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Typification of Papaver radicatum — a Nomenclatural Detective Story

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Although species and other categories of biota doubtless are realities in nature, it may be claimed that concepts of species and their delimitation are unstable abstractions altering with different stages of knowledge. As information grows regarding each taxon, particularly its heritable variations, notions of its place in the hierarchy of the living world inevitably change. These shifting concepts will sometimes necessitate division or amalgamation of taxa, but such requirements must not be allowed to disrupt continuity and stability in scientific nomenclature. Not only must every taxon bear a single correct name, but also this name must be permanently attached to the taxon in the original sense, as shown by the material studied by the author. To ensure such a continuity in a world of inexact or changing concepts, botanical legislators have invented the process of typification which controls the application of names of all plants.

A typified botanical name is a designation attached to a definite specimen or element or to a representation of such an element (Lanjouw & alii, 1961). It is the only real safeguard against confusion when changing concepts or increased knowledge command the alteration of a taxon or the re-definition of its limits; even a detailed diagnosis may fail to distinguish between essential variations because the author felt they were of little significance, but the type remains as an unchanging point of reference to the core of the original concept of the taxon.

The ideal condition is created when the author deliberately appoints a single element to typify his taxon and refers to this application in its first publication. This is required by the Code as of 1958. The value of the type method is, however, greatly hampered by the fact that it is a comparatively recent invention. It developed during the first half of the twentieth century, but before the end of the last century botanists rarely designated what we would regard as types for their new names. A few indicated several elements, often in the form of herbarium sheets or at least by mentioning definite localities for their taxa. In such cases, the selection of one of these elements as a lectotype is a relatively simple procedure under the guidance of the Code.

Although the author may not have designated any material as typical of his taxon, a lectotype may be selected from among whatever is still available of specimens that were used, or at least seen, by him when compiling his diagnosis, provided that the essential characters of the specimen chosen do not contradict the original description. A drawing or a picture of the taxon may also be selected as lectotype, provided, naturally, that it can be exactly identified; while, on the other hand, a good herbarium specimen, even of more recent origin, is to be preferred as neotype. When no material known to the author is available, and no picture drawn or approved by him is present, and when the description is inconclusive, then the choice of type must be guided by traditional and current usage. The application of many names rests firmly on tradition and other indirect evidence, and their typification on less certain grounds is unnecessary and directly confusing.

When types must be selected because of division of old taxa, strict adherance to the rules of typification is the best available safeguard against confusion, but these rules are not always easy to apply retroactively. Frequently the author deliberately phrased his description in such a way that it could embrace heterogeneous material of wide distribution, and he may have referred to this material in indefinite terms. Drawings following a description may be inconclusive because of lack of artistic skill, and they may, also intentionally, have been based on several specimens from different sources, and thus be abstractions of the wide concept of the author. Lack of accurate information of the geographical origin of specimens is a frequent disturbance. When such doubts are inevitable, it is especially important that the guidance of Article 8 of the International Code be followed:

> "The author who first designates a lectotype or a neotype must be followed, but his choice is superseded if the holotype, or, in the case of a neotype, any of the original material is rediscovered, or if it can be shown that the choice was based upon a misinterpretation of the original description."

If this advice of the Code is ignored, confusion cannot be avoided.

Although Linnaeus and his contemporaries tried to follow a species concept that is still valid even from biosystematic points of view (cf. Löve, 1962), many species described by them have since been found to be collective taxa which had to be divided into several species and races. As a rule the typification of most of these species is not difficult, so that the retention of the original name for one of the segregates is simple and easy. In a few cases, however, difficulties have arisen making the selection of a type an extremely delicate procedure, in which all available evidence must be taken into consideration. If the conclusions reached from such studies are challenged without very strong evidence, permanent confusion arises, the original name is victimized and it must be abandoned as a "nomen confusum", in accordance with Article 69 of the Code which states that:

> "A name must be rejected if it is used in different senses and so has become a long-persisting source of error."

The name that is involved in the study reported below seems to be dangerously close to this condition, from which it could only be saved by discovery of its holotype.

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1. The problem

In the genus *Papaver,* there is a group of taxa the taxonomy of which has been increasingly clarified by the aid of modern methods, at the same time as the confusion in its nomenclature has been proportionally aggravated. It is now evident that a taxon originally regarded as a single and widely spread species is, in fact, composed of several good species in the truly Linnaean and biosystematic sense (cf. Löve, 1962 a), each of which includes taxa at various lower levels. The difficulties in naming these species have, however, recently reached the stage where the original name risks rejection because of an unnecessary confusion. This is only in part caused by changes in species concepts. It is mainly due to a misinterpretation and misunderstanding of the intentions of the original author, and by a general ignorance of the fact that material unmistakably designated in the original publication as the type, even in the modern meaning of the term, is still available. The taxon is *Papaver radicatum,* which was described by Rottböll (1770) in a paper about plants from Greenland and Iceland.

It seems reasonably safe to conclude from the morphological and chorological observations of Nordhagen (1931) and Löve (1955), from the cytological studies by Ljungdahl (1922, 1924), Horn (1938), Flovik (1940), Fabergé (1942, 1944), Nygren (in Löve & Löve, 1948), Löve & Löve (1948, 1956, 1961, and unpubl.), Löve (1955, 1962 b, and unpubl.), Jörgensen, Sörensen & Westergard (1958), and Knaben (1958, 1959 a, b), that the taxon long regarded as the species *Papaver radicatum* from Greenland, Iceland, the Faeroes, and Scandinavia, consists in fact of several species. The North Atlantic complex of this group is composed of taxa with chromosome numbers 2n=56, 70 and 84, four of which are good species whereas the others are to be classified as only subspecies and varieties.

There is no doubt of the correct name and typification of one of the 70-chromosome species, *P. Dahlianum* Nordh., since it was described by Nordhagen (1931) on the basis of material from northern Norway. It is met with in arctic Norway, Spitsbergen, northern Greenland, and parts of the Canadian Arctic Archipelago, but was unknown to Rottböll (1770), though he mentioned Spitsbergen plants seen by others.

The difficulty arises in the naming of two other species of the North Atlantic complex: another 70-chromosome species from Iceland, the Faeroes and Scandinavia, morphologically and geographically distinct from *P. Dahlianum,* and a 56-chromosome taxon from Greenland and northern Scandinavia. Both of these were apparently included by Rottböll (l.c.) in his *P. radicatum,* and the problem is reduced to the question of whether his species, as originally described, is typified by Norwegian and Icelandic or by Greenland material.

This is the central problem, leaving for later consideration the several other species described from within the Atlantic area by Nordhagen (1931) and Löve (1955) and proved by Knaben (1959 a, b) to be better classed as intraspecific to these major species, as well as the 84-chromosome taxon from northern Greenland (Knaben, 1959 a), and other species from arctic North America, the Rocky Mountains, and northern Russia and Siberia described by D. Löve & Freedman (1956), Knaben (1959 a), and Tolmatchev (1923, 1927, 1930 a, b, 1931 a, b, 1932, 1953, 1954, 1958, 1960), respectively.

2. Discovery and description

Our first evidence of the recognition of a species of the genus *Papaver* native to the North Atlantic region appears in Flora danica, which shows in its Tab. XLI a drawing of a plant that on p. 9 of the text is identified and described by Oeder (1761) as follows:

"Papaver erraticum nudicaule flore flavo odorato. Dill. Elth. 302, t. 224, f. 291.
Papaver erraticum luteo flore, capite oblongo hispido. Amm. ruth. 61, n. 81.
Papaver nudicaule, capsula hispida, scapo unifloro hispido, foliis simplicibus pinnato sinuatis. Linn. S.N.Sp. pl. 4. Hall. Goet. 88.
Steden: Paa et eneste Sted og det endnu kun gandske faa paa Dovrefjeld ved Kongsvold, i Begyndelsen af Vaarstigen, i Brinkerne paa den höire Side af Veien; blomstrer i Begyndelsen af Julii-Maaned."

The information in Danish is that the plant occurs only in one place and there sparsely, on Dovre Mountain at Kongsvold, on the slopes at the right of the entry to the springpath; and that it flowers at the beginning of the month of July.

Here, describing a Norwegian plant, Oeder identified it, first, with *P. nudicaule* L., a species clearly typified by Linnaeus (1753) as based on Siberian material cultivated in the Botanical Garden at Uppsala, and illustrated by Dillenius (1732); and, second, with the Siberian taxon referred to by Ammann (1739), which is probably more closely related to the Norwegian plant than to *P. nudicaule*. In the second edition of Species plantarum, Linnaeus (1763) indicated his acceptance of the identity of these two elements by adding a reference to Oeder following that to Dillenius, but he continued to consider *P. nudicaule* a Siberian plant: "Habitat in Sibiria".

A few years after the description and picture of the Norwegian plant had been published, material of a *Papaver* from Greenland and Iceland was studied by the Danish botanist Rottböll. The results were published by him in an "Afhandling om en Deel enten gandske nye eller vel forhen bekiendte, men dog for os rare Planter, som i Island og Grönland ere fundne, tillige med en kort Indledning om Urtelærens Tilstand i Dannemark. Læst i de sidste Sammenkomster Aar 1766, og de förste af 1767 af Christen Friis Rottböll." In a footnote the remark is made that the paper has been revised: "I Begyndelsen af 1770 efterseet, og hist og her med Tillæg forbedret", and these revisions seem to be only as footnotes. The paper was published in "Skrifter, som udi det Kiöbenhavnske Selskab af Lærdoms og Videnskabers Elskere ere fremlagte og oplæste i Aarene 1765, 1766, 1767, 1768, og 1769. Tiende Deel, Kiöbenhavn 1770."

This long paper, which covers the pages 393—462, first discusses Danish botany in general and then gives detailed descriptions of plants from Greenland and Iceland, collected by others but studied by the author, who never visited these countries. Rottböll had seen several collections from western and southern Greenland, but most of his plants from this country seem to have belonged to a Herbarium vivum assembled by Paul Egede from his collections in the colonies of Christianshaab and Godthaab in western Greenland in 1739. In § 19, on p. 419, he thanks Professor Egede for the loan of this herbarium and says that if he had not seen it he would probably never have published anything about Greenland plants. This indicates that although a substantial number of the plants he discussed were recent collections from Iceland, the main purpose of his paper was to describe the plants from western Greenland found in this herbarium. In § 22, on p. 424, Rottböll says that his studies are on plants collected between the 60th and 70th parallels; most of these are from Iceland, in part collected by "the learned Icelanders" (i.e. Eggert Ólafsson and Bjarni Pálsson), who studied the conditions in the country in 1752—57, and in part by König, who travelled in Iceland in 1764—65; fewer are from Greenland, and for these he thanks first Professor Egede, then the Greenland missionaries Sverdrup, Gill and Larsen, and finally Studiosus Chirurgiæ Brasen.

The description of *Papaver radicatum* is given in § 45, on pp. 453—455. Since the publication is rare, and because some of those discussing the description have distorted essential facts by selecting from them only sentences supporting preconceived ideas, it is appropriate to reprint the entire text translated into English:

> "In *Polyandria* Linn. I find two plants that have been sent to us, which, although they at first glance seem to be obvious, nevertheless on closer study have given cause for reflection and many doubts; the first one is a *Papaver,* on which the leaves are feathery divided, and the stem ends in one yellow flower; since this now has all characters of *Pap. Nudicaule* Linnæi; since it also has been identified with it by two famous botanists, namely Mr. von Linnæ and our Professor Öder, then it might be felt that I, without hesitation, could let it remain so; but this, for quite important reasons, I cannot do. When I was in Uppsala, I received a *Papaver* under the name of *Nudicaule,* which I have reason to believe is the correct species, since it is rather close to the picture by Dillenius; the same is very different from ours in the leaves, the height of the stem and in hairiness; but particularly in the flower, which when dried has become a dark- or brown-yellow[1] colour with a large black spot at the base of the petal; whereas ours, on the contrary, of which I have more than 100 dried [specimens], all become light-green or whitish yellow

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[1] Darker than the flower of *P. cambrium.*

with a bluish spot at the base of the flower, so that in this it resembles *Papaver Alpinum* more than that from Uppsala. Amman, who describes his Siberian *Papaver,* which I believe is the same as ours, also doubts greatly that his (plant) is identical with that of Dillenius, both for the thickness of the root (which in our [plant] is like long, round, fleshy cords) and also for the lack of a smell in the flower, which has given rise to the name by Dillenius; Our species is also not identical with *Pap. Alpino,* although the dry flowers are more like this than the flowers of *Pap. Nudicaulis;* because the leaves in ours, variable as they otherwise are in size, hairiness, the form of the lobes, their incision and distance, still all agree in that the long leafstalk ends above in a 7-lobed leaf (never more divided), very rarely only 5-lobed; they [the leaves] could therefore by no means be called doubly pinnate (*bipinnata*), and are also much coarser and hairier than those of *Pap. Alpino,* which I have seen flower in the garden of Professor Crantz in Vienna; and own also because of his kindness a very complete specimen, which I have closely compared with my plant, and found it as little agreeing with this as with his and Seguir's drawings. Hence, since I have before me 3 species of *Papaver,* which all agree in that they are single-flowered and with naked stems, but differ otherwise so much from each other, as species as a whole usually do; Therefore I have thought it most safe, to unite ours neither with *P. Nudicaule* nor *Alpino,* but make of it a new species under the name of *Pap. radicato,* which is placed between them both. It grows also in profusion in our mountains. Professor Öder has found it in Norway. From Iceland it has been brought by all botanists who travelled there. It is present in Professor Egede's Greenland Herbarium, and has also, in a variety of forms, been sent in large numbers from the same place by Mr. Sverdrup,[2] yes, I suppose further that it occurs in the Swiss and Pyrenean mountains, and it maybe that Hall. *Papav.* 3 in enum. stirp. Helvet., which he regarded as *Alp.* Linn., is this species. The objections which he raises are, against the figures as having represented it [the plant] with leaves much too small and wide spread; against the description of the leaf as being made up of small and narrow oaklike pieces terminating the leafstalk; and against the note on the spotting at the base of the dried petals. All these points raised his doubts, and if it is well grounded, it eliminates the apparent contradiction in the colour of the flower [as described by] him and Mr. Linnæ.[3] It is otherwise strange that this plant, which on our mountains occurs far and wide in such numbers, is still not found on the Lappish or Swedish [mountains]; Regarding the size of the stem and leaves it is very variable, since it reaches from one finger's to a span's length and more, which is shown in Fig. XXIV, Tab. VIII, to which I want to add the following description:

Papaver radicatum, radicibus longissimis carnosis. Foliis simplicibus ovatis, pinnato-sinuatis, scapis unifloris, capsulisque hispidis.

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[2] It it also likely to be the white poppy about which Martens speaks in his Spitzberg Reise pag. 41 in this way: "Mit Willen aber habe ich ausgelassen den weissen Mohn, davon wir viele Blumen auf unsere Hüte steckten etc. Die ganze Pflanze war nur einer Spanne lang."

[3] Mr. Haller has in his last edition of Flora Helvetica brought this, my assumption, to certainty; Nevertheless he still makes one species of both, and where, formerly, the description mainly fitted our *Papaver,* it now seems to agree more with *P. Alpino.*

Radix cylindrica, crassa, ramosa, ramis longissimis loreis carnosis.

Scapi plures *digitalis, palmares, spithamei,* suberecti, teretes, pilis russis patulis a subappressis hirsutissimi.

Folia ad radicem plura. *Intima* in squamas mutata, *cætera,* in perfectis pollicaria, circumscriptione ovata; pilis decumbentibus hirsutissima, sinuato-pinnatifida; Pinnis 3 communiter parium cum impari, ovatis vel ovato lanceolatis; inferiore pare longius remoto; ut plurimum integris, sæpe altero, rarius utroque latere incisis.

Petioli plani, hirsutissimi, foliis longiores; basi dilatati, membranacei, continua supereqvitatione sociis superimpositi.

Flos terminalis unicus.

Perianthium, 2 phyllum, caducum; Foliis oblongis, concavis, hirsutis, nigricantibus, l. brunneis.

Corolla Petala 4 subrotunda, glabra, integerrima, decidua, striis venosis, lineae ab apice distantia anastomosi junctis, insignata; in *exsiccatis* coloris pallide flavi cum macula cærulescenti ad basin.

Stamina. Filamenta plura, plana, linearia, germini breviora, lutea; at exsiccatione cærulescentia. Antheræ compressæ, oblongæ, utrinqve emarginatæ, luteæ.

Pistill. Germen magnum, oblongum, pilis rigidis, erectis, muricatum. *Stylus* O. *Stigma* peltatum, Radiis 6 rarius 8 divaricatis, linearibus nigris, rarissime albis, l. albis cum margine atro."

Rottböll depicted his new species as Fig. XXIV in his Table VIII, which is reproduced here as Fig. 1. In the legend he says, in translation: Fig. XXIV. *Papaver radicatum.* (a.) The root, (b.) The stems, (c.) The leaf stalks, (d.) The leaves, (e.) The sepals, (f.) The flower, (g.) A stamen with the anther (h.), (i.) The ovule, (k.) The stigma.

3. Attempts at typification

A. Preamble

Although Rottböll (1770) had clearly shown that his plant from Greenland and Iceland and Oeder's plant from southern Norway as well could not be conspecific with *P. nudicaule* or *P. alpinum,* few later authors accepted his conclusions. The name *P. radicatum* was most frequently used for Greenland populations, only once (Mohr, 1786) for an Icelandic plant, whereas authors discussing Norwegian populations consistently ignored it and designated their plants as *P. nudicaule.* The name proposed by Rottböll was, however, used for Norwegian plants by De Candolle (1824), but only as a variety of *P. nudicaule*; it is evident that the author had not seen the original description and was unfamiliar with the plant except perhaps from the picture in Flora danica. Elkan (1837), in his monographic treatment of the genus, also failed to realize the importance of the plant, since he listed it under *P. nudicaule* as a variety β *radicatum* of his subspecies A: *arcticum.*

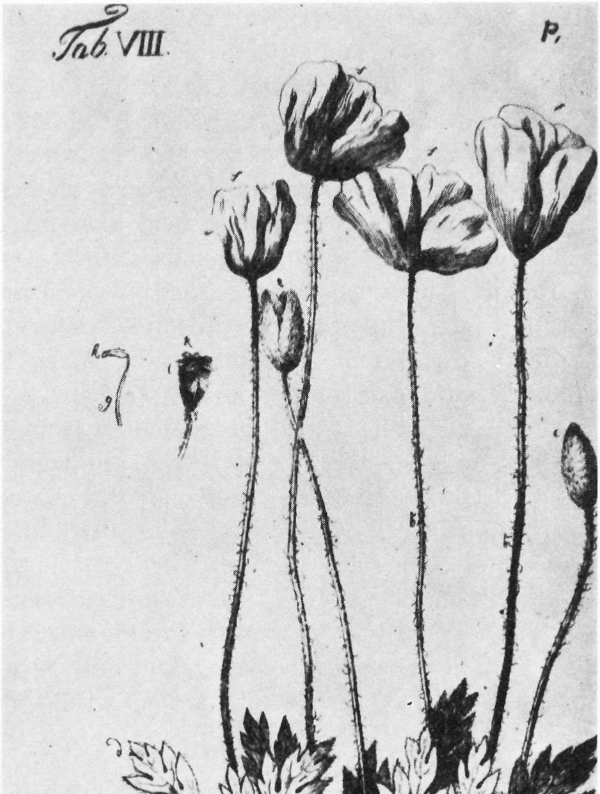


Fig. 1. *Papaver radicatum* Rottb. The picture of the plant in the original publication by Rottböll (1770). Explanations in the text.

It was Murbeck (1894) who rediscovered the significance of the species *P. radicatum* in the wide sense attributed to it by Rottböll himself. In connection with studies on hybrids between this taxon and *P. nudicaule* in the Bergian Botanical Garden in Stockholm, Murbeck pointed out: "Die arktische, durch doppelt niedrigere, bis 20 cm. lange mehr abstehend und wie die Blätter reichlicher behaarte Blütenstiele, durch spitzere Blattzipfel, bedeutend kleinere, bis 28 mm. lange, vornehmlich aber viel schmälere, schwefelgelbe (selten weisse) nach der Befruchtung meist noch als welk sitzen bleibende Petalen und kürzere, die Länge der breiter eiförmigen Kapsel meist nicht erreichende Staubblätter ausgezeichnete Art hat unter solchen Umständen den Namen *Papaver radicatum* Rottböll zu führen."

Almost all authors mentioning plants from Greenland, Iceland, the Faeroes and Scandinavia after the publication of Murbeck's paper followed his interpretation, and soon *P. radicatum* was regarded as an arctic-alpine species with circumpolar distribution. In fact, Fedde (1909) was almost alone in continuing to treat it as only a subspecies of *P. nudicaule.* The name *P. radicatum* was used almost exclusively in all treatments of the floras of the arctic and subarctic regions from the beginning of the present century, and only exceptionally was the name *P. nudicaule* also used for populations within the area.

B. Typification by Lundström

The work by Murbeck (1894) on the *Papaver* in the Botanical Garden in Stockholm was continued by Lundström (1914), who was of the opinion that Rottböll (1770) must have had the population from Dovre in mind when he described his species. Later, Lundström (1923) described several subspecies of *P. radicatum* and also of *P. nudicaule* from Scandinavia, Iceland, Greenland and Siberia, at the same time as he made a re-description of both species.

