciu klapy, otwierającej komorę nasienną. Obydwu ekologicznym cechom owoców (tj. hydrochorii i kserochazji) poświęcił autor wiele uwagi, przedstawiając je na szerszym tle porównawczym. W szczególności wykazał on, że mechanizm działania opisanych cech doskonalił się u *C. R.* stopniowo w procesie jednostronnie przystosowawczej ewolucji. Już w oligocenie wkroczył on wyraźnie na drogę wzmagającego się przystosowania do rozsiewania przez wodę i do kserochazji owocków, zaś w miocenie osiągnęły te cechy u *C. R.* największą, wybitnie jednostronną specjalizację, która przyczyniła się zapewne do wymarcia *C. R.* w czasie, gdy w dolnym pliocenie charakter klimatu i rozkład mórz uległy w Europie zasadniczym zmianom.

W rozdziale 6 zajął się autor dokładnie porównaniem cech *C. R.* z cechami charakterystycznymi dla owoców rodzaju *Toricellia* DC. Z badań tych wynikło jasno, że *C. R.* nie ma żadnych istotnych cech wspólnych z tym rodzajem, który — zdaniem autora — nie należy do rodziny *Cornaceae*, lecz do rodziny *Araliaceae*, zgodnie z zapatrywaniem odkrywcy rodzaju *Toricellia*, A. P. De Candolle (1828—1830).

W rozdziale 7 autor zajął się tezą wysuniętą przez Chandler (1926), że z *C. R.* spokrewniony jest górno-eoceński *Carpolithes* sp. 4. Po ponownym zbadaniu tego owocu kopalnego przez Chandler (1961) i zmianie jego nazwy na *Cornus quadrilocularis* Chandler 1961, należy przyjąć, że te oligoceńskie owoce nie mają nic wspólnego z *Carpolithes Rosenkjaeri.*

W rozdziale 8 przeszedł autor do zagadnienia ustalenia pozycji taksonomicznej kompleksu kopalnych owocków opisywanych pod nazwą *Carpolithes Rosenkjaeri.* Po dokładnym porównaniu *C. R.* z dziś żyjącymi rodzinami, doszedł on do wniosku, że *C. R.* zbliża się swymi cechami do dwu rodzin z rzędu *Myrtiflorae (Myrtales)*, a mianowicie do *Halorrhagidaceae* i do *Onagraceae*. Obydwie te rodziny, dziś jeszcze sąsiadujące ze sobą w systemie naturalnym, były w okresie trzeciorzędu jeszcze bliżej ze sobą zespolone, a kopalne taksony opisane jako *C. R.* należą bez wątpienia do pierwotnej grupy, jednoczącej w sobie w pewnym stopniu cechy charakterystyczne dla obydwu, dziś oddzielonych od siebie, rodzin. Biorąc pod uwagę właściwości anatomiczne *C. R.*, zwłaszcza obecność w kanale osiowym owocu tkanki korkowej oraz właściwości łożyska, autor doszedł do wniosku, że *C. R.* — choć wykazuje bez wątpienia pewne cechy wspólne z rodziną *Halorrhagidaceae* — należy zaliczyć do rodziny *Onagraceae*. W obrębie tej wielkiej i starej rodziny, należy — zdaniem autora — postawić kompleks form opisanych jako *C. R.* w pobliżu podrodziny *Jussieueae*, jako jedną z równolegle rozwijających się jej gałęzi (zapewne z wspólnych przodków).

Przechodząc do ustalenia rang taksonomicznych populacji form opisanych z trzeciorzędu pod nazwą *C. R.*, autor wypowiedział się za przyznaniem im rangi osobnego rodzaju w obrębie nowej podrodziny *Para-Jussieueae.*

W końcowym rozdziale 9 przedstawił autor swoje zapatrywania na przypuszczalny przebieg procesu ewolucji, jakiemu uległ kompleks trzeciorzędowych populacji *Carpolithes Rosenkjaeri* w czasie od oligocenu po górny pliocen.

Nowy rodzaj nazwał autor *Hartziella* n. gen. i wydzielił w nim trzy gatunki: *H. Rosenkjaeri* n. comb. (= *C. Rosenkjaeri* Hartz s. str.), *H. miocaenica* n. sp. (= *C. Rosenkjaeri* auct. div.) i *H. vindoboniensis* n. sp. (= *C. Rosenkjaeri* Berger 1952).