In connection with his re-description, Lundström (1923) had somehow acquired the misconception that *P. radicatum* must be the plant from southern Norway, which he consequently named f. *typicum.* For the purpose of typification he found the original description to be so indecisive in essential characters that it could also be used for *P. nudicaule* in the sense Lundström put into that species. As to the picture, he claims in a footnote on p. 405: "Die Figur in Rottböll'schen Abhandlung (Tab. VIII, fig. XXIV) zeigt kein *radicatum* von Formenkreis *typicum* (mihi), sondern wahrscheinlich eine grönländische oder isländische Pflanze (der Titel der Abhandlung angiebt ja das Pflanzenmaterial als aus Island und Grönland stammend). Die Kapsel ist ± trichterförmig und nackt (ohne daranhaftende, welke Blumenblätter!), der Stengel ist dünn — also eine nicht allzu characteristische *radicatum*-Pflanze. Man beobachte, dass Rottböll in seiner Original-Diagnose die Blüte u.a. mit folgenden Worten kennzeichnet: petala . . . decidua . . . (also abfallend so wie bei der Subsp. *færoënse* (mihi!))."

Since Lundström (1923) found the description of little use for the typification of the plant, he searched the Copenhagen Herbarium for the more than 100 specimens Rottböll (1770) claimed to possess. Only a single sheet designated "Herb. Rottböll" could be discovered, without any other information. Although the specimen was without fruit, Lundström ventured the opinion that "das Exemplar ist jedoch typisch *radicatum,* dem Habitus nach zu urteilen auf der Dovre-Kette gefunden", and this assumption was regarded as a further support for the selection of the Dovre race as the typical race of *P. radicatum.* This race, or f. *typicum* Lundstr., was reported to occur in the Dovre Mountains and in some north Scandinavian localities, whereas other Norwegian populations were classified as *P. nudicaule* ssp. *relictum* Lundstr., or *P. nudicaule*×*radicatum.* Icelandic plants were classified either as *P. radicatum* ssp. *færoënse* Lundstr. or *P. radicatum* f. *typicum* with its subf. *islandicum* Lundstr., or as the hybrid *P. nudicaule*×*radicatum,* and one collection was even named *P. radicatum*×*rubroaurantiacum,* though both the last-mentioned hybrids with some doubt. Greenland populations were classified as *P. radicatum* ssp. *occidentale* Lundstr., and *P. nudicaule*×*radicatum.*

Everyone must agree with Lundström on the inconclusiveness of the description by Rottböll, and the discordance between it and the picture of the plant. As will be seen later, Knaben (1958) disagrees with him on the identity of the plant from the Rottböll herbarium, though both identify it with different populations with similarly dogmatic arguments. As a matter of fact, the specimen cannot be identified by means of ordinary methods with any degree of certainty except perhaps as belonging to Icelandic *or* South Norwegian populations. The main point in this connection is, however, the fact that the selection of the Dovre taxon as the type for *P. radicatum* on the basis of this specimen must be rejected not only because the herbarium material cannot be properly identified, but also for the simple reason that there is nothing that indicates that it could not have been acquired by Rottböll after his description of the new species was published. Above all, however, such a typification must be rejected because it directly contradicts the scanty information in the original paper itself: Rottböll's original material of the plants described in his paper came from Greenland or Iceland and not from Norway; this is perhaps nowhere as clear as in his description and discussion of just this species.

C. Studies by Tolmatchev

Although Lundström (1923) studied material from widely different regions in the boreal-arctic zone, his conclusions must be judged in the light of an understanding of the inherent limitations of his approach, for his method was that of morphological examination alone, the material available was still inadequate, and its classification was badly hampered by the lack of a correlation of geographical information.

However, the year Lundström published his data, another approach to the problem of *P. radicatum* was initiated, and it soon resulted in a greatly improved and much increased understanding of the evolutionary history and relationships of these critical taxa. This new approach was based on the morphological-chorological method of Wettstein (1898). It was Tolmatchev (1923) who was the first to apply it to the problems of *Papaver,* and thus the first to express clear views on the evolutionary significance of the variations of this group.

In his first paper on the genus, Tolmatchev (1923) demonstrated, on the basis of material available in Petrograd, that *P. nudicaule* does not grow wild in Europe, and thereupon classified all the European populations so named earlier as *P. radicatum.* Since he did not agree with the preliminary typification by Lundström (1914), he described the Dovre race as the new ssp. *ovatilobum* Tolm., called a race from Russian Lappland ssp. *lapponicum* Tolm., another from Vaigatch and arctic northeastern Russia ssp. *jugoricum* Tolm., and classified the circumpolar arctic taxon as a collective ssp. *polare* Tolm. In a later paper, Tolmatchev (1927) reported the results of more detailed studies on material from Scandinavian herbaria. Then he joined issue with Lundström (1923) on several points, particularly the taxonomical significance of certain characters used by the latter as a major indication of specific distinctness. Most of the material classified by Lundström as f. *typicum* Tolmatchev still regarded as ssp. *ovatilobum,* in which he also included the race the former had named ssp. *færoënse* from the Faeroes and Iceland. Tolmatchev also transferred the ssp. *relictum* Lundstr. to *P. radicatum* and regarded it as a race of the same distinctness as ssp. *ovatilobum.* North Scandinavian populations not grouped with the last-mentioned race but regarded by Lundström as the hybrid *P. nudicaule*×*radicatum,* were identified by Tolmatchev with *P. radicatum* ssp. *polare.* His ssp. *lapponicum* included Lundström's ssp. *kvænangense,* in part, as well as some of the putative hybrids reported by Lundström, while collections from northernmost Norway, determined with doubt as the hybrid *P. nudicaule*×*radicatum* by Lundström, were given the new name of ssp. *brachyphyllum.* Tolmatchev maintained that these four subspecies could embrace all the material of *P. radicatum* from Scandinavia.

Tolmatchev (1930 a) later added some observations about the arctic *Papaver,* and has since (1930 b, 1931 a, b, 1932, 1953, 1958, 1960) made great efforts to clarify the relationships within and between Siberian taxa, mainly belonging to the *P. nudicaule* group but also related to ssp. *lapponicum*. Though of great importance to the understanding of the group as a whole, these studies are of lesser interest for the present problem. Tolmatchev (1927) rejected the typification by Lundström (1923) but he himself never explicitly typified the species described by Rottböll (1770). It may, however, perhaps be inferred from his inclusion of the Icelandic and Faeroeic populations in the same subspecies as the southern Norwegian taxon, that he was under the impression that the Rottböll specimens must have been from Greenland.

D. Typification by Nordhagen

Another great step towards a better understanding of the Scandinavian *P. radicatum* complex was taken through the detailed morphological-chorological studies by Nordhagen (1931). He distinguished four species in Scandinavia, i.e. *P. relictum* based on ssp. *relictum* of Lundström (1923), *P. lapponicum* based on ssp. *lapponicum* of Tolmatchev (1923), *P. Dahlianum,* which is ssp. *brachyphyllum* of Tolmatchev (1927), and *P. radicatum* with the three subspecies *dovrense* (=*ovatilobum* s.str.), *hyperboreum,* and *Læstadianum*. The last subspecies was later (Nordhagen, 1939) given specific rank on the basis of additional cytological evidence, and still later (Nordhagen, 1940) the ssp. *macrostigma* was added as a race of *P. radicatum*.

Although Nordhagen (1931) used the name *P. radicatum* for three of his Norwegian taxa, he was quite aware that none of the Norwegian races belong to the typical subspecies. As to the origin of the material described by Rottböll (1770), Nordhagen (1931, p. 4) stated: "Was nun die Art *Papaver radicatum* Rottb. betrifft, so geht aus der Abhandlung Rottböll's (1770) klar hervor, dass das Originalmaterial seiner neuen Art aus Grönland stammt. Durch Herbarstudien fand er aber, dass dieselbe auch in Island und Zentralnorwegen (Dovre) vertreten war. Die Blattform des von Rottböll abgebildeten Exemplars is indessen mit derjenigen der Dovrerasse nicht identisch; der Narbendiscus ist auch viel zu breit, und erinnert vielmehr an derjenigen gewisser nordskandinavischer Formen."

It is apparent that Nordhagen here typified *P. radicatum* with a Greenland taxon, closely related to some taxa from northern Norway, and selected as its type the picture in the paper by Rottböll (1770).

E. Typification by Hultén

In connection with his studies of the flora of Alaska and Yukon, Hultén (1945) also discussed the identity of the original material of *Papaver radicatum.* Though correctly stating that Rottböll "took the species in a very wide sense", Hultén erred in claiming that Nordhagen (1931) "considers that the Icelandic poppy should be regarded as *P. radicatum* proper, probably because Rottböll says that all collectors brought it from Iceland." In actual fact, Nordhagen, as related above, came to the same conclusion as Hultén, who expressed it as follows: "The Icelandic type, however, has an elliptical capsule and the capsule represented in Rottböll's plate is another type with flat stigmatic disc more closely akin to the Greenland type, which has a circumpolar distribution. It seems to me rational to take the plant figured in Rottböll's plate as the type of what he meant by *P. radicatum,* and I therefore regard the circumpolar plant common in Greenland as *P. radicatum.*" From Alaska and Yukon Hultén (l.c.) included in *P. radicatum* only ssp. *occidentale,* which he regarded as a high-arctic circumpolar race, a part of the ssp. *polare* s.lat. of Tolmatchev (1923, 1927); and this seems to be the plant he considered the type of the species in its strict sense.

F. Cytotaxonomical inferences

The first cytotaxonomical approach to the problem of the *Papaver radicatum* group was made by Horn (1938), who demonstrated that within the taxa of this complex the chromosome numbers 2n=28, 56, and 70 are met with. The number 2n=56 was found to be typical of *P. lapponicum* and *P. radicatum* ssp. *Læstadianum* from northern Norway, and also of *P. radicatum* from Greenland, whereas 2n=70 was reported from *P. Dahlianum* and *P. relictum* and also from races of *P. radicatum* from northern and southern Norway and the Faeroes. The last number had also been reported earlier from northern Sweden by Ljungdahl (1922, 1924). These results have since been confirmed on populations from Canada, Greenland, Iceland, the Faeroes, Spitsbergen, and different parts of Scandinavia and Siberia by various authors, and the numbers 2n=42 and 84 have been added from North America (cf. Knaben, 1959 a, b; Löve & Löve, 1961, and unpubl.).

Horn's chromosomal counts prompted Nordhagen (1939) to raise the taxon *Læstadianum* to the level of species. Although he must have realized that this conclusion, when linked with his earlier typification of *P. radicatum,* made necessary the choice of a new name for the 70-chromosome species in Norway, he avoided the issue and continued to refer to this taxon as "*P. radicatum* s.str."

During studies on the cytotaxonomy of the higher plants of Iceland, Löve (1955) made detailed observations on the variations of the *Papaver radicatum* group. It was confirmed that all Icelandic taxa of this group are characterized by the chromosome number 2n=70. Consequently, the evaluation of the taxonomical status of the taxa that could be distinguished within the Icelandic populations had to be based on the morphological-chorological method as used by Nordhagen (1931), since similarities in chromosome number and chromosome morphology do not necessarily indicate conspecificity. With the acceptance of the relative importance attributed by Nordhagen to certain morphological characters and their distribution, it was concluded that in this group in Iceland there are two taxa at the same level as the subspecies of *P. radicatum* described by Nordhagen from Norway, as well as two taxa at about the same level as his *P. relictum* in Norway. Accordingly, the two last-named taxa, from northwestern and southwestern Iceland respectively, were described as the species *P. Stefanssonianum* and *P. Steindorssonianum,* whereas the other two taxa were regarded as the ssp. *faeroeënse* and ssp. *islandicum* of the 70-chromosome species also represented in Norway by four subspecies distinguished by Nordhagen (1931, 1940).

Since Löve (1955) found no reason to challenge Nordhagen's and Hultén's typification of *P. radicatum* by the Greenland populations, he accepted it and pointed out, in connection with a discussion of the Rottböll description and picture of *P. radicatum*: "It is evident, however, from his picture of the new species, that his type material cannot have originated from Iceland or Norway (cf. Nordhagen, 1931; Hultén, 1945), since it is a plant with a small capsule, subcylindrical to oblong with a flat stigmatic disc the rays of which run almost to the middle of the capsule. The plant must have been from Greenland, and there is little doubt as to its identity with *P. radicatum* ssp. *occidentale* described by Lundström (1923) from Sabine Island and Pendulum Island in eastern Greenland, as well as with *P. nudicaule* ssp. *radicatum* γ *labradoricum* Fedde (1909), which is *P. radicatum* var. *labradoricum* (Fedde) Rousseau & Raymond (1952). This is the variable plant mentioned by Polunin (1940) from the Canadian Eastern Arctic, and it is correctly classified as *P. radicatum* s.str. It has yellow lactescence, and its chromosome number is 2n=56, determined by Horn (1938), Fabergé (1944) and Holmen (1952) and confirmed by the present writer on germinating seeds from northern Canada."

As a logical consequence of the typification of *P. radicatum* by the Greenland plant, and the demonstration that it differs not only morphologically and geographically but also cytologically from the Icelandic-Faeroeic-Scandinavian species with 70 chromosomes, the latter had been left without a name. This species was therefore described as *P. Nordhagenianum* with, as type subspecies, the somewhat variable ssp. *hyperboreum,* and, as a type specimen, a plant collected by H. Smith on the mountain Nissontjåkko in Torne Lappmark in Sweden, and kept in the Botanical Museum at Uppsala. The three other Scandinavian and one Icelandic-Faeroeic subspecies were then transferred to this new species, at the same time as one new Icelandic subspecies was described.

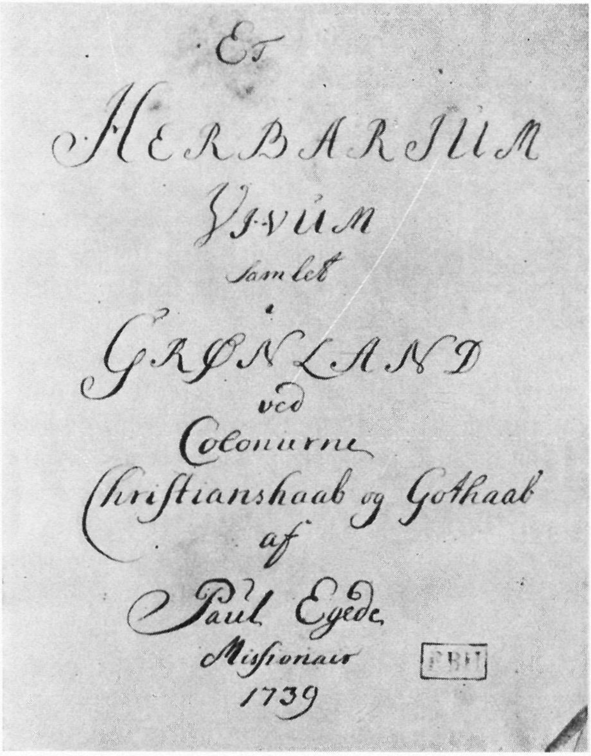
G. Knaben challenges the typification

In reporting her extensive experimental studies on the *Papaver radicatum* complex, Knaben (1958) challenged the typification of *P. radicatum* by a Greenland plant, because of differences in hairiness and form of leaves between the drawings by Rottböll (1770) and Lundström (1923) and the plants cultivated in Oslo. However, she ignored entirely the fact that the independent typifications by Nordhagen (1931) and Hultén (1945) were based on the characters of the flower and especially the gynoecium in the Rottböll picture. She agreed that the typification by Lundström (1923), based on a specimen marked as "Herb. Rottböll" in the Botanical Museum in Copenhagen, should be ignored, though her reasons for this are obscure and her conclusion that this specimen must be Icelandic, rather than Norwegian as supposed by Lundström, is only a guess as good as his. She pointed out that the diagnosis fits the Icelandic plant, and then claimed that it does not fit Greenland and Norwegian populations, a very doubtful conclusion, the consequences of which would be that the populations from Norway could not belong to the same species as those from Iceland. As a further support for her assumption that the plant in question must have come from Iceland, she noted that the next species described by Rottböll is explicitly Icelandic, and added: "Hvis den stammet fra Grönland, ville han ha angitt dette" (If it had originated from Greenland he would have pointed this out). Finally, there is certainly some confusion behind her statement that Rottböll's plants had flowered profusely in Copenhagen and so must have come from Iceland rather than from Greenland, since Rottböll nowhere even mentions that his *Papaver* had ever been cultivated there.

4. The solution and final typification

It is evident that when Knaben (1958) challenged the typification of *P. radicatum* by the Greenland plant she did not fulfil the requirements of the International Code for so serious an act. She criticized the identification of the picture as far as its leaves were concerned, but ignored the gynoecium, which was the main character used by Nordhagen (1931) and Hultén (1945); and it would be a great overstatement to claim that she had demonstrated "that the choice was based upon misinterpretation of the original description", as required by the Code. Her ill-supported claim that the only specimen available from the Rottböll herbarium must be from Iceland is of no importance, and she did not replace the type chosen by Nordhagen and Hultén with a better certified type. As long as other material is not detected on which the typification could be more securely based, it is, therefore, in concordance with the International Code to retain the first typification, or else drop the name *P. radicatum* as a "nomen confusum".

Since the publication of the challenge by Knaben, the present writer has made detailed investigations of the entire nomenclatural problem of this complex. He has studied the single specimen from the Rottböll herbarium mentioned by Lundström (1923) and Knaben (1958), and has come to the conclusion that it most likely belongs to the 70-chromosome species although its condition is such that it cannot be positively identified with either the Norwegian or the Icelandic races. He also agrees with Knaben that the leaf-form of the plant depicted by Rottböll is reminiscent of Icelandic plants, though it is also fairly similar to some of the Greenland specimens figured by Knaben (1959 a) from her own experiments. The taxonomically highly important stigmatic disc and gynoecium of the Rottböll picture are, however, without the slightest doubt those of the Greenland taxon. It may seem reasonable to suggest that Rottböll, in drawing his plant, idealized his species on the basis of specimens from both Greenland and Iceland, although this assumption cannot be verified. If this is the case, the use of this illustration for typification of the species could certainly be challenged. The Rottböll specimen of the 70-chromosome species might then be chosen as a lectotype or neotype, for its presence in his herbarium



Et
HERBARIUM
VIVUM
samlet
i
GRØNLAND
ved
Colonierne
Christianshaab og Gothaab
af
Paul Egede
Missionair
1739

Fig. 2. The title page of the Herbarium Vivum by Paul Egede.

might be taken as indication of his concept in spite of the strong possibility of its being a later addition to his collection.

However, the observation of one small detail makes the whole discussion superfluous. As in all good detective stories, Rottböll had already given the solution of the problem when he described his new species, though this has been overlooked by all but Nordhagen (1931). A careful reading of the Danish description of *P. radicatum* reveals that he had in fact typified the new species almost as precisely as do modern taxonomists who follow the advice of the International Code: "Den voxer ellers i Overflödighed paa vore Fjelde. Hr. Professor Öder har fundet den i Norge. Fra Island have alle did reiste Botanister bragt den. Den findes i Hr. Professor Egedes Grönlandske Herbario, og er sammesteds fra tillige med dens Afvigninger i Mængde nedsendt af Hr. Sverdrup." In translation this reads: "It grows also in profusion in our mountains (i.e. those of the Danish empire: Norway, Iceland, Greenland). Professor Öder has found it in Norway. From Iceland it

Fig. 3. Details of the holotype of *Papaver radicatum* Rottb.

has been brought by all botanists who travelled there. It is present in Professor Egede's Greenland Herbarium, and has also, in a variety of forms, been sent in large numbers from the same place by Mr. Sverdrup." Though most of this information tells only about the distribution of the specimens seen, the significant statement is that the plant described "is present in Professor Egede's Greenland Herbarium." This is the Herbarium Vivum that, according to Rottböll in the introduction to his paper, induced him to make the study of the plants he described, and there can be no doubt that this can be taken as a typification that follows strictly the requirements of the present International Code. Since the herbarium in question is conserved in the Botanical Museum in Copenhagen, the holotype of *P. radicatum* is still available (cf. our Fig. 2—3). Its rediscovery supersedes the use, as lectotype, of the controversial illustration in the Rottböll paper.

All the plants in the Egede herbarium were collected in 1739 in the colonies at Christianshaab and Godthaab in western Greenland, but no indication is given of which of these localities contributed the *Papaver*. From the fragmentary information on the distribution of the Greenland races given by Knaben (1959 a), and also from the data provided by Böcher, Holmen & Jakobsen (1957), it seems that the populations from both these places may belong to the ssp. *occidentale* as interpreted by Knaben (1959 a). The present writer regards it, thus, as reasonably safe to conclude that the specimen in the Egede herbarium represents the ssp. *occidentale* and, therefore, proposes that Christianshaab be regarded as its type locality. It follows that the name ssp. *occidentale* Lundstr., as employed by Knaben, will have to be regarded as synonymous with the typical ssp. *radicatum,* exactly as proposed by Hultén (1945). This is the race *b* in the flora by Böcher, Holmen & Jakobsen (1957), whereas their race *a* is ssp. *labradoricum* (Fedde) Fedde, and their race *c* the 84-chromosome species from northernmost Greenland seems to be identical with *P. cornwallisense* D. Löve (cf. D. Löve & Freedman, 1956). It is possible that further investigations may reveal that minor races of the typical subspecies from eastern and western Greenland are distinct enough to warrant their separation at the varietal level, in which case the name *occidentale* ought to be employed at that level for the East Greenland plant.

5. Taxonomical review

The circumpolar complex identified by Murbeck (1894) and later authors with the species *Papaver radicatum* has been found to include several species, some of which comprise some subspecies and varieties. Cytologically, these species are characterized by chromosome numbers ranging from the tetraploid number 2n=28 to the dodecaploid 2n=84. Only cytologically known taxa from the more Atlantic parts of North America and Eurasia are included in the present discussion, western American and eastern Asiatic species being ignored. For further references to the eastern Asiatic taxa, the treatment by Popov (1937) in the Flora SSSR as well as the numerous papers by Tolmatchev (1931 a, b, 1932, 1953, 1954, 1958, 1960) may be consulted, whereas information from western America is given in the recent publications by Hultén (1945), Porsild (1945, 1957), D. Löve & Freedman (1956), Moss (1959), and Knaben (1959 a). All these taxa ought to be studied as closely as the North Atlantic complex by aid of biosystematical methods, and the author would be grateful for seed material from any of them wherever collected.

The experimental investigations by Knaben (1959 a, b) on the Greenland-Iceland-Faeroes-Scandinavia populations, and similar unpublished studies by the present writer on material from Canada, the North Atlantic region, Russia and Siberia, clearly support the conclusion that, in the North Atlantic area, there are four distinct species belonging to the *radicatum* complex. Three of these species are composed of more or less distinct races. According to Knaben these races in two of the species are to be regarded as equivalent subspecies, though her evidence indicates that several of these ought to be classified only as varieties. One of these species is octoploid, with $2n=56$ chromosomes, two are decaploid, with $2n=70$, and one is dodecaploid, with $2n=84$ chromosomes.

The octoploid species was shown by Knaben to occur in Greenland, northern Canada, and northern Scandinavia, and the present writer can add races from Russia and Siberia; so it is truly circumpolar. As has been shown above, the correct name for this species is *Papaver radicatum* Rottb., and within our area seven of its many known subspecies occur and also four varieties of one of these races.

The decaploid taxa belong to two distinct species. One of these is the arctic *Papaver Dahlianum* Nordh. described by Nordhagen (1931); it includes at least two subspecies and three varieties (cf. Löve, 1955; Hadač, 1960), and its distribution area reaches from Spitsbergen and northern Scandinavia to northern Greenland and parts of the Canadian Arctic Archipelago. The other decaploid is a plant of the mountains in Iceland, the Faeroes, and southern as well as northern Scandinavia; it remained nameless until described as the species *Papaver Nordhagenianum* by Löve (1955). Its fourteen known intraspecific races seem to be best classified as five subspecies, three of which include three, four, and five varieties, respectively.

The dodecaploid taxon is a rare plant, described as *Papaver cornwallisense* by D. Löve (in D. Löve & Freedman, 1956). Its general distribution is insufficiently known, but it seems to be confined to high-arctic regions in North America, in northernmost Greenland and some islands of the Canadian Arctic Archipelago.

A nomenclatural summary of the species and races just mentioned is being published elsewhere (Löve, 1962 b). The delimitation of the categories in that summary follows the definitions given by Löve & Löve (1961).

Summary

The original material used by Rottböll (1770) when describing his new species *Papaver radicatum* has been re-discovered: the holotype is a plant in the Herbarium Vivum collected by Paul Egede in 1739, most likely at Christianshaab in western Greenland, and it is still kept in the Botanical Museum in Copenhagen. It belongs to the 56-chromosome circumpolar complex. The two 70-chromosome species of the group are, thus, correctly named *Papaver Dahlianum* and *Papaver Nordhagenianum,* whereas the 84-chromosome taxon from high-arctic America is to be named *Papaver cornwallisense.*

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Cytochimeras in Ribes

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Introduction

After colchicine treatment of germinating seeds and growing plants chromosome doublings very often take place. These doublings as a rule occur in a single cell and at first only that cell is affected. Tissue deriving from such a cell is found to be polyploid and plant organs from that tissue are different from the rest of the treated plant. Thus a plant subjected to colchicine treatment often comprises shoots with different chromosome numbers and then one has a sectorial chimera. As a rule, the polyploid tissue is slower in development than the diploid one, which usually becomes preponderant. Due to the different speed of development the plants easily revert to diploidy. A stable polyploid chromosome number is not secured until the next generation after sexual propagation. Colchicine treatment of growing points sometimes affects one layer of cells which becomes polyploid, while other tissues remain normal. In that case a type of periclinal chimera is developed. These periclinal chimeras are very often overlooked. Dermen (1960) described several cases of chimeras with different chromosome numbers in different tissues and he suggested the name cytochimeras. By studying the genus *Ribes* several chimeras were found, all as results from colchicine treatments.

Material and methods

Since 1940 a great material of the genus *Ribes* has been studied with crosses within as well as between different species. All spontaneous material has been found to have the diploid chromosome number 16. By investigation of 60 different species also Zielinski (1953) found only the diploid number 16. As no divergence has appeared, it is stated with great likelihood that no natural polyploids of *Ribes* occur.

By colchicine treatment a great number of polyploids have been developed both in pure species and in species hybrids, which is reported previously (Nilsson 1944, 1951 a and b).

Both sectorial and periclinal chimeras have appeared. From sectorial chimeras diploid and tetraploid cuttings have been taken and rooted. Periclinal chimeras have so far been obtained in two species hybrids, which repeatedly were treated by strong solutions of colchicine. These two hybrids are *Ribes nigrum*×*Ribes grossularia* and *Ribes grossularia*×*Ribes divaricatum*.

The cross *R. nigrum*×*R. grossularia* was made already in 1939 and the varieties were *Boskoop Giant* and *Early Sulphur*. The behaviour of the hybrid was previously described (Nilsson 1955). Vegetative propagation was made on a large scale in 1952 and during the following spring rooted cuttings were treated with colchicine in the concentration of 0.5 and 1.0 %. The common symptoms of polyploidy appeared. The development slowed down and the leaves were thickened. Many plantlets died but surviving ones showed leaves with coarser lobes, partly covering each other. In some cases leaves indicated symptoms of disease reminding of virus effect in *Ribes nigrum* (Nilsson 1944). By grafting and by renewed propagation of cuttings pure tetraploids were developed. These tetraploids were fertile and the progeny had the chromosome number 32.

The hybrid *R. grossularia*×*R. divaricatum* has already been described by Janczewski (1907). The senior author developed hybrids from similar crosses. In 1942 a cross was made between the gooseberry variety *Achilles* and a seedling of *R. divaricatum*. Altogether 11 fully fertile hybrid plants developed. The germinating seeds were treated with colchicine and several plants with polyploid characters were found. Among them two tetraploid plants were revealed. A new cross was made in 1948 and the gooseberry variety used was *British Hero*. Germinating seeds were treated with a strong solution of colchicine (0.5—1.0 %). Many seedlings died and the surviving ones were affected with stopped growth and shrinkled leaves.

Polyploidy can be recognized by morphological observations but these are not reliable. Changes in fertility often occur and are easily revealed in flowering plants. In most cases there is a change in length of stomata and by taking measurements of them a very good indication of polyploidy can be obtained. By studying the pollen grains changes in chromosome number can be detected due to the pollen grains generally being greater in polyploids than in diploids.

In the *Ribes* material measurements of stomata and pollen grains were made. After staining with aceto-carmine differences in pollen grain development are easily seen. In order to determine cytological differences microscopic investigations are necessary. Fixations were made according to different methods. As a rule root tips were fixed in Navashin-Karpechenko solution and stained with Crystal-violet. In recent years root tips were also prepared by squashing and staining in accordance with the method described by von Rosen (1949).

In order to determine chimeras of periclinal type young shoot tips were fixed in a solution of 6 p. isopropylalcohol, 3 p. propionic acid, 1 p. acetone, 1 p. dioxane, 1 p. petroleum ether (Newcomer 1953). After embedding in paraffin the shoot tips were cut to a thickness of 10 μ. For staining the Feulgen-technique was used, partly also Haidenhains hematoxylin. Fixations were made on a large scale in the spring of 1960, when buds were taken at an early stage. Somewhat later also Feulgen- and nigrosin squash slides were prepared. In those cases the young tips were pre-treated in 0.001 M solution of oxy-quinoline for three hours with the aim of getting chromosome contraction (Tjio & Levan, 1950).

Results

Ribes nigrum × *Ribes grossularia*

Morphological observations indicated that some plants apparently were sectorial chimeras, which could be detected in different ways. Tetraploid shoots were fertile, but diploids constantly were sterile. The progeny of fertile and presumed tetraploid shoots were found to have the chromosome number 32 in root tips. From observations some plants were assumed to be periclinal chimeras. In the material one plant (200-XXV) was stated to be different from both diploids and tetraploids. The stomata were smaller than in tetraploids. The fertility was comparable to that of tetraploids. By cytological studies it was found that different chromosome numbers occur in epidermis and in the subepidermal tissue. The cells and the nuclei are different in size as can be seen in figure 1. Smaller nuclei generally have a lower chromosome number and in this case there are 16 chromosomes in the cells of the epidermis and 32 in those of underlying tissue. The plant is a periclinal chimera composed of a diploid cell layer around the tetraploid.

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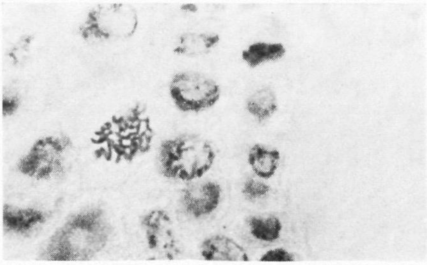

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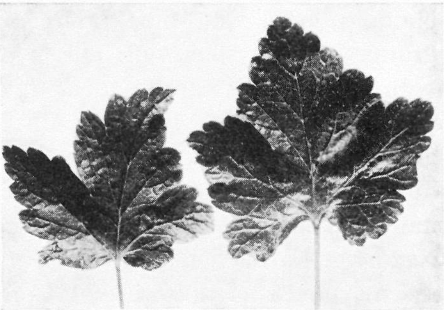

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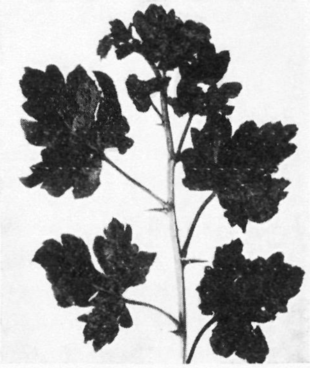

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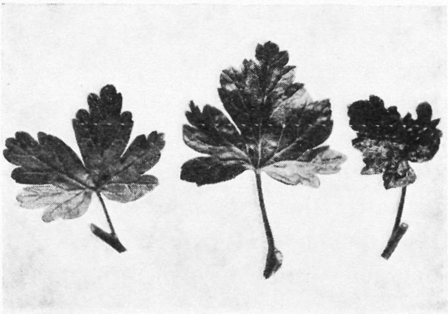

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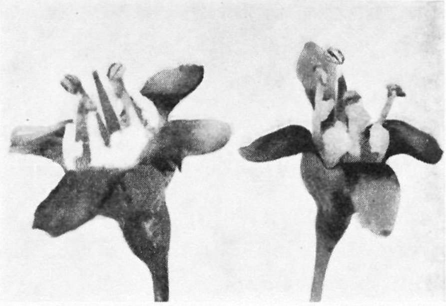

Fig. 1. Chimera of *Ribes nigrum*×*Ribes grossularia* no. 200-XXV. Transverse section of young leaf. Magn. 1500×. — Fig. 2. Leaves of *Ribes nigrum*×*Ribes grossularia*. Leaf at left diploid, at right tetraploid. — Fig. 3. Tetraploid *Ribes grossularia*×*Ribes divaricatum*. — Fig. 4. Leaves of diploid (left), tetraploid and cytochimera (right) of *Ribes grossularia*×*Ribes divaricatum*. — Fig. 5. Cytochimera (no. 575-25) with a lateral sport at right. — Fig. 6. Flowers of chimera no. 575-25. At left flower from a sporting shoot.

By vegetative propagation this condition is kept constant. Since the development of egg cells and pollen grains always originates from the subepidermal tissue, a chimera of this kind is fertile and gives rise to tetraploid progeny.

Ribes grossularia × *Ribes divaricatum*

After colchicine treatment seedlings of this hybrid showed a great variation in development. Apparently the colchicine had caused a change in chromosome number in whole plants or parts of them. Among the plants some were revealed as pure tetraploids and some as pure diploids but two plants could not be recognized as tetraploids although they certainly were greatly affected by the treatment. In a previous paper (Nilsson 1959) they were mentioned as presumed chimeras. The field numbers of these two plants were 575-25 and 575-32. They were somewhat dwarfy with retarded development, short internodes, thickened and shrinkled leaves, much smaller than those of normal sibs. They had certain characters in common but differed from another in growth. Plant no. 575-25 was very dwarfy and in 1961 it was only 90 cm high, while at the same time 575-32 reached the height of almost 2 m. Both plants showed very shrinkled leaves with a specific serration. In figure 4 the leaf type is seen in comparison with diploid and tetraploid sib plants. In spring and in autumn the leaves are purely green and healthy, but during the summer they often show necrosis, which is very similar to a damage by *Lygus* sp. These symptoms begin as small cracks, but develop into a russet appearance of the leaf surface. They seem to be caused by physiological disturbances. Similar necrosis due to sun scald appears in *Ribes grossularia* leaves in very hot summer days. The flowers were thick and short (figure 6). Plant number 575-32 so far did not show any variation in the shoots, while plant no. 575-25 on several occasions produced mutations. These mutations appeared as lateral shoots with bigger leaves, which also have a more normal shape. They resemble very much the leaves of tetraploid plants. Such mutations also occur on cuttings, particularly after cutting back the shoot tips.

In order to detect different stages of polyploidy stomata measurements were taken. Stomata of normal diploid plants had a value of 10.4, tetraploids 12.3 and the plants 575-25 and 575-32 had 22.1 and 18.0 respectively. These values indicate different chromosome numbers. After fixation and sectioning it was found, that the epidermis cells of these two plants were larger than those of underlying tissue. Also the nuclei had different size, which can be seen from figures 7 and 8. This is an indication of a chimeral condition, which was confirmed by counting the chromosomes. Tetraploid and diploid plants showed the same size of the nuclei in all cell layers.

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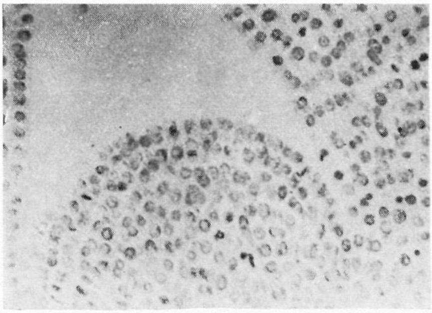

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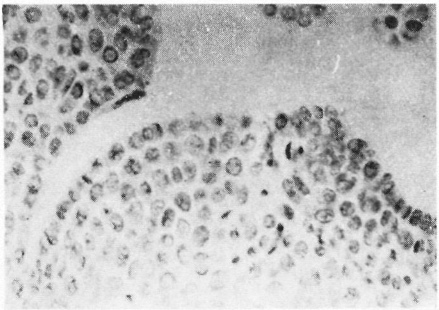

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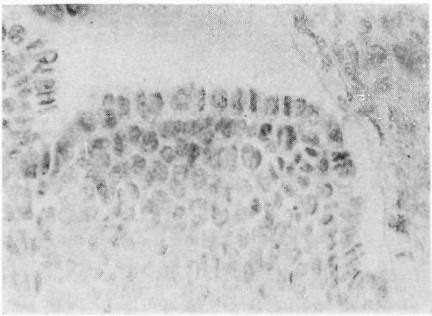

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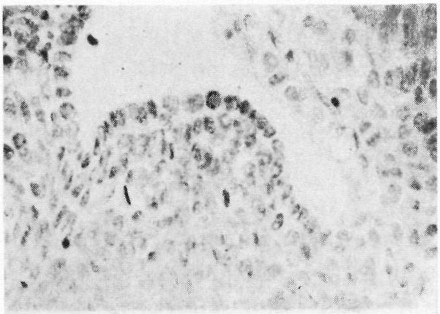
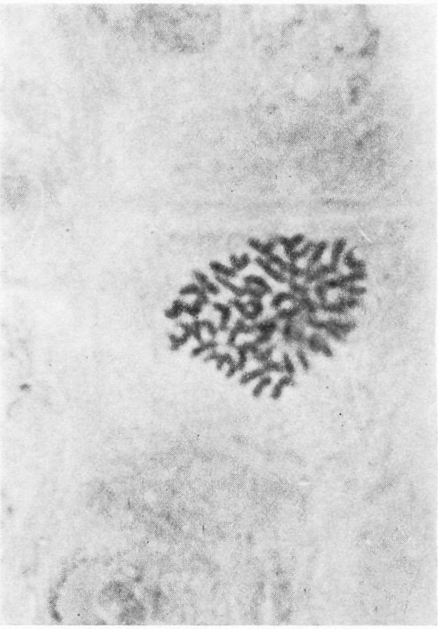


Fig. 7. Apex of diploid no. 575-8. Magn. 450×. — Fig. 8. Apex of tetraploid no. 575-23. Magn. 450×. — Fig. 9. Apex of chimera no. 575-25. Magn. 450×. — Fig. 10. Apex of chimera no. 575-32. Magn. 450×.

Plant 575-32 showed the chromosome number 46 in epidermis, while the inner tissue had the tetraploid number 32. A few seedlings from no. 575-32 were raised and these were found to be tetraploid.

Plant 575-25 also had the chromosome number 32 in the inner tissue, but in epidermis cells of different shoots varying chromosome numbers were counted. On the original plant the chromosome number of epidermis was found to be 64 but very often it was lower. As already mentioned this plant produces lateral shoots, which are called mutants due to different types of leaves and longer internodes. By studying the chromosome number in epidermis of these mutants a great variation was found. The chromosome number seems to be very unstable and many different numbers between the tetraploid and octoploid ones were counted. In some cells of one shoot the hexaploid number 48 was stated, but in many other shoots the chromosome number is not a multiple of 8. There was also found a correlation between chromosome number and type of leaf. In general the leaves become larger when the chromosome number is reduced towards 32. The most abnormal leaves with



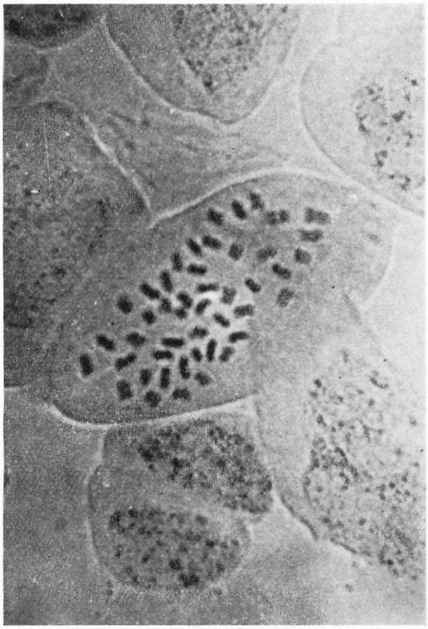


Fig. 11. Epidermis-cell of no. 575-25 with 64 chromosomes. Magn. 3000×. — Fig. 12. Feulgen leaf tip squash of no. 575-32. Cell with 46 chromosomes. Magn. 3000×.

very small, shrinkled and revoluted blades belonged to shoots with more chromosomes in epidermis cells (compare figure 13). The stomata were also smaller in epidermis of leaves with a lower chromosome number. As the chromosome number is greater in the original plant no. 575-25 and smaller in the mutants it can be assumed that the variation is due to a reduction.