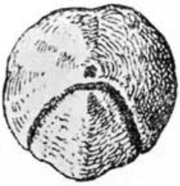
Plate I

1— 7. *Carpolithes Rosenkjaeri* Hartz. Original pictures from N. Hartz: Bidrag till Danmarks tertiaere og diluviale Flora, København 1909.
Fruits seen: 1 — from above; 2 — from beneath; 3 — from the side with valve; 4 and 5 — from above with two valves; 6 — fruit in cross-section; 7 — inside of seedchamber.
8—10. C. *Rosenkjaeri* from Copenhagen (Oligocen).
8 — fruit seen from above; × 13.
9 — the same from beneath; × 13.
10 — the same from the side with valve; × 13.
11 and 12. C. *Rosenkjaeri* from Gliwice Stare (Miocene)
11 — fruit seen from above; × 13.
12 — from beneath; × 13.
13. Pear-shaped fruit from Rypin (Miocene); × 13.
14. Fruit from Gliwice Stare with spongy epicarp well preserved; × 13.
15. Fruit from Copenhagen with two valvate seedchambers; × 13.

Tablica I

1— 7. *Carpolithes Rosenkjaeri* Hartz. Oryginalne rysunki z dzieła N. Hartza: Bidrag till Danmarks tertiaere og diluviale Flora, København 1909.
Owoce widziane: 1 — z góry; 2 — z dołu; 3 — z boku od strony klapy; 4 i 5 — z góry, z dwoma klapami; 6 — owoc w przekroju poprzecznym; 7 — wnętrze komory nasiennej.
8—10. C. *Rosenkjaeri* z Kopenhagi (oligocen).
8 — owoc widziany z góry; × 13.
9 — ten sam owoc z dołu; × 13.
10 — ten sam owoc od strony klapy; × 13.
11 i 12. C. *Rosenkjaeri* z Gliwic Starych (miocen).
11 — owoc widziany z góry; × 13.
12 — z dołu; × 13.
13. Owoc z Rypina (miocen) kształtu gruszkowatego; × 13.
14. Owoc z Gliwic Starych z dobrze zachowanym gąbczastym epikarpem; × 13.
15. Owoc z Kopenhagi z dwoma komorami nasiennymi opatrzonymi klapami; × 13.

Plate I
Tablica I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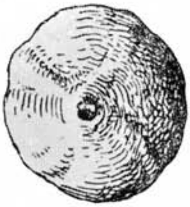
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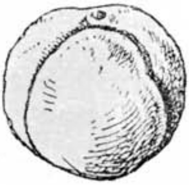
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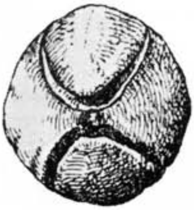
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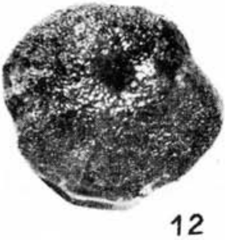
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W. Szafer 1963

Plate II

1— 5. *Carpolithes Rosenkjaeri* from Gliwice Stare (Miocene).

1 — Fruit seen from above with sessile stigma well preserved; × 13.

2 — seedchamber from inside with protruding basal part of placental aperture and radiantly arranged pearl-like sculpture; × 13.

3 — seedchamber from inside with placental aperture laying in depression; × 13.

4 — cross-section of 3-chambered fruit, a little deformed by compression: above, on the left side protruding placenta with some abortive ovulae, beneath one part of seedchamber with characteristic sculpture; the axial-canal flattened; × 13.

5 — cross-section with axial-canal well preserved, the vascular bundles arranged around it; × 13.

6 and 7. C. *Rosenkjaeri* from Rypin (Miocene); × 13; the fruit seen from above and beneath.

8—11. C. *Rosenkjaeri* from Vienna (Lower Pliocene).

8 — inside of seedchamber with subapical placental aperture; × 13.

9 — side-view of fruit with short peduncle; × 13.

10. — the same seen from beneath; × 13.

11. — the same fruit seen from above with sessile stigma without valve; × 13.

Tablica II

1— 5. *Carpolithes Rosenkjaeri* z Gliwic Starych (miocen).