Discussion

By colchicine treatment very often sectorial chimeras arise, from which polyploid and diploid shoots can be propagated. Also periclinal chimeras appear but are very often overlooked. Dermen (1960) described several cases of such chimeras. Also in *Ribes* some periclinal chimeras were studied. Very likely this type of chimeras occurs as often as the sectorial chimeras but it is not so easily distinguished. In the senior author's work with *Ribes* several polyploid types have been produced. On some occasions chimeras were presumed but not revealed. In this paper two certain periclinal chimeras are described. The one case is

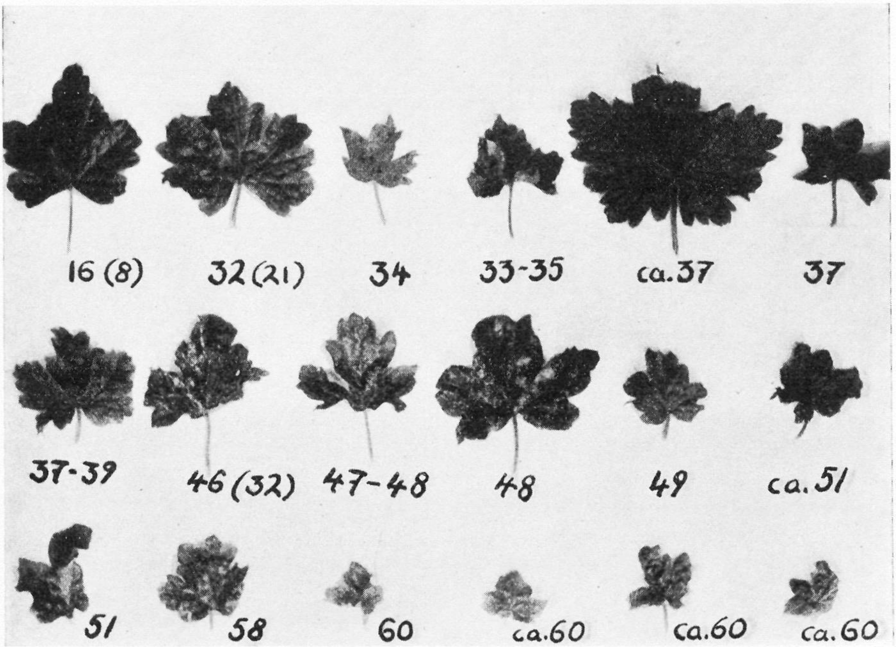


Fig. 13. Leaves from branches with different chromosome numbers. All leaves from no. 575-25 except three leaves with numbers in brackets.

a hybrid plant of *Ribes nigrum*×*Ribes grossularia* with diploid epidermis and tetraploid inner tissue. This plant was compared with sister plants of pure diploid and pure tetraploid type. The stomata were small as in diploids but the habitus was more like tetraploids. The flowers were fertile and gave rise to tetraploid progeny. In this case the colchicine treatment has resulted in a change of the chromosome number in a subepidermal cell from which the tetraploid tissue has developed. The epidermal cell layer has the unchanged diploid stage.

The other case of chimeras is more complicated. Among treated seedlings of *R. grossularia*×*R. divaricatum* tetraploid and diploid plants arose and besides two plants were found peculiar in habitus, leaf shape, size of stomata and so on. Being assumed to be chimeras the latter were studied thoroughly and the periclinal type of chimeras was detected. Both plants had tetraploid inner tissue and epidermis with a still higher chromosome number, the one with the stable chromosome number 46 and the other one with an unstable chromosome number varying between 32 and 64. From colchicine treatment doublings often occur and more than one doubling can take place.

In the periclinal chimera of *Ribes nigrum*×*Ribes grossularia* the epidermis was not affected but the inner tissue was doubled. The two chimeral plants of *Ribes grossularia*×*Ribes divaricatum* very likely arose by doubling twice of epidermis and by doubling once of the underlying tissues. The octoploid number 64 was detected in some epidermis cells and must have been the right number of the young seedlings. During the development changes have occurred visible as mutations with a varying chromosome number in epidermis. As the octoploid number apparently is non-optimal a reduction slowly takes place. In one case the chromosome number seems to be stabilized to 46 but in the other case it is still unstable and probably cuttings with different chromosome number in epidermis can be produced. Vaarama (1947, 1949) described variations in the chromosome number of tetraploid *Ribes nigrum*. Also in that case there was a reduction of the chromosome number explained by Vaarama as a mutagen effect of colchicine. The chromosome number was reduced from tetraploid to diploid in a pure species. In the present cases of chimeras there is a reduction from octoploidy to a lower level taking place by producing lateral shoots with different characters. In our opinion it is very likely that *Ribes* species have an optimal chromosome number. If this optimum is surpassed, the plants seem to have a possibility of reducing the chromosome number to a lower level. The reduced number is in no case lower than 32 which must be closer to optimum than 64. Haskell & Tun (1961) report a cytologically unstable *Rubus* hybrid, which originated as a seedling in F_2 from the cross of two tetraploid *Rubus* species, *R. craniensis*×*R. proserus*. The actual seedling was not subjected to colchicine treatment but showed a variation in chromosome number from 9 to 46, the most common number being the pentaploid 35. The study was limited to root tips, but it indicates a reduction or elimination of chromosomes. The cause of unstability was however not established. If the plant was a chimera or not was not investigated.

Summary

After colchicine treatment of *Ribes* seedlings chimeras of different types were found and reported. In *Ribes nigrum*×*Ribes grossularia* one cytochimera with diploid epidermis and tetraploid inner tissue was found. Among treated seedlings of *Ribes grossularia*×*Ribes divaricatum* besides tetraploids also two chimeras were found. One of these was tetraploid with an epidermis with 46 chromosomes, while the other

one was tetraploid and had an epidermis with chromosome numbers varying between 32 and 64. All evidence indicates that there is a reduction in chromosome number of epidermis. Very likely the chromosome number was doubled twice. As the octoploid number was unstable it was reduced resulting in mutations. There is a tendency of reduction towards the tetraploid number, but stabilization can also take place on a higher level. The conclusion is that the octoploid chromosome number is greater than optimum.

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Die spättertiären Fagus-Arten Europas

(With a summary in English)

Von HANS TRALAU

Naturhistoriska Riksmuseets paleobotaniska avdelning, Stockholm 50

Inhalt

1. Einleitung

Im Frühjahr 1961 hatte der Verfasser die Gelegenheit u.a. am Fundort der oberpliozänen Flora von Willershausen (Westdeutschland) fossile Pflanzen zu sammeln. Später hat Dr. Adolf Straus von Berlin-Dahlem, der seit über 30 Jahren an dieser Stelle gesammelt hat, das ganze bekannte *Fagus*-Material von Willershausen zur Bearbeitung zur Verfügung gestellt.

Früher publizierte Literatur über den Fundort findet sich unter Wegele (1914), Straus (1930, 1935, 1952, 1954, 1956) und Frantz (1961).

Die Durchsicht des fossilen *Fagus*-Materials von Willershausen ergab, dass die Blätter sich in zwei Gruppen teilen liessen, von denen die eine dem Formenkreis der nordamerikanischen Art *F. grandifolia*, die andere dem von *F. silvatica* und anderen nahestehenden Arten entsprach.

Im Folgenden soll nun der Versuch gemacht werden, die Beziehungen dieser spättertiären Blätter zu anderen europäischen, pliozänen und miozänen *Fagus*-Vorkommen zu beleuchten und ihr Verhältnis zu den rezenten Arten darzustellen. Hierbei wurde alle bekannte Literatur über tertiäre *Fagus*-Blätter in die Studie einbezogen und in die oben erwähnten Formengruppen unterteilt. Die unten folgenden Synonymlisten über die europäischen Vorkommen bringen daher in der ersten Abteilung Angaben, die nach Auffassung des gegenwärtigen Verfassers sicher erscheinen, in der zweiten Abteilung Angaben, die nicht durch Abbildungen verifiziert sind und in der dritten Abteilung Angaben, die mehr oder weniger sehr zweifelhaft sind. In diese Abteilung sind auch die intermediierenden Formen gestellt. Exemplare, die mit Sicherheit nicht zu den erwähnten Gruppen gehören, aber in der Literatur als solche angegeben sind, werden im Text dementiert.

Das in dieser Weise auf den Verbreitungskarten niedergelegte Resultat erscheint, wenn man dieses mit einer früheren Karte über die fossile Verbreitung von *Fagus* (Meusel 1953, S. 40) vergleicht, ausserordentlich mager. Die bis jetzt zweifelhaften und völlig unbewiesenen Vorkommen von *Fagus* in der Arktis u.a.m. fallen aus. Die grönländischen Vorkommen von „*Fagus*“ sind, falls es sich wirklich um *Fagus* handelt, viel älter als aus dem Miozän. Es ist aber zu hoffen, dass die hier publizierten Karten, auch wenn sie unromantisch und mager sind, ein einigermassen zuverlässiges Bild der Wirklichkeit geben.

II. Gruppe Fagus silvatica L.

Fagus silvatica. — Bianconi 1838, Tafel XII, Fig. 1; S. 443; Senigallia; Miozän

Fagus Deucalionis. — Unger 1847, Tafel XXVII, Fig. 6; S. 103; Putschirn; Unteres Miozän

Fagus sylvatica. — Gaudin & Strozzi 1858, Tafel VI, Fig. 6; S. 31; Val d'Arno; Pliozän

Fagus Chiericii. — Massalonga in Massalonga & Scarabelli 1858, Tafel XXXII, Fig. 5; S. 207; Senigallia; Miozän

Fagus Deucalionis. — Massalonga in Massalonga & Scarabelli 1858, Tafel XXX, Fig. 9; S. 203—204; Senigallia; Miozän

Fagus Gussonii. — Massalonga in Massalonga & Scarabelli 1858, Tafel XXV, Fig. 2, 5; S. 202—203; Senigallia; Miozän

Fagus Marsilii. — Massalonga in Massalonga & Scarabelli 1858, Tafel IX, Fig. 19; Tafel XXI, Fig. 18; S. 201—202; Senigallia; Miozän

Fagus sylvatica. — Gaudin & Strozzi 1859, Tafel I, Fig. 20; S. 20; Casciana; Pliozän

Fagus pliocenica ceretana. — Rèrolle 1884/85, Tafel V, Fig. 1—6; S. 258 ff; Cerdagne; Pliozän (Oberes Miozän?)

Fagus pliocenica. — de Saporta 1884, Tafel VI, Fig. 5; S. 88 ff; Cantal; Tertiär (Pliozän?)

Fagus intermedia. — Nathorst 1888, Tafel XI, Fig. 3—5; S. 29; Ushigatani, Tertiär (Pliozän?)

Fagus sylvatica. — Nathorst 1888, Tafel IX, Fig. 1—2; S. 33; Shiobara; Tertiär (Pliozän?)

Fagus japonica. — Nathorst 1888, Tafel IX, Fig. 3—8; S. 33; Shiobara; Tertiär (Pliozän?)

Fagus sylvatica. — Nathorst 1888, Tafel XII, Fig. 1—10; S. 37; Yokohama; Tertiär (Pliozän?)

Fagus silvatica. — Bouley 1892, Tafel III, Fig. 8; S. 57; Mont-Dore; Pliozän

Fagus pliocenica. — Krašan 1894, Tafel I; S. 45—48; Cantal; Pliozän

Fagus sinuata. — Peola 1896, Tafel III, Fig. 4; S. 146—147; Annone d'Asti; Pliozän

Fagus Antipofi. — Sordelli 1896, Tafel XVII, Fig. 2, Tafel XVIII, Fig. 11, S. 118 ff; Montescano; Miozän

Fagus Marsiglii. — Sordelli 1896, Tafel XVIII, Fig. 14; S. 120—121; Montescano; Miozän

Fagus silvatica. — Marty 1903, Tafel V, Fig. 9—16, S. 125; Joursac; Miozän

Fagus pliocenica. — Marty 1904, Tafel III, Fig. 4; S. 17; Capels; Miozän

Fagus pliocenica. — Laurent in Laurent & Marty 1904—1905, Fig. 15; S. 129—132; St. Vincent; Unteres Pliozän

Fagus pliocenica. — Marty 1905, Tafel II, Fig. 8—17; S. 116; Las Clausades; Pliozän

Fagus ferruginea miocenica. — Menzel 1906, Tafel III, Fig. 5; S. 48 ff; Senftenberg; Miozän

Fagus pliocaenica. — Engelhardt & Kinkelin 1908, Tafel XXIX, Fig. 7 a—w, Tafel XXX, Fig. 1 a—c, 2 a—c; Niederrad; Oberes Pliozän

Fagus silvatica var. *pliocenica.* — Laurent in Laurent & Marty 1908; S. 37; Niac; Pliozän

Fagus sp. — Lauby 1910, Tafel VIII, Fig. 4; S. 92; Sant-de-Jujieu; Tertiär (Miozän?)

Fagus orientalis fossilis. — Palibin 1915, Tafel II; Fig. 2, 3, 6; S. 34, 270; Kermal-Naftalan; Pliozän

Fagus pliocenica. — Depape 1922, Tafel VI, Fig. 1—5; S. 143—145; St. Marcel; Pliozän

Fagus silvatica fossilis. — Laurent & Marty 1923, Tafel XI, Fig. 1—6, 8; S. 35—37; Reuver; Pliozän

Fagus pliocenica. — Laurent & Marty 1927, Tafel III, Fig. 4; Tafel XVII, Fig. 3; S. 74; Cheylade; Pliozän

Fagus pliocenica. — Marty 1931, Tafel VII, Fig. 1, 2; Tafel IX, Fig. 11, 12; S. 184; Aubrac; Oberes Miozän

Fagus silvatica. — Weyland 1934; S. 54; Fischbach; Oberes Pliozän

Fagus orientalis. — Stefanoff & Jordanoff 1935, Fig. 37; Tafel VIII, Fig. 6, 7; Tafel IX, Fig. 2—5; S. 36—38; Sofia; Pliozän

Fagus cf. *silvatica.* — Straus 1935, Tafel XXXIII, Fig. 7; S. 182; Willershausen; Oberes Pliozän

Fagus pliocenica. — Marty in Bout & Marty 1936, Tafel III, Fig. 1, 2; S. 25; Perrier; Miozän

Fagus pliocenica. — Marty in Marty & Glangeaud 1936, Tafel B, Fig. 3; Tafel C, Fig. 1; S. 22; La Bourboule; Miozän

Fagus orientalis var. *fossilis.* — Kryshtofovitch 1937, Fig. 14; S. 161

Fagus decurrens. — Mädler 1939, Tafel VII, Fig. 28, 29; Abb. 24—26; S. 85—86; Frankfurt am Main; Pliozän

Fagus pliocaenica. — Berger 1952, Tafel I, Fig. 35; Tafel II, Fig. 33; S. 89; Brunn-Vösendorf; Unteres Pliozän

Fagus orientalis var. *fossilis.* — Pimenova 1954, Tafel IX, Fig. 3—5; S. 43—45; Amvrosijevka; Miozän

Fagus pliocaenica. — Berger 1955 b, Fig. 57—60; S. 91; Laaerberg; Unteres Pliozän

Fagus pliocenica. — Grangeon 1958, Tafel I, Fig. 5, 13; Tafel VII, Fig. 4—8; S. 71—75; Coiron; Oberes Miozän

Fagus aperta. — Andreánszky 1959, Tafel XXV, Fig. 5, Abb. 79; S. 95; Balaton; Miozän

Fagus latissima. — Andreánszky 1959, Tafel XXV, Fig. 7, Abb. 80; S. 96; Balaton; Miozän

Fagus oblonga. — Andreánszky 1959, Tafel XXV, Fig. 6; S. 95—96; Saly; Miozän

Fagus palaeojaponica. — Andreánszky 1959, Tafel XXV, Fig. 4; S. 96; Balaton; Miozän

Fagus pliocenica var. *ceretana.* — Carez 1908; S. 3085, 3155; Cerdagne; Miozän

Fagus dentata. — Principi 1908; S. 42; Senigallia; Miozän

Fagus palaeosilvatica. — Principi 1908; S. 42; Senigallia; Miozän

Fagus cfr. *silvatica.* — Stoller in Fliegel & Stoller 1913; S. 244; Beisselsgrube, Weilerswist; Pliozän

Fagus silvatica. — Straus 1930; S. 331; Willershausen; Oberes Pliozän

Fagus pliocenica. — Rey & Depape 1949; S. 76; St.-Flour; Mio-Pliozän

Fagus pliocenica. — Berger 1955 a; S. 75; Brunn-Vösendorf; Unteres Pliozän

Fagus cfr. *orientalis.* — Varga 1955; S. 39; Banfalvi; Miozän

Fagus cfr. *orientalis.* — Bócsa 1955; S. 59; Balaton; Miozän

Fagus orientalis. — Paschkov 1959; S. 658; Nordkaukasus; Unteres Pliozän

?*Fagus Deucalionis.* — Unger 1847, Tafel XXVII, Fig. 5; S. 103; Putschirn; Unteres Miozän

?*Alnites venosa.* — Massalonga 1854, Tafel IV, Fig. 2; S. 12; Senigallia; Miozän

?*Fagus sylvatica.* — Gaudin & Strozzi 1858, Tafel VI, Fig. 7; S. 31; Val d'Arno; Pliozän

?*Fagus ambigua.* — Massalonga in Massalonga & Scarabelli 1858; Tafel XXXVI, Fig. 1; S. 204—205; Senigallia; Miozän

?*Fagus betulifolia.* — Massalonga in Massalonga & Scarabelli 1858, Tafel XXX, Fig. 10; S. 206; Senigallia; Miozän

?*Fagus incerta.* — Massalonga in Massalonga & Scarabelli 1858, Tafel XXX, Fig. 3; S. 205—206; Senigallia; Miozän

?*Fagus sylvatica.* — Gaudin & Strozzi 1859; Tafel I, Fig. 19; S. 20; Galleraje; Pliozän

?*Rhamnus Eridani.* — Heer 1859, Tafel CXXVI, Fig. 1; S. 80; Teufen-Appenzell; Tertiär

?*Rhamnus deletus.* — Heer 1859, Tafel CXXIII, Fig. 19; S. 79; Eriz; Tertiär

?*Fagus Deucalionis.* — Sismonda 1865, Tafel XIII, Fig. 1—3; Tafel XIX, Fig. 1; S. 435; Guarène; Miozän

?*Fagus Antipofi.* — Nathorst 1888, Tafel V, Fig. 2—4; S. 16; Kita-Aiki; Tertiär (Pliozän?)

?*Fagus intermedia.* — Nathorst 1888, Tafel XI, Fig. 2; S. 29; Ushigatani; Tertiär (Pliozän?)

?*Fagus Antipofi.* — Sordelli 1896, Tafel XVII, Fig. 3—5, Tafel XVIII, Fig. 8—10; S. 118 ff; Montescano; Tertiär

?*Fagus ambigua.* — Sordelli 1896; S. 145; Annone d'Asti, S. Damiano d'Asti; Pliozän

?*Fagus ferruginea miocenica.* — Menzel 1906, Tafel VII, Fig. 4, 10; S. 48 ff; Senftenberg; Miozän

?*Fagus lanceolata.* — Principi 1908, Fig. 2, 3; S. 41—42; Senigallia; Miozän

?*Fagus pliocenica.* — Berger 1952, Tafel II, Fig. 34; S. 89; Brunn-Vösendorf; Unteres Pliozän

?*Fagus pliocenica.* — Teixeira 1952, Tafel VI, Fig. 7, 7 a; S. 56; Vale de Santarém; Pliozän

?*Fagus orientalis* var. *fossilis.* — Pimenova 1954, Tafel X, Fig. 1, 2; S. 43—45; Amvrosijevka; Miozän

?*Fagus* sp. — Pimenova 1954, Tafel X, Fig. 3, 4; Amvrosijevka; Miozän

?*Fagus pliocenica* var. *ceretana.* — Menendez Amor 1955, Tafel XXIV, Fig. 1, 2; 72—73; Cerdana; Pliozän

?*Fagus* cf. *orientalis.* — Cziffery 1955, Tafel VIII, Fig. 28; S. 27—28; Erdöbénye; Miozän

?*Fagus orientalis.* — Vörös 1955, Tafel XVII, Fig. 5; S. 66; Rózsaszentmárton; Miozän

?*Fagus Antipovii.* — Usnadse 1957, Tafel III, Fig. 3, Tafel IV, Fig. 5, 6, Tafel V, Fig. 2; S. 223; Nord-Priaral; Tertiär

Bearbeitetes Fossilmaterial von Willershausen: Geologisch-Paläontologisches Institut der Universität Göttingen: 2632 (=Tafel III, Fig. A), 2686 (=Tafel II, Fig. E), 3559 (=Tafel II, Fig. H), 3563 (=Tafel II, Fig. B), 5140 a (=Tafel III, Fig. E), 5923 a (=Tafel III, Fig. D), 5971 (=Tafel II, Fig. A), 6932 a (=Tafel III, Fig. B, C), 6940 a (=Tafel II, Fig. C), 8335 (=Tafel II, Fig. D), 9284 (=Tafel II, Fig. G), Tafel I ohne Nummer. Botanisches Museum, Berlin-Dahlem: 2130, 2234, 2273, 2282?, 2299, 2299 a, 2403, 2447, 2447 a, 2458, 2511, 2512, 2632?, 2641?, 2657, 2686 a, 2739, 2776, 2813, 3204, 3328, 3341, 3351, 3543, 3543 a, 3545 a, 3550, 3551, 3552, 3553, 3557?, 3558?, 3775, 3997, 4053, 4100 a?, 4113, 4144?, 4146?, 4297, 4302, 4427?, 4438, 4503, 4861, 4881, 4914 a, 4972, 4990, 5140, 5269, 5342, 5383?, 5684?, 5856, 5895, 5923, 5934, 5934 a, 5990, 6792, 6933 a, 6934?, 6936, 6939, 6941 a, 6942?, 6945?, 7215, 7215 a, 7339, 7438, 8126, 8270?, 8295, 8380, 8381?, 8383, 8404?, 8415?, 8498, 8517, 8573, 8613?, 8614, 8615, 8616, 8617, 8719, 8739 a, 8822, 8927, 8987, 8987 a, 9063, 9063 a, 9113, 9117, 9275, 9286, 9417, 9486?, 9935?, 9935 a?, 9936?, 9936 a?, 9937, 9947, 9949. Naturhistoriska Riksmuseets paleobotaniska avdelning, Stockholm: 3344, 8133, 8493, 8825?, 9607, 3/6: 1—5.