1 — Owoc widziany z góry z siedzącą, dobrze zachowaną, guzikowatą szyjką słupka; × 13.

2 — komora nasienna od zewnątrz ze smoczkowato wystającą podstawą otworu łożyskowego i z promieniście ułożonymi perełkowatymi wypukłościami epidermy; × 13.

3 — komora nasienna od wewnątrz z wgłębionym otworem łożyskowym; × 13.

4 — przekrój poprzeczny owocu trójkomorowego, nieco zniekształconego przez zgniecenie; z lewej strony wystające łożysko z szczątkowymi zalążkami, poniżej część komory nasiennej z charakterystyczną perełkową rzeźbą; w środku spłaszczony kanał osiowy; × 13.

5 — przekrój poprzeczny z dobrze zachowanym kanałem osiowym oraz wiązkami ułożonymi wokół niego; × 13.

6— 7. C. *Rosenkjaeri* z Rypina (miocen) — owoc widziany z góry i z dołu; × 13.

8—11. C. *Rosenkjaeri* z Wiednia.

8 — wnętrze komory nasiennej z otworem łożyskowym umieszczonym podszczytowo; × 13.

9 — owoc z krótką szypułką; × 13.

10 — to samo z dołu; × 13.

11 — ten sam owoc widziany z góry, z siedzącą szyjką, bez klapy; × 13.

Plate II
Tablica II


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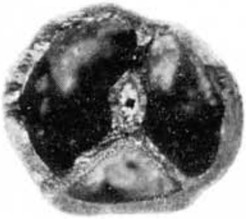
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W. *Szafer 1963*

Plate III

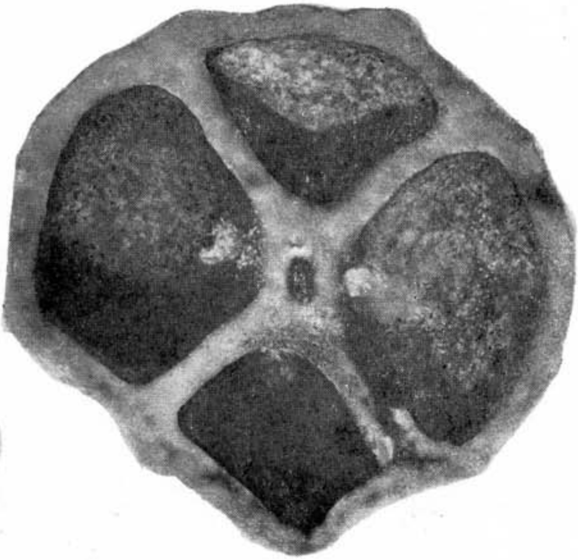
1 and 2. *Carpolithes Rosenkjaeri* from Copenhagen (Oligocene).
1 — four-chambered fruit with the protruding placenta in both sterile chambers; × 13.
2 — the same; × 35.
3—6. C. *Rosenkjaeri* from Gliwice Stare (Miocene); three-chamber-fruits with the seedchamber located beneath; inside it a whitish membrane is seen; × 13.
7. C. *Rosenkjaeri* from Vienna (Pliocene); subapical aperture of the placenta in axial part of seedchamber; × 64.

Tablica III

1 i 2. *Carpolithes Rosenkjaeri* z Kopenhagi (oligocen).
1 — czterokomorowy owoc z wystającymi, kołnierzykowatymi łożyskami w dwóch płonnych komorach; × 13.
2 — to samo; × 35.
3—6. C. *Rosenkjaeri* z Gliwic (miocen); trójkomorowe owoce z komorą nasienną umieszczoną u dołu; wewnątrz komory nasiennej widoczna jest biaława błona; × 13.
7. C. *Rosenkjaeri* z Wiednia (pliocen); subapikalnie położony otwór łożyskowy w komorze nasiennej; × 64.

Plate III
Tablica III


1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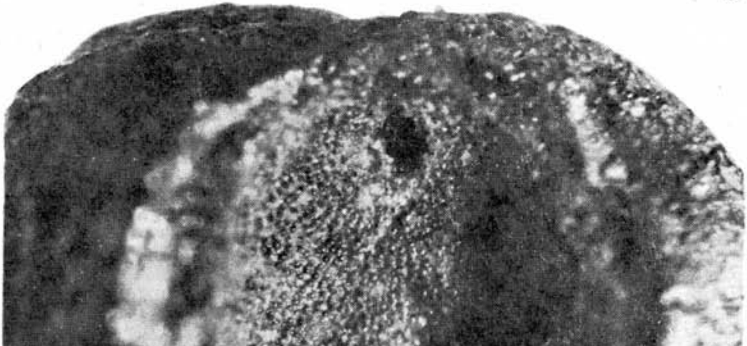

W. Szafer 1963

Plate IV

1 and 2, 5 and 6. *Carpolithes Rosenkjaeri* from Vienna (Pliocene).

1 — cross-section of fruitchambers; the surface of pericarp is tuberculate; × 22.

2 — the parenchyma-tissue in the upper part of pericarp; m — mebrane of the seedchamber; × 22.

5 — cross-section of a funneled type of placentation in the seedchamber, with remains of vascular tissue in the central canal; × 22.

5a — the same magnified; × 60.

6 — in the central canal one part of the cork-tissue is visible; × 22.

3 and 4, 7 and 8. C. *Rosenkjaeri* from Gliwice Stare (Miocene).

3 and 4 — fruit in longitudinal section; both epicarp and pericarp well visible; at the basis the parenchym thick; in the central canal remains of vascular bundles; × 22.

7 and 8 — in two sterile chambers are located placental protrudings filled with cork-tissue; 7 — × 22; 8 — × 50.

Tablica IV

1 i 2, 5 i 6. *Carpolithes Rosenkjaeri* z Wiednia (pliocen).

1 — przekrój poprzeczny owocu; powierzchnia perykarpu jest guzkowata; × 22.

2 — tkanka parenchymatyczna w górnej części perykarpu; m — część śluzowatej błony; × 22.

5 — przekrój poprzeczny przez owoc, widać lejkowaty typ łożyska w komorze nasiennej ze szczątkami tkanki naczyniowej w kanale centralnym; × 22.

5a — to samo × 60.

6 — w kanale centralnym widoczna jest część tkanki korkowej; × 22.

3 i 4, 7 i 8. C. *Rosenkjaeri* z Gliwic (miocen).

3 i 4 — owoc w przekroju podłużnym; widoczny epikarp i perykarp; u nasady parenchyma, w kanale centralnym szczątki wiązek naczyniowych; × 22.

7 i 8 — w dwóch płonnych komorach znajdują się wystające łożyska typu kołnierzykowatego, wypełnione tkanką korkową; 7 — × 22; 8 — × 50.

Plate IV
Tablica IV


1

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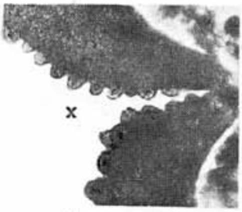
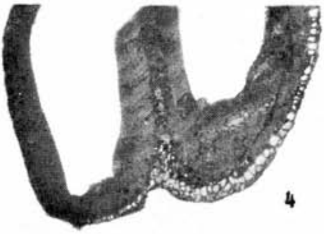
3



5a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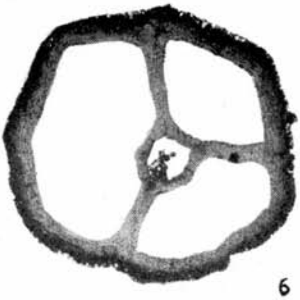
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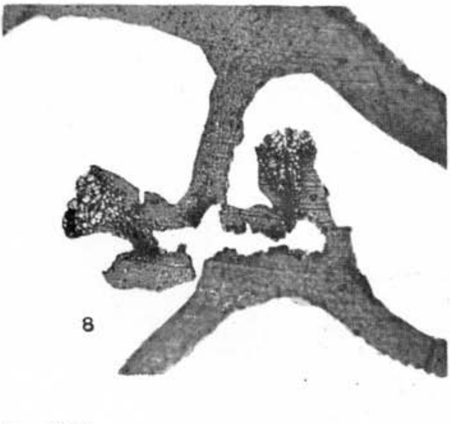
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7

W. Szafer 1963

Plate V

1 — 3. *Carpolithes Rosenkjaeri* from Copenhagen (Oligocene).
   1 — Fruit with two valves seen from above; at the apex the flattened stigma; × 60.
   2 — difference in sculpture of the wall of the seedchamber (left) and of the sterile chamber × 50.
   3 — suberized tissue in central canal; × 15.