Neuzeitliche Vergleichsarten: *Fagus silvatica* L., *F. orientalis* Lipsky (=*F. Hohenackeriana* Palib.), (*F. taurica* Popl.=*F. silvatica*×*F. orientalis*), *F. asiatica* DC, *F. crenata* Blume (=*F. Sieboldii* Endl., *F. ferru-*

ginea Siebold), *F. japonica* Maxim., *F. engleriana* Seemen, *F. longipetiolata* Seemen (=*F. sinensis* Oliv.) u.a. nahestehende.

Die Verbreitung der neuzeitlichen Vergleichsarten ist bizentrisch, d.h. europäisch-vorderasiatisch und ostasiatisch.

In Europa ist *F. silvatica* von S England im Westen bis Mittelpolen im Osten verbreitet. Von S Skandinavien erstreckt sich die Verbreitung nach Süden bis N Spanien, Sizilien und dem mittleren Balkan.

Die Verbreitungsgrenze für spontanes Vorkommen von *F. silvatica* in England ist lange unklar gewesen. Viele Verfasser glaubten diese Grenze nach S Schottland verlegen zu müssen, wie es noch Meusel (1959) tat. Aber schon Bertsch (1935) hat eingesehen, dass die Grenze für spontane Vorkommen von *F. silvatica* in England im Süden des Landes liegen müssen. Nach Tansley (1939) liegt diese Grenze in der Gegend von London und südlich von Worcester im Norden und reicht im Westen bis in die Gegend von Bristol-Bournemouth. Godwin (1956) hat anhand von postglazialen Fossilvorkommen nachgewiesen, dass *F. silvatica* bis ungefähr Oxfordshire und Norfolk im Norden und im Westen wenigstens bis Exeter spontan vorkommt.

Auch die NO Grenze für spontanes Vorkommen der Art ist lange diskutiert worden (siehe Literatur unten) ohne dass bis jetzt klar ist, wo diese liegt (vergl. auch Firbas 1949, S. 229 ff).

Über die Ursprünglichkeit des Vorkommens in Norwegen vergl. Fægri (1954).

Die Biologie von *F. silvatica* ist eingehend von Lindquist (1931) beschrieben worden und es kann in diesem Zusammenhang auf diese Arbeit verwiesen werden.

F. orientalis ist verbreitet vom mittleren Balkan, der N Türkei und dem ganzen Kaukasus bis nach N Persien und hat einige isolierte Vorkommen in der S Türkei.

In Asien ist *F. crenata* und *F. japonica* in Japan und *F. engleriana* und *F. longipetiolata* in China verbreitet. Es finden sich andere nahestehende Arten in diesem Gebiet, die alle durch Übergangsformen nahe mit einander verwandt sind.

Die Verbreitung ist kartiert u.a. in folgenden Werken: Andersson 1903, Fig. 4; Bertsch 1935, Abb. 40; Christiansen 1953, Nr. 785; Hanna Czeczott 1932; S. 387; Fægri, Gjærevoll, Lid & Nordhagen 1960, Fig. 22; Enquist 1924, Fig. 2; Enquist 1933, Fig. 6; Erdtman 1932, Fig. 1; Hegi 1957, Fig. 87; Hjelmqvist 1940, Fig. 9; Holmboe 1913, Fig. 16; Hueck 1937, Abb. 6, 18; Hueck 1940, Taf. VI (1); Hultén 1950, Nr. 600; Hultén 1960, Fig. 61; Kirchner, Loew & Schröter 1911, Fig. 1; Kulczýnski 1930, Fig. 15; Köppen 1888, Karte I; Lindquist 1959, Fig. 5, 6, 7 a—f, 8, 9, 10, 13, 14, 15, 16; Markgraf 1932, Abb. 2; Meusel 1959, Abb. 2; Oltmanns 1922, Karte 8; Saxer 1955, Fig. 26; Scharfetter 1938, Abb. 21; Schmucker 1942, Fig. 87; Schoenichen 1933, Abb. 33; Szafer 1930, Fig. 20; Szafer 1932, S. 177; Szafer 1935, S. 239.

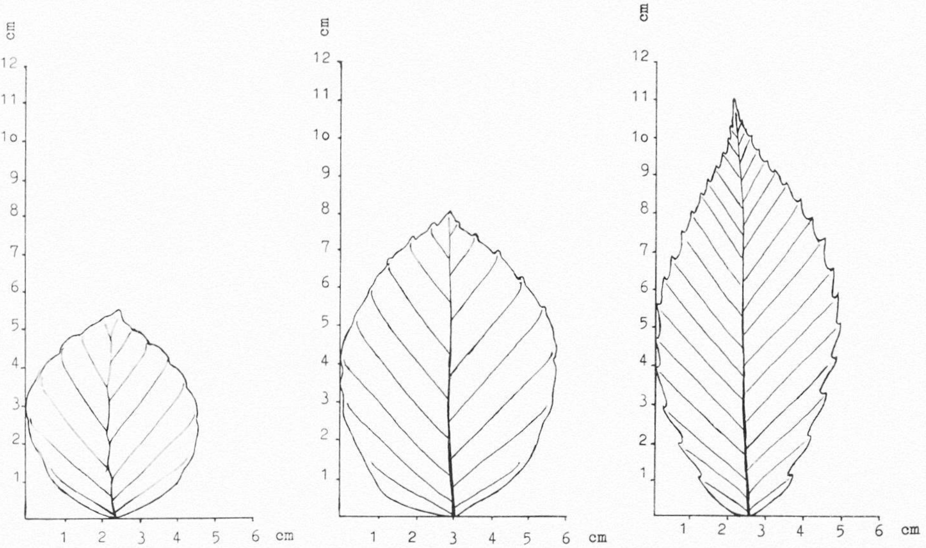

Fig. 1: Blatt von *Fagus silvatica* (*crenata*-Typ). — Fig. 2: Blatt von *Fagus silvatica* (*dentata*-Typ). — Fig. 3: Blatt von *Fagus grandifolia*.

F. silvatica ist als polymorphe Fossilart in Europa wenigstens seit dem Miozän bekannt. Im Pleistozän verschwindet sie völlig von Mittel- und Nordwesteuropa. Sie ist dagegen bekannt aus interglazialen Ablagerungen in O und SO Europa.

Im Holozän verbreitet sich *F. silvatica* wieder über fast ganz Europa. Die nacheiszeitliche Ausbreitung ist von Firbas (1949, S. 229—248, Abb. 32 a—c) eingehend beschrieben und es kann auf diese Publikation hingewiesen werden. Weitere Quellenangaben finden sich dort.

Die neuzeitlichen europäisch-vorderasiatischen Arten *F. silvatica* und *F. orientalis* sind was die Blattformen betrifft, von einander nicht mit Sicherheit zu unterscheiden. Auch die Blattformen der asiatischen Arten finden sich häufig in den Formenelementen der europäischen Population wieder. Besonders häufig ist z.B. die *crenata*-Form von *F. japonica* und *F. crenata* bei *F. silvatica* und *F. orientalis*. Gleichzeitig finden sich bei u.a. *F. longipetiolata* und *F. crenata* Ostasiens deutliche *dentata*-Formen, die von denen von *F. silvatica* nicht zu unterscheiden sind (vergl. Fig. 1 & 2).

Aber auch das tertiäre Fossilmaterial zeigt eine Variationsbreite, die der Variabilität der rezenten *Fagus*-Populationen Europas nicht nachsteht. Auf Grund dieser Schwierigkeiten soll das Fossilmaterial,

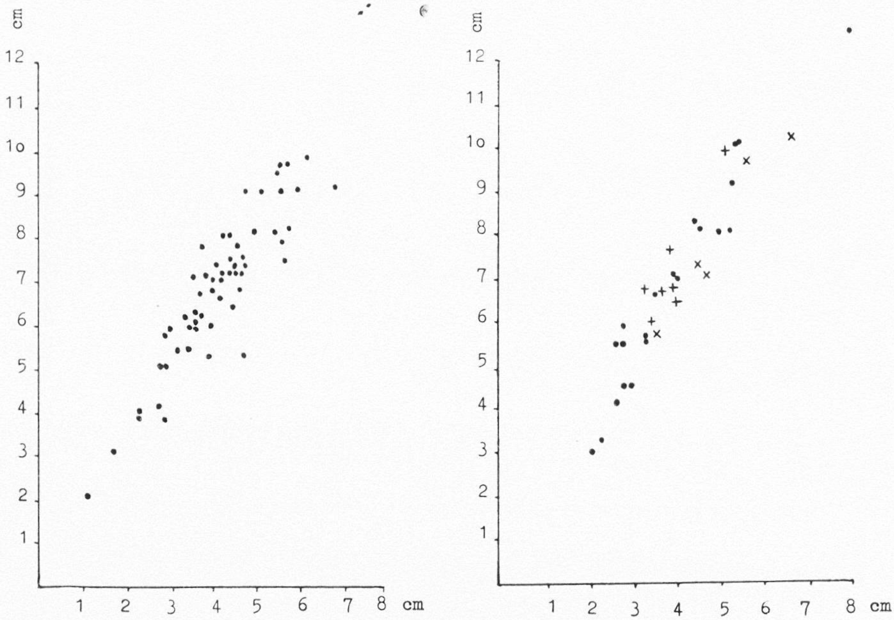

Fig. 4: Längen-Breitenvariation bei rezenten Blättern von *Fagus silvatica.* — Fig. 5: Längen-Breitenvariation bei fossilen Blättern von *Fagus silvatica* aus Willershausen (+ = Länge rekonstruiert, × = Breite rekonstruiert).

das in die Variationsbreite der rezenten europäischen *Fagus*-Arten fällt unter der (Arten-)Gruppe *F. silvatica* zusammengefasst werden.

Die morphologischen Differenzen der rezenten eurasiatischen *Fagus*-Arten gegenüber *F. grandifolia* N Amerikas sind allerdings genügend gross. Der Längen-Breiten-Index von *F. silvatica* beträgt 1.5 ± 4 : 1 (vergl. Fig. 4). Die hier untersuchten fossilen Blätter der Gruppe *F. silvatica* fallen alle in die natürlichen Variationsbreite der rezenten Art(en) (vergl. Fig. 5).

Das fossile Material von Willershausen enthält Blätter, die schwach gezähnt sind (Tafel I) und die man häufig bei *F. silvatica* findet. Aber auch Blätter mit *crenata*-Form sind ebenso wie bei der rezenten Art *F. silvatica* häufig (vergl. Tafel II, Fig. E, G, H; Tafel III, Fig. A, D, E). Tafel II, Fig. D stellt ein Blatt dar, das an *F. longipetiolata* erinnert.

Breitblättrigkeit dominiert bei diesen fossilen Blättern (vergl. Tafel II, Fig. B, u.a.).

Schmalblättrige Formen wie sie Tafel III, Fig. B & C representieren sind selten. Diese Form scheint auch mit dem Pliozän aus Europa zu verschwinden. Die Blätter sind ungezähnt und oft von *crenata*-Form und erinnern an gewisse Blattformen der ostasiatischen *F. japonica* und *F. engleriana*. Im europäischen Tertiär sind sie mehrfach gefunden worden; so z.B. von Rèrolle (1884/85, Tafel V, Fig. 5), Peola (1896, Tafel III, Fig. 4) und vor allem Grangeon (1958, Tafel I, Fig. 5 & 13; Tafel VII, Fig. 4—8) u.a.m.

Sordelli (1896, Tafel XVII, XVIII) stellt unter *F. Antipofi*[1] diese schmalblättrigen Exemplare mit solchen der Gruppe *F. grandifolia* zusammen.

Das von Menzel (1906, Tafel III, Fig. 5) abgebildete und mit *F. ferruginea miocenica* bezeichnete Blatt gehört ganz sicher zu *F. silvatica*. Das Blatt ist nämlich zu breit und die Zähne zu kurz und stumpf, als dass es sich hier um *F. grandifolia* handeln könnte. Diese Form tritt wenigstens bei rezenten Exemplaren nie auf. Auch sind weitere von Menzel (1906, Tafel III, Fig. 4 & 10) abgebildete Blätter typischer für *F. silvatica* als für *F. grandifolia*. Besonders Fig. 10 stellt ein Blatt dar, das zu *F. silvatica* gestellt werden könnte. Leider ist dieses Blatt sehr fragmentarisch.

Berger (1952), der in den pliozänen Ablagerungen von Wien zwei *Fagus*-Arten — *F. attenuata* Goepp. und *F. pliocenica* Sap. — unterscheidet, stellt unter *F. pliocenica* offenbar ein Exemplar (Tafel II, Fig. 34), das wahrscheinlich besser zur Gruppe *F. grandifolia* (=*F. attenuata* Goepp.) gestellt werden sollte.

Von Andreánszky's (1959) miozänen *Fagus*-Arten gehören *F. aperta, F. latissima, F. oblonga* und *F. palaeojaponica* mit Sicherheit zur Gruppe *F. silvatica*.

Nach von Ettingshausen (1894, S. 2) soll *Rhamnus deletus* und vielleicht auch *Rh. Eridani* (Heer 1859) hierher gehören. Die von Heer publizierten Abbildungen sind allerdings für *F. silvatica* oder eine andere naheverwandte Art nicht typisch genug.

In Eurasien ausserhalb Europas sind mehrfach fossile Blätter publiziert worden, die mit Sicherheit zur Gruppe *F. silvatica* zu stellen sind.

F. Antipofii (Schmalhausen 1886—87, Tafel XX, Fig. 10, S. 204—205) aus den wahrscheinlich pliozänen Ablagerungen vom Altai gehört ohne Zweifel hierher.

Das Gleiche gilt für *F. Sieboldi fossilis* (Nathorst 1883, Tafel XV, Fig. 6; S. 84) und *F. japonica fossilis* (Nathorst 1888, Tafel IX, Fig. 3—8; S. 227) aus den tertiären Ablagerungen von Japan. Später haben

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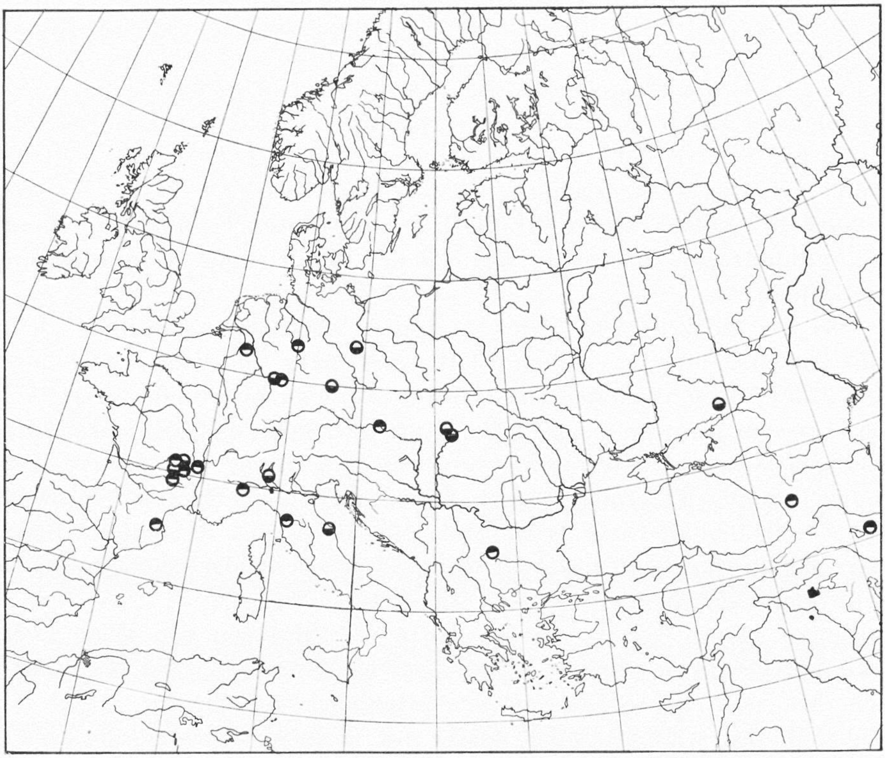
[1] Diese „Art" ist aufgestellt von Heer 1858 (in Abich, Palaeontologie des asiatischen Russlands, Tafel VIII, Fig. 2; S. 572).



Karte 1: Die Verbreitung von *Fagus silvatica* in Europa: miozäne Vorkommen (◒) und pliozäne Vorkommen (◓).

Japaner selbst mehrfach Reste beschrieben, die hierher gehören. Diese sind unter den Namen *F. japonica* (Murai 1958, Tafel II, Fig. 1—3; S. 20), *F. protojaponica* (Suzuki 1959, Tafel II, Fig. 10 und Tanai 1961, Tafel XV, Fig. 5, 6; S. 308—309) und *F. palaeojaponica* (Tanai 1960, Tafel I, Fig. 1, 8 und Tanai & Onoe 1961, Tafel VII, Fig. 3—5; S. 308—309) beschrieben worden.

Ganz zweifellos ist auch das tertiäre Vorkommen in der Kirgisen-Steppe (Palibin 1904, Tafel V, Fig. 1). Palibin bezeichnet sein Exemplar mit *F. Antipofii*; doch scheint auch sein *Carpinus grandis* (Tafel V, Fig. 2) zur Gruppe *F. silvatica* zu gehören. Kryshtofovitch (1921 b, Tafel I, Fig. 8; S. 6) bildet ein fossiles Blatt vom Primorsk Gebiet ab, das er mit *F. Deucalionis* bezeichnet und das man mit ziemlicher Sicherheit hierher rechnen kann. Heer berichtet über (miozäne?) Fagus-Vorkommen auf Sachalin. Auch wenn nicht alle Exemplare des heer-

Karte 2: Die Verbreitung von *Fagus silvatica* und *F. orientalis* und *F. longipetiolata*, *F. engleriana*, *F. crenata*, *F. japonica* u.a. nahestehende in Eurasien und das Vorkommen von *F. silvatica* (◒=miozäne Vorkommen, ◓=pliozäne Vorkommen, ○=Vorkommen unbekannten Alters).

schen Materials der Sammlung des Naturhistoriska riksmuseet in Stockholm wirklich *Fagus* representieren, so sind doch sicher einige Abdrücke zur Gattung *Fagus* zu rechnen. *F. Antipofi* (Heer 1878 a, Tafel VII, Fig. 5; S. 36) ist trotz der dichten Nervatur sicherlich *Fagus*. Das Fossil erinnert stark an gewisse rezente Formen von *F. japonica*. Auch die weiteren mit *F. Antipofi* benannten Stücke (Heer 1878 b, Tafel II, Fig. 7 d; Tafel III, Fig. 1—3; S. 7) gehören zur Gruppe *F. silvatica*. Die von Heer (Tafel II, Fig. 7 d) dargestellte Zähnung des Blattrandes ist am Original nicht zu erkennen, sondern offenbar nur durch

Bruch des Stückes entstanden. Die Exemplare schliessen sich recht gut an rezente ostasiatischen Arten an.

Dagegen gehört *F. Antipofii* vom Possiet-Bay (Kryshtofovitch 1921 a, Tafel II, Fig. 3—5 a; S. 20) sicher nicht zu *Fagus*. Brown (1937 a, Tafel 55, Fig. 2, 3; S. 179) hat sehr ähnliche Blätter aus dem mittleren Eozän von Wyoming zu *Rhus longipetiolata* gestellt.

Ausserordentlich zweifelhaft ist ebenfalls ob *F. Pyrrhae* und *F. macrophylla* (Engelhardt 1894, Tafel III, Fig. 1—5; S. 179) aus dem Tertiär von Podvin überhaupt Fagus ist. In die fossile Gruppe *F. silvatica* gehören die Resten jedenfalls nicht.

Die tertiären Reste von Aralsee, die Palibin (1907, Tafel II, Fig. 10; S. 12—14) mit *F. Antipofii* bezeichnet, müssen nicht notwendigerweise zu *Fagus* gehören. Auch Krasnovs Angaben (Krasnov 1910, S. 182) sind wegen der schlechten Abbildungen zweifelhaft. Janishevskij (1915, Tafel I, Fig. 8; S. 9—10) bildet einen schlecht erhaltenen Blattabdruck aus miozänen Ablagerungen von Tomsk ab und bezeichnet das Exemplar mit *F.* cf. *Antipofii.* Auch hier ist es völlig unsicher, ob es sich um ein *Fagus*-Blatt handelt.

Völlig von der Gattung *Fagus* auszuschliessen sind auch: *F. atlantica* Unger (1847, Tafel XXVIII, Fig. 2), die offenbar zu *Zelkova* gehört, *F. Deucalionis* Unger (1852, Tafel XVIII, Fig. 24) und *F. pristina* Pilar (1883, Tafel V, Fig. 5).

Ausserhalb Eurasiens kommen typische Reste der Gruppe *F. silvatica* nicht vor.