4. C. *Rosenkjaeri* from Gliwice Stare (Miocene) — three-chambered fruit. Left: the sterile chamber with the wall composed of two parts the contact of which is indicated by *x*; in the central canal the remains of cork-tissue, beneath in the seedchamber is visible a part of the slime membrane; × 15.
5. Cross-section of fruit of the recent *Toricellia tiliaefolia* Oliv.; on the right side is well visible the contact of epicarp and pericarp; in the axial part central canal is lacking; × 15.

6 and 7. Cross-sections of the fruits of *Halorrhagis prostrata* Forst. × 15.

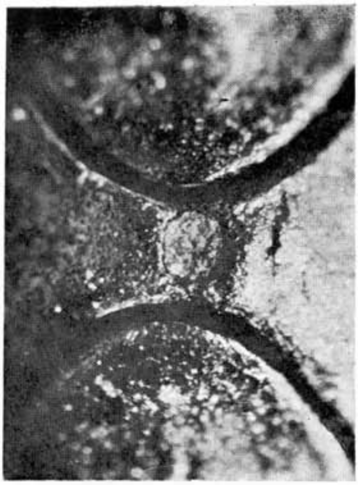
Tablica V

1 — 3. *Carpolithes Rosenkjaeri* z Kopenhagi (oligocen).
   1 — Owoc z dwoma klapami widziany z góry; na szczycie guzikowata szyjka znamię?); × 15.
   2 — różnica w rzeźbie epidermy komory nasiennej (z lewej strony) i komory płonnej; × 50.
   3 — pochwa korkowa w kanale centralnym; × 15.

4. C. *Rosenkjaeri* z Gliwic Starych (miocen) owoc trójkomorowy; z lewej strony płonna komora ze ścianą złożoną z dwóch owocolistków, miejsce zetknięcia się ich jest zaznaczone literą *x*; w kanale centralnym szczątki tkanki korkowej, u dołu w komorze nasiennej widoczna jest część śluzowatej błony (m); × 15.
5. Przekrój poprzeczny owocu współczesnej *Toricellia tiliaefolia* Oliv.; z prawej strony dobrze widoczne zetknięcie się epikarpu i perykarpu; w części osiowej nie ma kanału centralnego; × 15.

6 i 7. Przekrój poprzeczny owoców *Halorrhagis prostrata* Forst; × 15.

Plate V
Tablica V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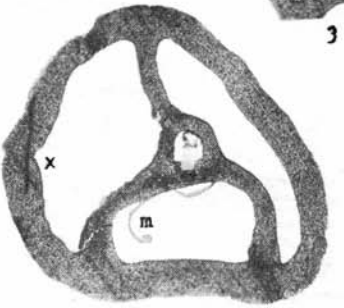

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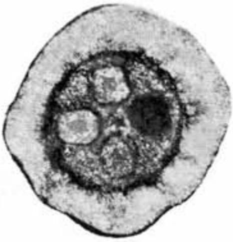
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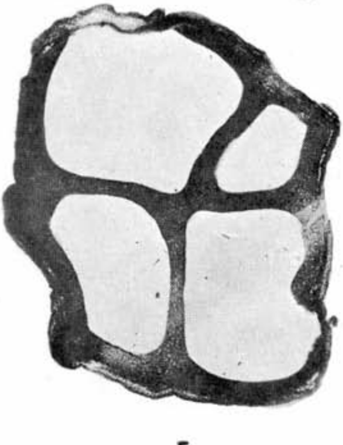
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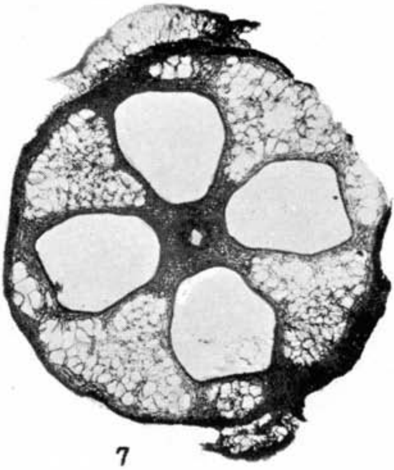
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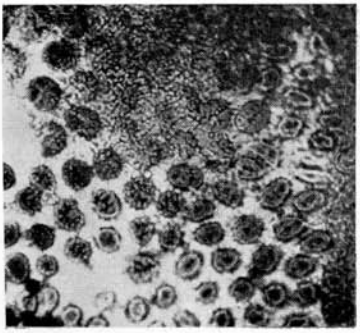
Plate VI

1a. Fragment of a seedchamber of *Carpolithes Rosenkjaeri* from Vienna seen from above; characteristic pearl-like cells are covered with a wrinkled membrane of dried slime; × 135.
1b — the same in an optical cross-section; × 135.
2. Cross-section through the wall of a seedchamber of C. *Rosenkjaeri* from Copenhagen with pearl-like cells; × 135.
3. Cross-section through the wall between the seedchamber and sterile chamber of C. *Rosenkjaeri* from Gliwice Stare; beneath are visible remains of the spongy epicarp; × 90.
4. Wall of a seedchamber of C. *Rosenkjaeri* from Copenhagen with partly detached dried out slime membrane covering the pearl-like cells; × 175.
5a and 5b. Similar fragments magnified × 350.

Tablica VI

1a. Fragment komory płodnej *Carpolithes Rosenkjaeri* z Wiednia widziany z góry; charakterystyczne komórki perełkowe są pokryte pomarszczoną błoną zeschniętego śluzu; × 135.
1b — ten sam fragment widziany w przekroju optycznym; × 135.
2. Przekrój przez ścianę komory płodnej C. *Rosenkjaeri* z Kopenhagi z perełkowatymi komórkami; × 135.
3. Przekrój przez przegrodę między komorą płonną i płodną C. *Rosenkjaeri* z Gliwic Starych; u dołu szczątki gąbczastego epikarpu; × 90.
4. Ściana komory płodnej C. *Rosenkjaeri* z Kopenhagi z odrywającą się błoną śluzową, pokrywającą komórki perełkowe; × 175.
5a i 5b — analogiczne fragmenty powiększone × 350.

Plate VI
Tablica VI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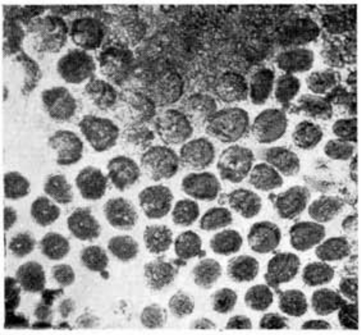
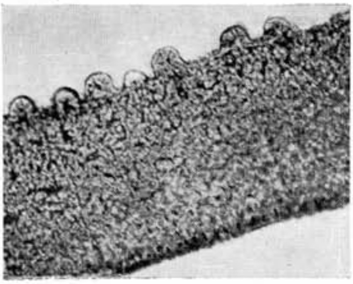

1b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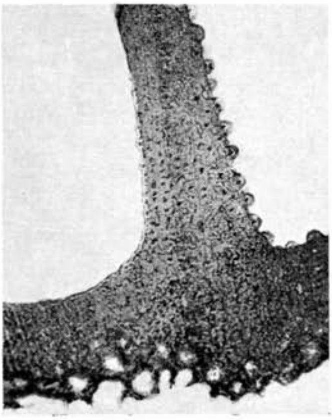
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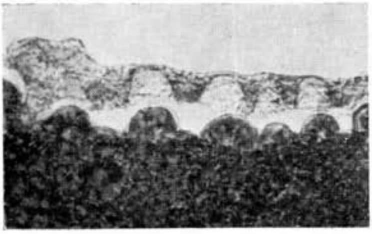
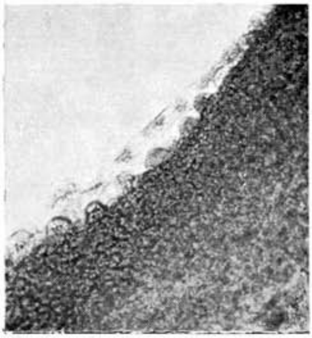
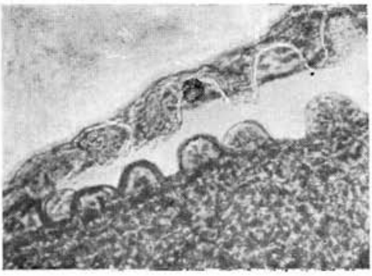

5a

4



5b

W. Szafer 1963