Von Grönland sind *Fagus*-Vorkommen publiziert worden. Heer (1880, Tafel IV, Fig. 2, 3; S. 10) nennt *F. Deucalionis.* Wenn Fig. 2 wirklich *Fagus* darstellt, ist das Exemplar jedenfalls nicht zur Gruppe *F. silvatica* gehörig zu rechnen. Fig. 3 macht wegen der Sekundär- und Tertiärnervatur in der rechten, unteren Blatthälfte nicht wahrscheinlich, dass das Exemplar zu *Fagus* gehört. *F. cordifolia* (Heer 1883, Tafel XCII, Fig. 1) von Grönland ist wahrscheinlich keine *Fagus.* Es gibt wenigsten innerhalb der Gattung *Fagus* gegenwärtig keine Art, die eine solche Blattbasis und Tertiärnervatur ausbildet. Es kann allerdings bei *F. crenata* z.B. selten vorkommen, dass sich die Sekundärnerven der Blattbasis in einer Weise teilen, wie es bei *F. cordifolia* von Grönland der Fall ist. Dieses ist immerhin so selten, dass man die Nervatur von *F. cordifolia* als untypisch bezeichnen muss. Nathorst (1907) hat ähnlich Abweichungen bei frostbeschädigten *Fagus*-Blättern beschrieben. Solche Ausnahmen könner allerdings keinen Beweis bei palaeobotanischem Material liefern. Auch *F. Antipofi* (Heer 1883, Tafel XCIV,

Fig. 7) ist ganz sicher nicht näher mit *F. silvatica* verwandt. *Fagus*-Cupulae sind von Grönland nicht bekannt und das wirkliche Vorkommen von *Fagus* auf Grönland daher bis jetzt nicht bewiesen.

Das Gleiche gilt für Spitzbergen. *F. Deucalionis* Heer (1876, Tafel XV, Fig. 5 b, 6, Tafel XVIII, Fig. 1 b, Tafel XXXI, Fig. 7) beweist nicht das frühere Vorkommen von *Fagus* auf Spitzbergen.

Auch von N Amerika sind keine fossilen Reste bekannt, die sich mit *F. silvatica* oder einer anderen rezenten, naheverwandten Art direkt vergleichen lassen.

F. silvatica hatte somit während des Miozäns und Pliozäns eine eurasiatische Verbreitung und ist im Gebiet seiner rezenten Verbreitung in geographisch getrennten, systematisch schwach von einander differenzierten Typen erhalten.

Die stratigraphische Verbreitung erstreckt sich in Europa mit Sicherheit vom Miozän bis in die Gegenwart. Eine Verarmung der Formenelemente scheint ständig, besonders aber beim Übergang vom Pliozän zum Pleistozän stattgefunden zu haben, d.h. wir haben hier eine Artenbildung durch geographische Isolation.

III. Gruppe Fagus grandifolia Ehrh.

Fagus castaneaefolia. — Unger 1847, Tafel XXVIII, Fig. 1; S. 104—105; Loeben, Wartberg; Tertiär

Fagus castaneaefolia. — von Ettingshausen 1851, Tafel I, Fig. 21—23; S. 13; Wien; Miozän

Fagus attenuata. — Goeppert 1855, Tafel V, Fig. 9; S. 18; Schossnitz; Miozän

Fagus castaneaefolia. — Sismonda 1865, Tafel X, Fig. 4; S. 435; Turin; Miozän

Fagus pliocenica. — de Saporta 1884, Tafel VI, Fig. 1—4; S. 88 ff.; Cantal; Tertiär

Fagus attenuata. — von Schlechtendal 1896, Tafel V, Fig. 1—5; S. 200 ff; Senftenberg; Miozän

Fagus Antipofi. — Sordelli 1896, Tafel XVII, Fig. 6, Tafel XVIII, Fig. 7, 13; S. 118; Montescano; Miozän?

Fagus ferruginea miocenica. — Menzel 1906, Tafel III, Fig. 11—12, Tafel VIII, Fig. 15; S. 48 ff; Senftenberg; Miozän

Fagus attentuata. — Reichenbach in Kräusel 1920, Tafel XI, Fig. 4, 5, Tafel XII, Fig. 22, Textfig. 11, 12, 13; S. 123 ff; Kokoschütz, Schossnitz, Dyhernfurt; Miozän

Fagus attentuata. — Weyland 1934, Tafel V, Fig. 1, 4, 5; S. 53—54; Fischbach; Pliozän

Fagus grandifolia. — Straus 1935, Tafel XXXIII, Fig. 6; S. 182; Willershausen; Oberes Pliozän

Fagus ferruginea fossilis. — Mädler 1939, Tafel VII, Fig. 21, 22; Abb. 27, 28; S. 83—84; Frankfurt a.M.; Pliozän
Fagus attentuata. — Berger 1952, Tafel I, Fig. 31, 32; S. 88—89; Brunn-Vösendorf; Pliozän
Fagus cfr. *grandifolia.* — Andreánszky 1959, Tafel V, Fig. 3, Tafel XXVI, Fig. 1, 2; Textabb. 81, 82; Balaton; Sarmatien

Fagus feroniae. — Engel 1908; S. 562; Heggbach; Oberes Miozän
Fagus pristina. — Lauby 1908; S. 155; l'Aubrac; Miozän
Fagus pristina. — Principi 1908; S. 40—41; Senigallia; Miozän
Fagus pristina. — Lauby 1910; S. 92; Sant-de-Jujien; Tertiär (Miozän?)
Fagus Feroniae. — Kettner 1911; S. 5; Klinec; Tertiär (Miozän?)
Fagus ferruginea fossilis. — Stoller in Fliegel & Stoller 1913; S. 243—244; Beisselsgrube; Pliozän
Fagus pristina. — David 1916; S. 86; Harsova; Pliozän
Fagus attenuata. — Kräusel 1920; S. 407, 409, 410; Kokoschütz, Schossnitz, Dyhrenfurt; Miozän
Fagus attenuata. — Pax 1922; S. 308; Ueskūb; Miozän
Fagus attenuata. — Juhnke 1932; S. 113; Wohlau; Tertiär
Fagus pliocenica. — Rey & Depape 1949; S. 76; St.-Flour; Mio-Pliozän
cf. *Fagus attenuata.* — Berger 1953; S. 144; Wien-Hernals; Miozän
Fagus haidingeri. — Bócsa 1955; S. 59; Balaton; Miozän
Fagus haidingeri. — Józsáné Czár 1955; S. 36; Mikófalva; Miozän

?*Fagus attentuata.* — Gaudin & Strozzi 1859; Tafel V, Fig. 7; S. 41; Val d'Arno; Pliozän
?*Fagus castaneaefolia.* — Sismonda 1865, Tafel 13, Fig. 2—3; Tafel XIV, Fig. 1; Tafel XV, Fig. 3; S. 435; Guarène; Miozän
?*Fagus castaneaefolia.* — von Ettingshausen 1867, Tafel XVI, Fig. 1—2; S. 128; Bilin; Miozän
?*Fagus intermedia.* — Nathorst 1888, Tafel XI, Fig. 2; S. 29; Ushigatani; Tertiär (Pliozän?)
?*Fagus Antipofi.* — Sordelli 1896, Tafel XVIII, Fig. 12; S. 118; Montescana; Tertiär
?*Fagus pliocenica.* — Marty 1903, Tafel V, Fig. 5—7; S. 124—125; Joursac; Miozän
?*Fagus ferruginea miocenica.* — Menzel 1906, Tafel III, Fig. 4, 10; S. 48 ff.; Senftenberg; Miozän
?*Fagus silvatica.* — Laurent & Marty 1923, Tafel XI, Fig. 7; Reuver; Pliozän
?*Fagus grandifolia.* — Straus 1935, Tafel XXXIII, Fig. 9; S. 182; Willershausen; Oberes Pliozän
?*Fagus attenuata.* — Müller-Stoll 1936, Tafel III, Fig. 8; S. 110; Rhön; Miozän
?*Fagus ferruginea* var. *miocenica.* — Dotzler 1937, Tafel VII/VIII, Fig. 21; S. 15; Miesbach; Oligozän
?*Fagus pliocenica.* — Berger 1952, Tafel II, Fig. 34; S. 89; Brunn-Vösendorf; Unteres Pliozän
?*Fagus attenuata.* — Hantke 1954, Tafel II, Fig. 2, 3; S. 45; Oehningen; Oberes Miozän

?*Fagus pliocaenica.* — Berger 1955 b, Fig. 56; S. 91; Laaerberg; Unteres Pliozän

?*Fagus* (*Castanea*) *castaneaefolia.* — Menendez Amor 1955, Tafel XXV, Fig. 1; S. 74—75; Badés, Padro; Miozän

?*Fagus pristina.* — Menendez Amor 1955, Tafel XXIV, Fig. 3, 4; S. 75; Coll del Saig; Miozän

?*Fagus Antipovii.* — Usnadse 1957, Tafel III, Fig. 3, Tafel IV, Fig. 5, 6; Tafel V, Fig. 2; S. 223; Nord-Priaral; Tertiär

?*Fagus angusta.* — Andreánszky 1959, Tafel XXVI, Fig. 3, Abb. 83; S. 97—98; Mikófalva; Miozän

?*Fagus* cfr. *grandifolia.* — Andreánszky 1959, Abb. 82; S. 96—97; Balaton, Sarmatien

Bearbeitetes Fossilmaterial von Willershausen: Geologisch-Palaeontologisches Institut der Universität Göttingen: 2129 (=Tafel IV, Fig. A), 2412 (=Tafel IV, Fig. B), 4165 (=Tafel IV, Fig. C). Botanisches Museum, Berlin-Dahlem: 2129 a, 2176?, 2423?, 3151, 3387?, 3723?, 3764 a, 3833?, 3833 a?, 3843?, 4167?, 4183, 4249, 4249 a, 4294?, 4298?, 4299?, 4301?, 4445?, 4968?, 5339?, 5840, 5858?, 6791?, 6811?, 6932?, 7104, 7285?, 8267?, 8366, 8366 a, 8670?, 9110?, 9282?, 9497, 9827?, 9912, 9933 a, 9938. Naturhistoriska Riksmuseets Paleobotaniska avdelning, Stockholm: 3556?, 3562?.

Neuzeitliche Vergleichsart: *Fagus grandifolia* Ehrh. Syn.: *F. ferruginea* (Dryand.) in Ait., *F. americana* Sweet, *F. sylvestris* Michx., *F. heterophylla* Rafin., *F. virginiana* Hort. Möglicherweise kann auch *F. lucida* R. & W. von Kweichow Provinz, China hierher gerechnet werden. Diese Art intermediiert zwischen *F. grandifolia* und *F. longipetiolata.*

Die rezente Verbreitung von *F. grandifolia* in Nordamerika erstreckt sich von S New Brunswick, S Ontario bis N Florida im Osten und von O Wisconsin bis O Texas im Westen. Die Art kommt in ozeanisch betonten Klimagebieten vor und ist im Flachland an Wasserläufen u.s.w. verbreitet.

Die Verbreitung ist kartiert in folgenden Werken: Hough 1957, S. 133; Nichols 1935, S. 408; Munns 1938, Karte 87; Martin & Harrell 1957, S. 471, Karte 4.

In N Amerika ist *F. grandifolia* mit Sicherheit seit dem Oligozän bekannt, d.h. von Oregon (Chaney 1920, Contr. of the Walker Mus., 2, Tafel XI, Fig. 1, S. 167; Chaney 1927, Pub. Carnegie Inst. Washington, 346, Tafel X, Fig. 6—9; Brown 1937, Journ. Washington Acad. of Sci., 27) und von British Columbia (LaMotte 1935, Pub. Carnegie Inst. Washington, 455). Aus spättertiären Ablagerungen — d.h. aus dem Miozän und Pliozän — ist *F. grandifolia* von den U.S.A. und British Columbia bekannt. Die fossilen Blätter sind allerdings unter sehr verschiedenen Namen z.B. *Amygdalus alexanderi* (Berry 1929), *Castanea lesquereuxi* (LaMotte 1936), *Sorbus chaneyi* (Hollick 1927) und *F. washoensis* (LaMotte 1936) publiziert worden.

Die miozänen und pliozänen Vorkommen in N Amerika sind: Beck 1938, Fig. 3; Berry 1929, Fig. 1; Berry 1934, Tafel XIX, Fig. 6; Berry 1938; Berry 1952; Brooks 1935; Brown 1937 b, Tafel LI, Fig. 1, 2, 3, 8, 9, 10; Brown 1940; Hollick 1927, Tafel XXX, Fig. 3, 4, Tafel XXXI, Fig. 3; Tafel XXXII, Fig. 2, 3; LaMotte 1936, Tafel VIII, Fig. 2, 3, 5, Tafel IX, Fig. 4, 5, 9; Oliver 1934; Smith 1939, Tafel XI, Fig. 2, 3, 4, Tafel XIII, Fig. 5, 7, 9; Smith 1941, Tafel XI, Fig. 5.

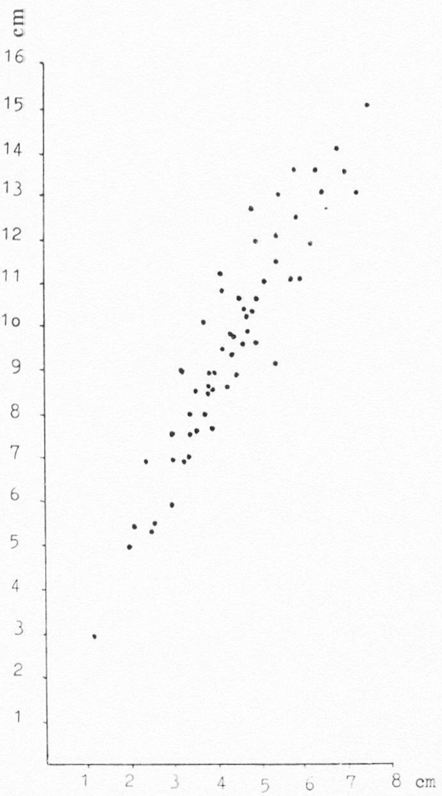
Vielleicht gehört auch *F. antipofii* von Kenai Peninsula (Alaska) Hollick 1936, Tafel LIII, Fig. 1, S. 95—96) hierher.

Im Pleistozän ist die Art so gut wie vollständig an ihr rezentes Verbreitungsgebiet gebunden und ist u.a. aus den Staaten New Jersey, Massachusetts, Maryland, Pennsylvania, West Virginia, North Carolina, Tennessee und Alabama bekannt.

Angaben über das fossile Vorkommen im Pleistozän (inkl. Holozän) N Americas finden sich bei: Berry 1907, Journ. Geol., 15; Berry 1907, Amer. Naturalist, 41; Berry 1909, Amer. Naturalist, 43; Berry 1915, Torreya, 15; Berry 1926, U.S. Geol. Survey, prof. paper, 140; Berry 1927, Torreya, 27; Berry 1940, Journ. Washington Acad. Sci., 30 & 31; Brown 1938, Louisiana Geol. Survey, Geol. Bull., 12; Emerson 1898, U.S. Geol. Survey, Geol. Atlas, fol. 50; Hollick 1906, Maryland Geol. Survey, Pliocene and Pleistocene, 226; Knowlton 1896, Amer. Geol., 18; Lesquereux 1859, Amer. Journ. Sci., 27; Lesquereux 1869, Geol. Tennessee, 427; Mercer 1899, Journ. Philad. Acad., 11.

Die neuzeitliche Art *F. grandifolia* zeigt geringe Variabilität und ist gut von anderen *Fagus*-Arten unterschieden. Ausser dieser Art gibt es keine andere, innerhalb der Gattung, die vollständig ähnliche Blätter ausbildet. Ähnliche Blätter finden sich allerdings bei Arten der Gattungen *Castanea* und *Quercus,* sodass Verwechslungen bei Fossilien möglich sind.

Abgesehen von anderen morphologischen Differenzen z.B. der Zähnung u.s.w., die die rezenten Blätter von *F. grandifolia* und *F. silvatica* u.a. unterscheiden, findet man im Längen-Breiten-Index der beiden Arten sichere Unterscheidungsmerkmale (vergl. Fig. 6), die besonders bei der Identifizierung von fossilem Material von Bedeutung sein kann. Der Längen-Breiten-Index der Blätter von *F. grandifolia* beträgt nämlich bei rezentem Material (Naturhistoriska Riksmuseets botaniska avdelning, Stockholm) 2.4 ± 0.6 : 1. Die hier untersuchten fossilen Blätter (vergl. S. 163) fallen in die natürliche Variationsbreite der rezenten Art (vergl. Fig. 7) und müssen daher auf Grund sowohl der Zähnung



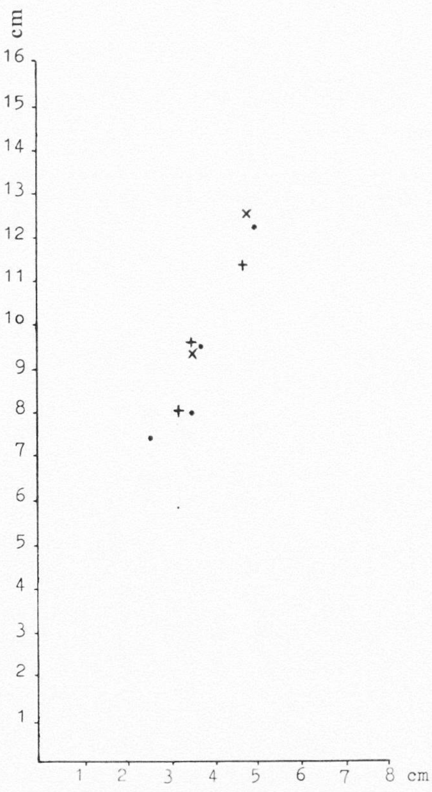
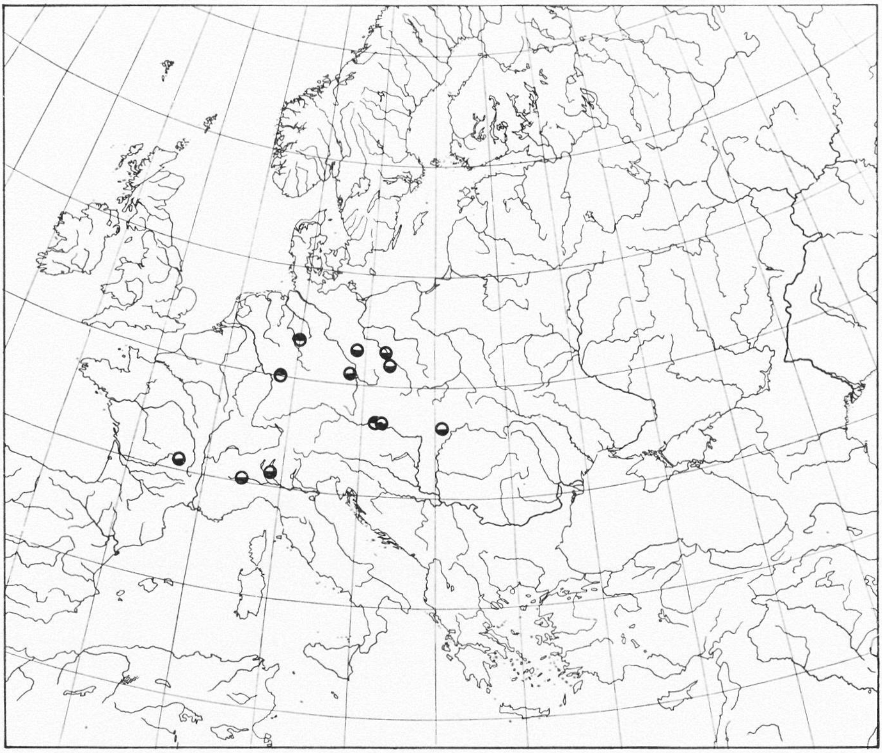


Fig. 6: Längen-Breitenvariation bei rezenten Blättern von *Fagus grandifolia*. — Fig. 7: Längen-Breitenvariation bei fossilen Blättern von *Fagus grandifolia* aus Willershausen (+ = Länge rekonstruiert, × = Breite rekonstruiert).

als auch wegen des Verhältnisses von Länge-Breite zu *F. grandifolia* gezogen werden.

Ein Teil der früher abgebildeten Fossilien ist sehr typisch und es kann kein Zweifel daran bestehen, dass die im ersten Teil der Liste angeführten Blätter von Unger (1847), von Ettingshausen (1851), Goeppert (1855), u.s.w. zu *F. grandifolia* gehören. Sie sind alle ähnlich den auf Tafel IV, Fig. A—C abgebildeten fossilen Blättern und stimmen gut überein mit den rezenten Blättern von *F. grandifolia*.

Eine ganze Reihe von fossilen Blättern, die von verschiedenen Verfassern mit der nordamerikanischen *F. grandifolia* verglichen wurden, haben allerdings nur wenig Ähnlichkeit mit dieser. So hat Hanna Czeczott (1934) nachgewiesen, dass *Fagus feroniae* (Unger 1847, Tafel



Karte 3: Die Verbreitung von *Fagus grandifolia* in Europa: miozäne Vorkommen (◒) und pliozäne Vorkommen (◓).

XXVIII, Fig. 3, 4; S. 106) aus den miozänen Ablagerungen von Bilin eine *Alnus*-Art ist. Auch die Funde von v. Ettingshausen (1867, Tafel XV, Fig. 12—20, 22; S. 126—128) und von Marty (1903, Tafel V, Fig. 8; S. 125—126) sind auszuschliessen. Es ist so z.B. auch ausgeschlossen, dass *F. dentata* (Goeppert 1855, Tafel V, Fig. 11, S. 18) wegen der runden Breitblättrigkeit und der doppelten Zähnung hierher gehört, die allerdings u.a. von Hantke (1954, S. 45) ohne Motivierung mit der *F. attenuata* Goepperts zusammengefasst wird. Goepperts „*Fagus*“ *dentata* ist ganz sicher nicht einmal Fagus.

C. von Ettingshausen (1867, Tafel XV, Fig. 12, 13, 16, 17) bildet unter dem Namen *F. Feroniae* fossile Blätter ab, deren systematische Stellung unsicher erscheint und die mit den übrigen wohl nicht zu nur einer Art gehören. Auch Sordelli (1896) fasst unter dem Namen *F. Antipofi* Exemplare, die zu *F. grandifolia* gestellt werden sollten, mit solchen, die deutlich zu der fossilen Gruppe *F. silvatica* gehören, zusammen. Von den von Menzel (1906) abgebildeten fossilen Blättern, die er als *F. ferruginea miocenica* bezeichnet, hat wenigstens ein Blatt (Tafel III, Fig. 5) auffallende Ähnlichkeit mit *F. silvatica* und es dürfte sich sehr wahrscheinlich um diese handeln. Lediglich zwei Abbildungen (Tafel III, Fig. 11, 12) dürften wirklich *F. grandifolia* repräsentieren.

Zu *F. grandifolia* gehört nicht das von Kovats (1856) unter *F. castaneaefolia* abgebildete Blatt. Hier handelt es sich entweder um *Ulmus* sp. oder *Carpinus* sp. Hantke (1954, Tafel II, Fig. 1—4) veröffentlicht unter dem Namen *F. attenuata* fossile Blätter aus den miozänen Ablagerungen von Oehningen, von denen ein Exemplar (Tafel II, Fig. 4= Fig. 1 nach Hantke) mit Sicherheit nicht zu *F. grandifolia* gehört, da diese Art, wie es bei dem abgebildeten fossilen Exemplar der Fall ist, keine nach aussen gebogenen Zähne hat. Es mag sich hier um eine *Castanea*-Art handeln. Nach aussen gebogene Zähne kommen z.B. bei *Castanea sativa* und *C. dentata* vor.

Nach Lesquereux (1878, S. 146) soll *Ulmus quercifolia* (Unger 1847, Tafel XXV, Fig. 5, S. 96) sowie *Quercus myricaefolia* (Unger 1852, Tafel XVII, S. 37) hierher gehören. Diese Ansicht ist jedoch falsch. „*Ulmus quercifolia*“ ist doppeltgezähnt und kommt daher als *Fagus* nicht in Frage.

Fagus attenuata (Sismonda 1865, Tafel XVII, Fig. 3, S. 435) aus den miozänen Ablagerungen von Piemont ist ebenfalls ganz sicher kein *Fagus*.

Auch *F. feroniae* von Engelhardt (1902, Tafel II, Fig. 29, 33, 35, 39; S. 270—271) von Himmelsberg gehört mit Sicherheit nicht zu *Fagus* wegen der doppelten Zähnung.

Im Willershausener Material findet sich ein fossiles Blatt (Botanisches Museum, Berlin-Dahlem Nr. 4129 & 4129 a), das grosse Ähnlichkeit mit *Fagus angusta* (Andreánszky 1959, Abb. 83; Tafel XXVI, Fig. 3; S. 97—98) zeigt. Andreánszky vergleicht dieses Blatt mit *F. grandifolia*. Es scheint aber sehr unsicher — oder wenigstens nicht bewiesen — ob diese Exemplare überhaupt zur Gattung *Fagus* gehören.

Tertiäres *Fagus*-Pollen von *grandifolia* (ferruginoidem) Typ wurden u.a. von Leschik (1951, S. 15, Tafel IV, Fig. 10—12) gefunden. Wie sicher diese von *Fagus*-Pollen von *silvatica* Typ zu unterscheiden sind, entzieht sich der Kenntnis des gegenwärtigen Verfassers.

Nach Zlatarski (1927) und Konjarov (1932) (beide zitiert nach Stefanoff & Jordanoff 1935, S. 123) soll *F. grandifolia* (unter *F. Feroniae*)

Karte 4: Die Verbreitung von *Fagus grandifolia* (schraffiert) und das fossile Vorkommen von *F. grandifolia* (◒=miozäne Vorkommen, ◓=pliozäne Vorkommen, ○=Vorkommen unbekannten Alters).

auch in den miozänen Ablagerungen von Oranovo-Simitli in Bulgarien gefunden worden sein.

In Asien sind der *F. grandifolia* ähnliche Fossilien gefunden worden. Schmalhausen (1886—87, Tafel XXI, Fig. 1—4; S. 206) beschreibt eine *F. ferruginea* mut. *altaica* aus tertiären, wahrscheinlich pliozänen Ablagerungen vom Altai. Von den fragmentarischen Blättern sind wenigstens zwei oder drei (Tafel XXI, Fig. 1, 2, 3) ziemlich typisch. Fig. 4 hat für die angegebene Art allerdings zu abgerundete Zähne und ist sicher kein *Fagus*-Blatt, es könnte zu *Zelkova* gehören.

Nathorst (1883, Tafel IV, Fig. 21; Tafel V, Fig. 1, 5) bildet typische Blätter von *F. grandifolia* aus wahrscheinlich oberpliozänen Ablagerungen von Mogi in Japan ab. C. von Ettingshausen (1883, S. 5) stellt die von Nathorst zum grössten Teil gut auseinander gehaltenen Reste von *F. grandifolia* und der Gruppe *F. silvatica* zusammen unter seine imaginäre „gemeinsame Stammart" dieser beiden und bezeichnet sie mit *F. Deucalionis* Ung. G. de Saporta (1884, S. 88 ff) führt die Reste von Mogi unter seine ebenso polymorphe Art *F. pliocenica* und identifiziert sie mit denen von Frankreich.

Auch Florin (1920, Tafel I, Fig. 3—12) bildet sehr typische Blätter von *F. grandifolia* aus Japans Tertiär ab und stellt sie zu dieser Art.

Weitere Funde aus dem Neogen Japans bestätigen die Angaben von Nathorst und Florin. So publizierten Miki (1941, Fig. 11; S. 270) als *F. ferruginea,* Endo (1955, Tafel XXXII, Fig. 6) als *F. americana* und Tanai (1961, Tafel XV, Fig. 1, 8, Tafel XVI, Fig. 9; S. 306) als *F. antipofi* und *F. palaeocrenata* Reste, die direkt mit *F. grandifolia* vergleichbar sind.

Fagus? *feroniae* Ung. aus der alttertiären Flora der südlichen Mandschurei (Florin 1922, Tafel I, Fig. 5—7, S. 12) gehört nicht hierher.

Heers Angaben über das Vorkommen von gezähnten *Fagus*-Blättern in Grönland beziehen sich — wenn es überhaupt *Fagus*-Blätter sind — nicht auf *F. grandifolia.* Heer (1880, Tafel IV, Fig. 2, 3; S. 10) verzeichnet zwei Blätter von denen besonders Fig. 3 durch die Tertiärnervatur für *Fagus* untypisch ist. Fig. 2 hat einen für *Fagus* ungewöhnlich breiten Stengelansatz. Später (Heer 1883, Tafel XCV, Fig. 8—10) verzeichnet er wiederum unter dem Namen *F. Deucalionis* gezähnte Blätter. Die Fig. 9 stellt unter keinen Umständen *Fagus* dar. Die Zähne und die unregelmässige Sekundärnervatur schliessen das Blatt von der Gattung *Fagus* aus. Die beiden übrigen Figuren sind ebenfalls nicht typisch genug, um eine definitive Bestimmung zuzulassen. Die grönländischen Ablagerungen sind ausserdem ohne zweifel älter als aus dem Miozän.

F. grandifolia hatte somit während des Miozän und Pliozän eine zirkumpolare Verbreitung und ist im Gebiet seiner rezenten Verbreitung ein tertiäres Relikt.

Die stratigrafische Verbreitung von *F. grandifolia* in Europa erstreckt sich mit Sicherheit vom Miozän bis ins späte Pliozän. Wahrscheinlich starb die Art mit der ersten Kalt- oder Eiszeit aus.

IV. Theorien über die Phylogenie der Fagus-Arten

Schon 1883 hat A. G. Nathorst erkannt, dass im Pliozän Japans zwei *Fagus*-Arten vorhanden waren, von denen die eine *F. grandifolia* und die andere *F. silvatica* (*F. Sieboldii*) entspricht. Auch Fliche (1886) schliesst sich, was die europäischen Reste betrifft, dieser Auffassung an und sieht in der *F. Deucalionis* aus dem europäischen Miozän *F. silvatica.*

Als Nathorst (1883) seine zweite tertiäre Japanflora publiziert hatte, antwortet noch im gleichen Jahre v. Ettingshausen (1883) und führt die von Nathorst gut auseinander gehaltenen Arten zu einer „tertiären Stammart“ zusammen. Krašan (1894) und v. Ettingshausen (1894) erklären dann später, dass die europäische Art im Tertiär *F. Feroniae* Ung. sei, die sich an *F. prisca* Ett. der Kreideperiode anschliessen soll. *F. Feroniae* Ung. gehört aber, wie von Hanna Czeczott (1934) nachgewiesen, in die Gattung *Alnus*! Aus dieser „tertiären Stammart“ sollen sich dann die neuzeitlichen Arten entwickelt haben. Eine wirklich erstaunliche Metamorphose in Floras Reich. Eine im Grunde gleiche Auffassung vertreten Menzel (1906) und Zablocki (1927) indem sie unter *F. ferruginea miocenica* die Formenelemente von *F. silvatica* und *F. grandifolia* zusammenfassen. Die Entwicklungsreihe für *Fagus* sieht nach Krašan so aus: *F. pristina* - *F. ferruginea* - *F. pliocenica* - *F. silvatica.* Während die Entwicklung also in N America für *F. grandifolia* stagnierte, bildete sich in Eurasien „*F. pliocenica*“ und *F. silvatica* aus. Rérolle (1884—85) denkt sich eine erweiterte *F. mio-pliocenica* und hat im übrigen eine ähnliche Theorie wie z.B. de Saporta (1884), der meint, dass sich *F. silvatica* und andere naheverwandte Arten aus *F. grandifolia* entwickelt hätten. Laurent (1904—05) gibt eine noch mehr komplizierte Theorie über die Phylogenie der rezenten *Fagus*-Arten. Er nimmt zwei Entwicklungslinien für *F. grandifolia* an. Diese sind 1.: *F. polyclada* Lesq. (*F. cretacea* Newb.) - *F. pristina* Sap. (=*F. antipofi* Heer) - *F. grandifolia* und 2.: *F. prisca* Ett. - *F. pliocenica* (sens. lat.) - *F. grandifolia.* Für die eurasiatischen Arten nennt er folgende Reihe: *F. prisca* Ett. - *F. pliocenica* (sens. lat.) - *F. silvatica fossilis* - *F. silvatica* (inkl. die übrigen eurasiatischen Arten).

Man wird sich nun mit Recht fragen können, ob es notwendig ist so komplizierte Systeme auf so schwachem Material aufzubauen. Hier soll jedenfalls aus verschiedenen Gründen die nathorstsche Idee zur Geltung kommen. Denn so viel ist sicher, dass die europäischen *Fagus*-Vorkommen wenigstens im Miozän und Pliozän in zwei Gruppen teilbar sind. Die Mehrheit dieser Vorkommen entsprechen — trotz schwerbestimmbarer Zwischenformen — der nordamerikanischen Art *F. grandifolia* und den eurasiatischen Arten, von denen *F. silvatica* die weiteste Verbreitung hat und auch im Übrigen am representativsten ist.

F. grandifolia ist in N Amerika aus praemiozänen Ablagerungen bekannt und war während des Miozäns und Pliozäns eine zirkumboreale Art, wie z.B. *Brasenia Schreberi* (Tralau 1959). Die Art gehört somit in die häufig diskutierte Gruppe der tertiären, zirkumborealen Pflanzen.

Von *F. silvatica* gibt es keine Spur im nordamerikanischen Miozän und Pliozän. Diese hat sich offenbar ausschliesslich in Eurasien entwickelt. Das Gleiche gilt z.B. auch für *Parrotia persica* (Tralau 1961).

Ein direkter Zusammenhang zwischen den hier diskutierten *Fagus*-Arten und den aus der Kreide bekannten Arten ist wegen der Sporadizität der Vorkommen bis jetzt nicht zu rekonstruiren.

Zum Schluss will ich Professor Olof H. Selling, Naturhistoriska Riksmuseet, Stockholm 50, meinen warmen Dank sagen für die freundliche und zuverlässige Unterstützung während meiner Arbeit, ohne die das vorliegende Resultat wenigstens nicht jetzt erreicht worden wäre. Auch für die Hilfe der Herren Dr. A. Straus von Berlin und Dr. E. Koch von Kopenhagen danke ich herzlich.

V. Summary

The Late-Tertiary Fagus Species of Europe

During a travel through Western Europe in the spring of 1961 the present author had the opportunity to collect fossil plants at the Upper Pliocene sites of Willershausen (Western Germany). Later the investigator of those sites, Dr. A. Straus of Berlin-Dahlem, put his own extensive collection of *Fagus* at my disposal.

Most of the material could be arranged in two separate groups, one resembling the formelements of the Northamerican *F. grandifolia* Ehrh. and the other as having features in common with the European *F. silvatica* L. and other closely related species of Eurasia. An attempt was made to follow these formelements downwards into the Tertiary as long as possibility permitted.

With reference to the last group mentioned the following could be stated. In the European Tertiary deposits containing leaves of *F. silvatica* simultaneously leaves which were resembling those of Eastasiatic species such as *F. crenata* and *F. japonica* occurred. But this fact does not appear to be abnormal as even in the recent European population of *Fagus* such leaves occur viz. leaves of *F. silvatica*-type are present in the Eastasiatic species. That is to say the variation of these species overlap because of their close relationship. Because of the simultaneous occurrence of all these forms in one and the same area including the European Miocene and Pliocene *Fagus* compared with *F. silvatica* must have been a more polymorphic species than it is now.

A depauperation of formelements taking place probably during the Pliocene and most likely in a more extensive way during the Quaternary ice-ages caused a species formation by isolation.

In Europe *F. silvatica* can be followed downwards to the Miocene and has been restricted to the temperate zones of Eurasia according to our present knowledge. No finds of fossil *Fagus* comparable with *F. silvatica* are known, neither from the Arctic of Eurasia or the Americas.

As to the fossil occurrence of *F. grandifolia* in Europe we have very good evidence that some leaves comparable with this species really belong to it. Although some species of other genera, as for instance *Quercus* and *Castanea*, have leaves similar to that of *F. grandifolia* also that intermediate forms between *F. silvatica* and *F. grandifolia* occur, those specimens cited in the first part of the list (see above) represent fossil *F. grandifolia*. Even in Asia typical remains of Late-Tertiary *F. grandifolia* have been found. In N America *F. grandifolia* is present from pre-Miocene sites upwards to the present time. Thus the species is a Tertiary relic within the area of its present distribution.

According to our present knowledge the stratigraphic distribution of the species in Europe stretches from the Miocene to the Upper Pliocene. The species accordingly became extinct at the very end of the Tertiary period or at the very beginning of the Quaternary during the advance of the first glaciation.

VI. Literatur

Abkürzungen:

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KVA=Kgl. Vetenskapsakademien, Stockholm.
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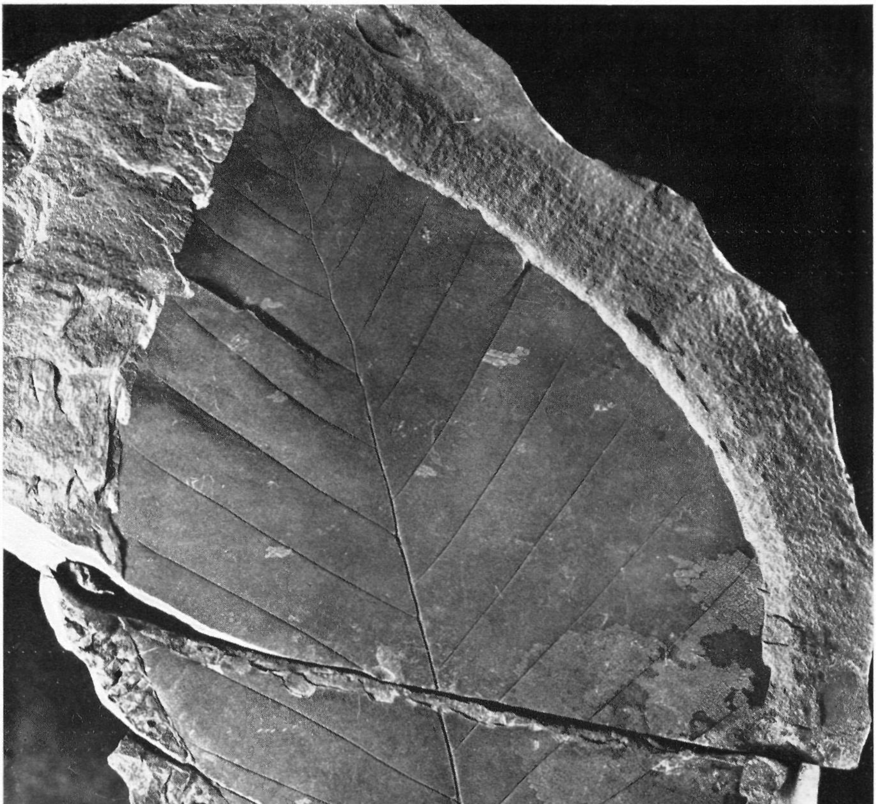
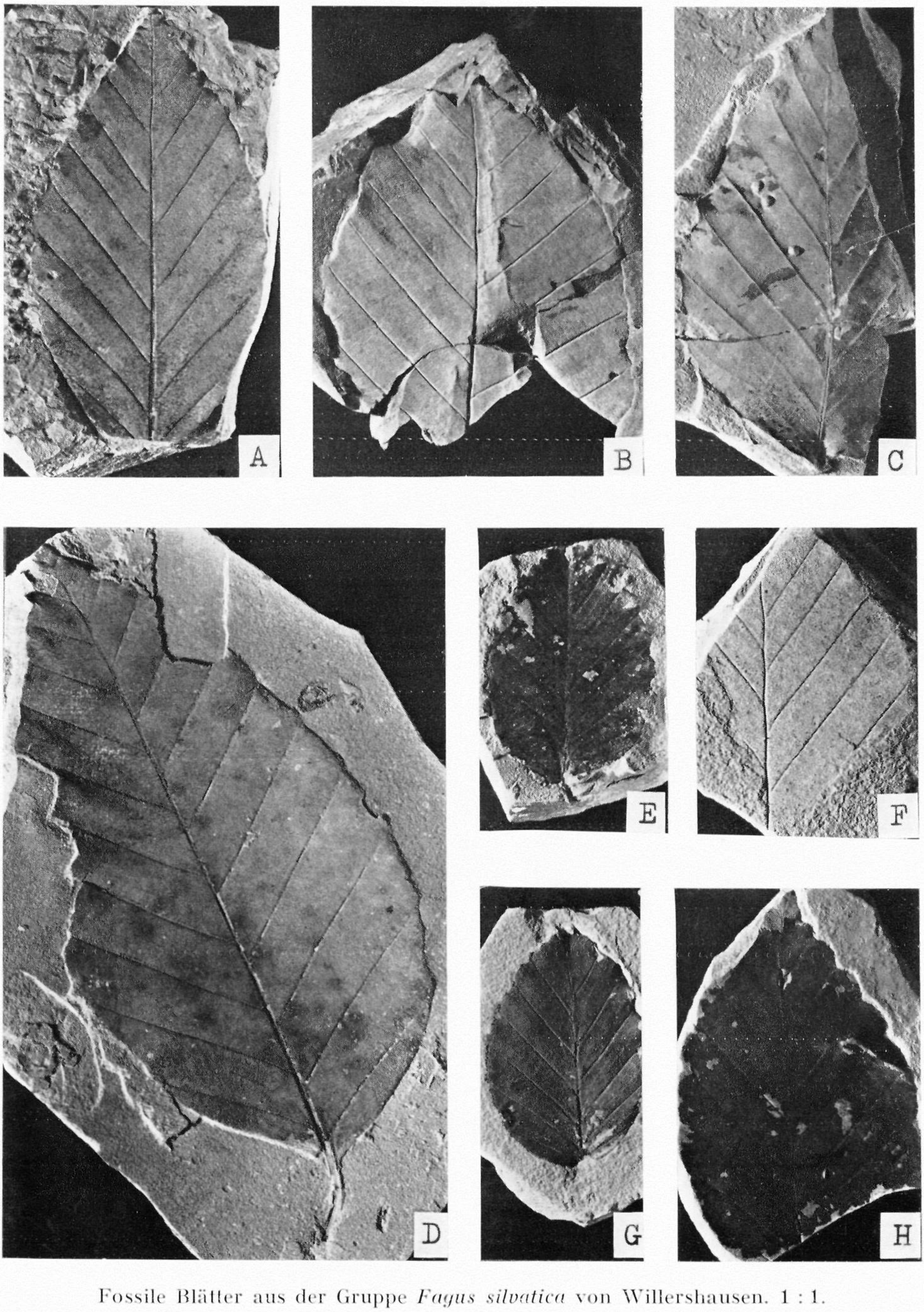


Fossiles Blatt aus der Gruppe *Fagus silvatica* von Willershausen. 1 : 1.
Foto: K. E. Samuelsson.



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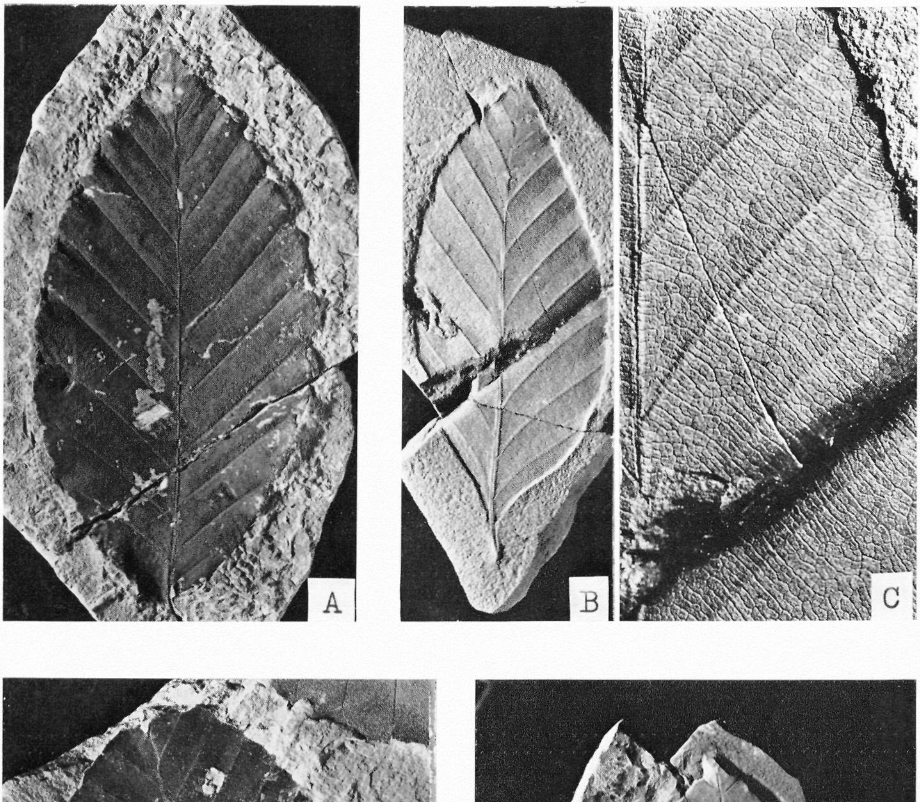

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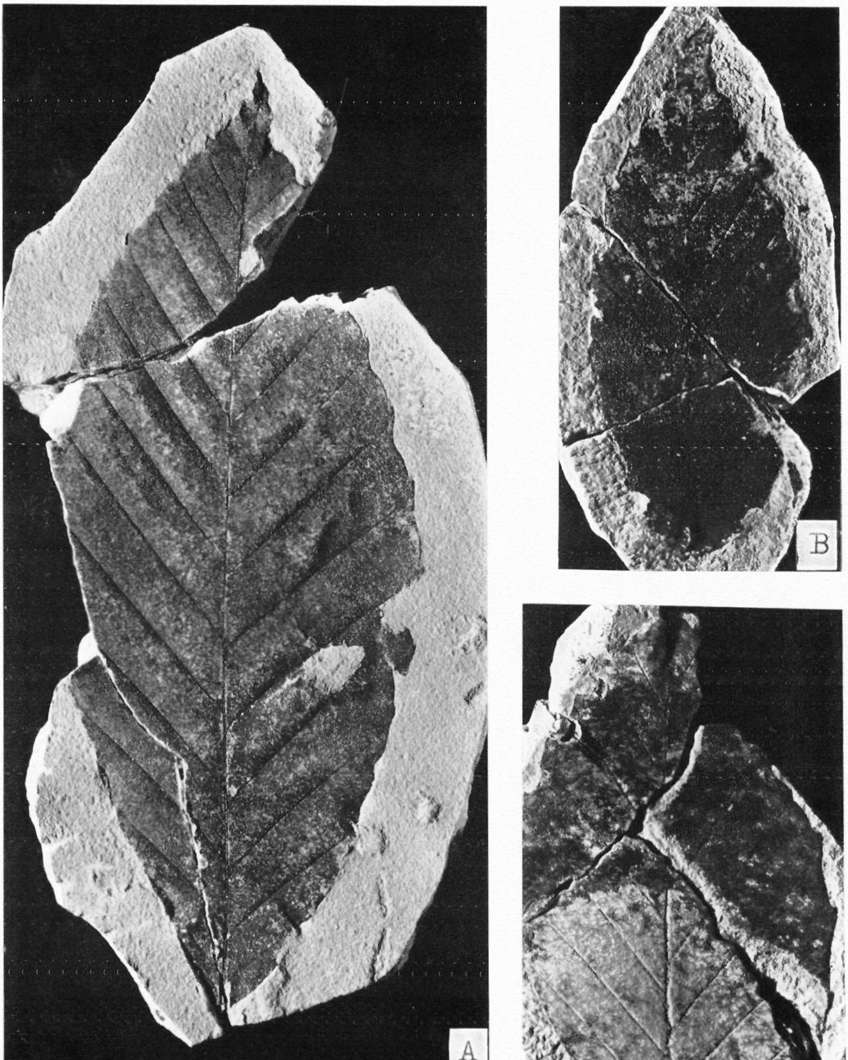

Fossile Blätter aus der Gruppe *Fagus grandifolia* von Willershausen. 1 : 1.
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A Revision of Pteris dentata and Related Species

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(Meddelande från Lunds Botaniska Museum, Nr 162)

Introduction

During excursions in the Aegean in 1958 a remarkable fern was found along two small streams in the south-western part of the island of Ikaria. This fern has been identified as *Pteris dentata* Forsk., a mainly South-African species not previously recorded north of Ethiopia and Yemen.

As the specimens collected deviate in some details from South-African material a revision was undertaken on available herbarium material. In this revision also the Macaronesian species *P. arguta* Ait., as well as the Australian and Pacific species *P. tremula* R. Br., were included, as they have often been confused with *P. dentata*.

Fronds

The species treated are in habit rather similar. From a short rhizome several tufted, 0.5—1.5 m long fronds, with a ± horizontal blade and a ± drooping apex, extend. The petioles are as long as the blade or longer. The blade is narrowly deltoid, glabrous, and 2-pinnate (at least the basal pair of pinnae partly further subdivided), usually with 8—15 pairs of pinnae in acute angles to the rhachis. Fertile and sterile blades are not very different. The fertile ones, however, have narrower segments and are often smaller and more erect. Even if the species are alike in habit, they can easily be distinguished in sterile material by minor characteristics.

In *P. arguta* all pairs of pinnae are simply pinnatifid, excepting the lowermost one, in which 1—3 of the basal segments, directed downwards, are transformed into pinnatifid pinnulae (fig. 1 A). If only one such pinnula is developed in each of the basal pinnae, it is usually very large, giving almost an impression of a dichotomous subdivision of the pinna.

In *P. tremula* (Macaronesian and at least part of the south-hemispheric material) only the uppermost pinnae are simply pinnatifid, while the other ones have at least the basal pair of segments transformed into pinnatifid pinnulae. In the lowermost pair of pinnae usually 2—6 pairs of segments are further subdivided in this way (fig. 1 B). In such a pair there is little difference in size between the two pinnulae.

In *P. dentata* the central and uppermost pinnae are simply pinnatifid, while at least the basal pairs have some segments transformed into pinnatifid pinnulae (fig. 1 C). Usually several such pinnulae, directed downwards, occur in the basal part of the blade, and not rarely a few pairs of pinnatifid pinnulae are found. In such a pair there is always a considerable difference in size between the pinnulae (those directed upwards being smaller).

Characteristic for the segments of the species treated is the decurrent base, the small, prickle-like scale at the base of the upper side of the midrib, and the free veins, which are once forked, with the exception of the basal ones which may be further subdivided (especially common in *P. arguta*), and the apical ones which are undivided. The form of the segments varies considerably even within the same taxon. However, in *P. arguta* they are always relatively broad ($\geqq 5$ mm) and very often short and narrowly deltoid (fig. 1 A, D). In *P. tremula* (Macaronesian and part of the south-hemispheric material) the segments are small and narrow (c. 3 mm), with a rounded apex, and at least many of them are somewhat contracted towards the base (fig. 1 E). In *P. dentata* there is a considerable variation in length and breadth of the segments. However, in ssp. *dentata* they are often longer and narrower than in ssp. *flabellata*.

The margin of the segments is smooth in fertile sections. In sterile segments and sterile parts of fertile ones the margin is crenate to denticulate in *P. arguta, P. tremula,* and *P. dentata* ssp. *dentata* (fig. 1 D, E, H), while it is serrate to serrulate with ± hooked teeth in *P. dentata* ssp. *flabellata* (fig. 1 F, G). There is, however, a considerable variation in the denticulation of the segments within ssp. *flabellata*. The material from Ascension and part of that from St. Helena and South Africa has thus a more deeply serrate margin with less hooked teeth than the rest of the material.

Fig. 1. Basal pinnae ($\times 1/3$): A. *Pteris arguta*, B. *Pteris tremula*, C. *Pteris dentata* ssp. *dentata*. — Segments from pinnae in central part of the blade ($\times 1.5$): D. *Pteris arguta* (fertile segments with pseudoindusia not yet fully developed), E. *Pteris tremula* (old fertile segments), F, G. *Pteris dentata* ssp. *flabellata* (F sterile segments, G fertile ones), H. *Pteris dentata* ssp. *dentata* (fertile segments).

The texture and colour of the blades vary considerable. *P. arguta* has dark green, coriaceous blades, which are ± glossy on the upper side. In the other species the surface is mat. *P. tremula* and *P. dentata* ssp. *dentata* (excepting part of the material from Ethiopia) have greyish green, subcoriaceous blades, while *P. dentata* ssp. *flabellata* and part of the material of ssp. *dentata* from Ethiopia have green, herbaceous ones. The colourless marginal supporting strand of the segments is more strongly developed in *P. arguta* than in the other species.

The petioles in all treated species are smooth, ± glossy, and with a colour varying from reddish brown to straw-coloured. In transversal sectioning the petiole is usually rounded with an insertion on the lateral side in *P. arguta* and *P. tremula,* while it is U- or V-shaped in *P. dentata.*

The petiole is glabrous, except for the very base which has small scales, easily seen at least in young fronds. The scales are only a few mm long and have the same texture and approximately the same cell type and cell size in the different species.

Sori and Sporangia

The extension of the sori as well as the breadth of the pseudoindusia covering them seem to be essential taxonomic characters in the species group treated.

In *P. arguta* the sori cover between $^1/_3$ and $^2/_3$ of the basal part of the margin of the segment, while in *P. dentata* and *P. tremula* the whole margin, excepting the very tip and the sinuses, is often covered by sporangia. The sori are broader, having more numerous sporangia in *P. arguta,* than in other species.

The pseudoindusia in *P. arguta* are broad (1.0—1.5 mm) and persistent, almost wholly covering even fully developed sori. *P. dentata* has narrow (0.3—0.5 mm) and rather ephemeral pseudoindusia, which are hardly visible in fully developed sori. In *P. tremula* the margin of fertile parts of segments is often somewhat undulate, with ± subcontinuous pseudoindusia.

The sporangia are similar, with 16—24 indurated cells in the annulus, in the different species. However in *P. tremula* opened sporangia are divided into two cup-formed parts connected solely by the annulus, while in *P. arguta* and *P. dentata* the sporangial wall is irregularly broken when sporangia open.

Spores

Spore material in herbarium specimens of the species treated has been investigated. The spores were kept in a filtered medium of gum arabic, glycerine, and chloral hydrate (gum arabic 30 g, glycerine 20 cc, chloral hydrate 50 g, distilled water 50 cc).

The values of the spore size given are the mean of measurements of 20 spores. The spores were measured in the equatorial zone from an angle to the middle point of the opposite side, including the equatorial ridge.

The spores of the species treated are all light brown, anisopolar, ± radiosymmetric, trilete, with a biconvex profile. The length of the leasure seems to vary considerably in all species as well as the sculpture of the margo. The equatorial ridge has a smooth zone on each side separating it from the sculptured parts. For the terminology of spore structures see Harris (1955).

P. arguta. The shape of the spores (fig. 2 A) is triangular in polar view, with concave to straight sides (at least one of the three sides is concave). The exine is muricate with very low, ± irregular, apparently minutely rugulose verrucae. There seems to be no or little difference in sculpture between distal and proximal sides. The smooth equatorial ridge is broader (4—6 μ) than in other species. It is widest in between the angles, thus changing the outline of the spore from concave to convex.

In size the spores vary from 42 to 48 μ (fig. 3 D).

The variation in spore size and surface sculpture is small in *P. arguta,* even in collections from different geographic areas.

The drawing of spores of *P. arguta* in Maire et. al. (1952, fig. 40) is very simplified and partly incorrect (unripe spores?).

P. tremula. The shape of the spores (fig. 2 B) is triangular in polar view, with convex to straight sides (not more than one side is straight in a single spore). The distal side of the spores has very prominent low ridges, most of which are united, forming a network. The proximal side has a few scattered papillae or short ridges. The equatorial ridge has a ± undulate margin, and is usually 2—3 μ broad, and equally wide around the spore.

The spore size varies from 42 to 46 μ (fig. 3 C).

The variation in spore sculpture in the material studied is without importance (even in morphologically deviating material from, e.g., Norfolk Island). However, the development of the network on the distal side varies to some extent.

The drawing of a spore of *P. tremula* by Harris (1955, pl. 7: 9) is very simplified.

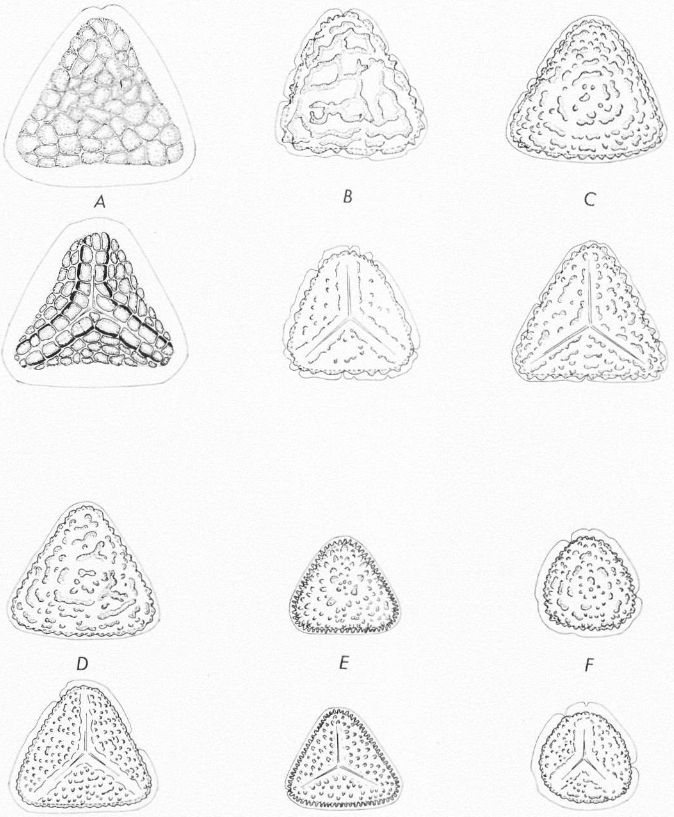

Fig. 2. Spores from distal and proximal sides: A. *Pteris arguta,* B. *Pteris tremula,* C, D. *Pteris dentata* ssp. *dentata* (C from Greece, D from Ethiopia), E, F. *Pteris dentata* ssp. *flabellata* (F deviating type from Ascension).

P. dentata ssp. ***dentata.*** The shape of the spores (fig. 2 C, D) is triangular in polar view, with slightly convex to straight sides (at least one of the sides of a spore is convex). The distal side of the spores has low prominent ridges of ± confluent exine elements, combined with low papillae. Sometimes a few ridges unit, but they never form a network. Not rarely the ridges are situated in ± concentric figures. The proximal side may be similar to the distal one, but usually it does not have so many ridges and more numerous papillae. The equatorial ridge is smooth or somewhat undulate, 1—3 μ broad, and equally wide around the spore.

The spore size varies from 38 to 42 μ (fig. 3 B).

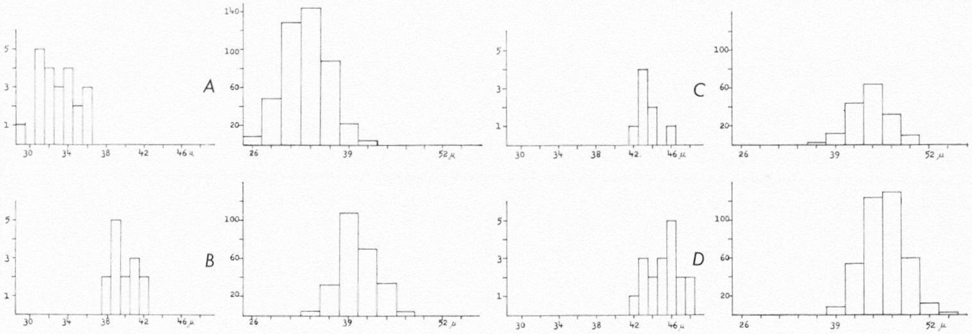

Fig. 3. Measurements of spore diameter in equatorial zone (including equatorial ridge). To the left the mean values of 20 spores from each herbarium specimen (on the vertical axis the numbers of collections measured). To the right the individual values of all spores from each taxon (on the vertical axis the number of spores measured). — A. *Pteris dentata* ssp. *flabellata,* B. *Pteris dentata* ssp. *dentata,* C. *Pteris tremula,* D. *Pteris arguta.*

The variation in spore sculpture is considerable within ssp. *dentata.* Especially the proportions between ridges and papillae, as well as the length of the ridges, vary.

P. dentata ssp. ***flabellata.*** The shape of the spores (fig. 2 E) is triangular to almost globose in polar view, with strongly convex to straight sides. The distal side of the spores has high papillae, rarely confluent, forming a few short ridges. The proximal side is similar to the distal one. The equatorial ridge has smooth or undulate to ± irregularly formed margin, 1—3 μ broad and equally wide around the spore.

The size of the spores varies from 29 to 36 μ (fig. 3 A).

The variation in spore size is rather great even in material from neighbouring localities. Rarely specimens intermediate in spore characters between ssp. *flabellata* and ssp. *dentata* occur. Thus one specimen from Ascension (fig. 2 F) has low papillae and ridges like those in ssp. *dentata,* but the spore size (31 μ) of ssp. *flabellata.* Other specimens from the same island are in spore sculpture not different from typical ssp. *flabellata.* A collection from Angola also has spores with low ridges and papillae resembling those of ssp. *dentata.* Even in this case the spore size (35 μ) falls within the variation range of ssp. *flabellata.* However, even in other characters this collection is intermediate between the subspecies.

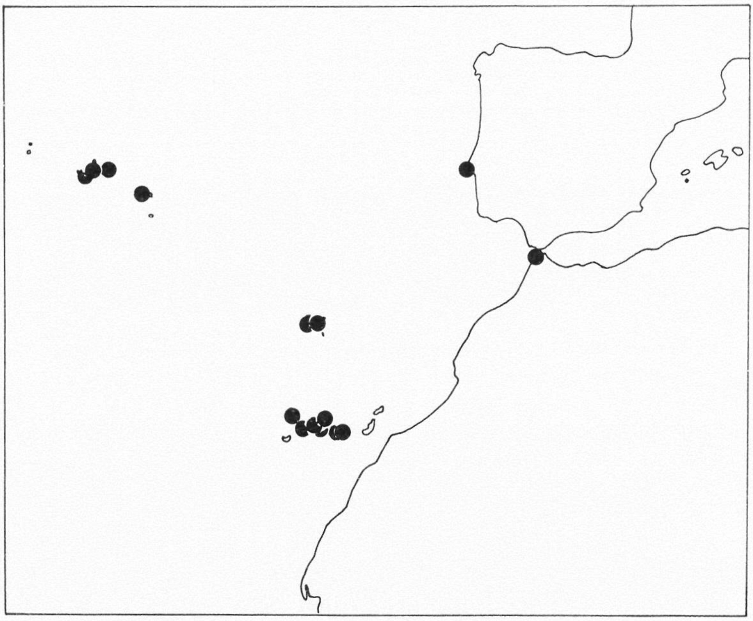

Fig. 4. The distribution of *Pteris arguta.* The locality in Portugal (Lisboa, Sintra) is not regarded as spontaneous by Sampaio (1946).

Ecology

The species treated grow exclusively in areas with a subtropic climate. Their main distribution is concentrated to areas with a humid macroclimate (Macaronesia, New Zealand and adjacent areas, humid parts of South Africa, the subtropic rain-forest belt of high mountains in Central Africa, and small oceanic islands).

According to the literature and labels on herbarium sheets they seem to require a humid microclimate. They grow mainly in the shade of trees, along small streams or rapids. In extremely humid areas they also seem to occur in forests and on shady cliffs.

Distribution

Pteris arguta seems to be wholly restricted to the Macaronesian area (fig. 4), where it occurs abundantly on the Atlantic islands. Old records for this species from Yemen, Ethiopia, and South Africa are due to confusion with *P. dentata.* The occurrence in Portugal (Lisboa, Sintra) is hardly spontaneous according to Sampaio (1946).

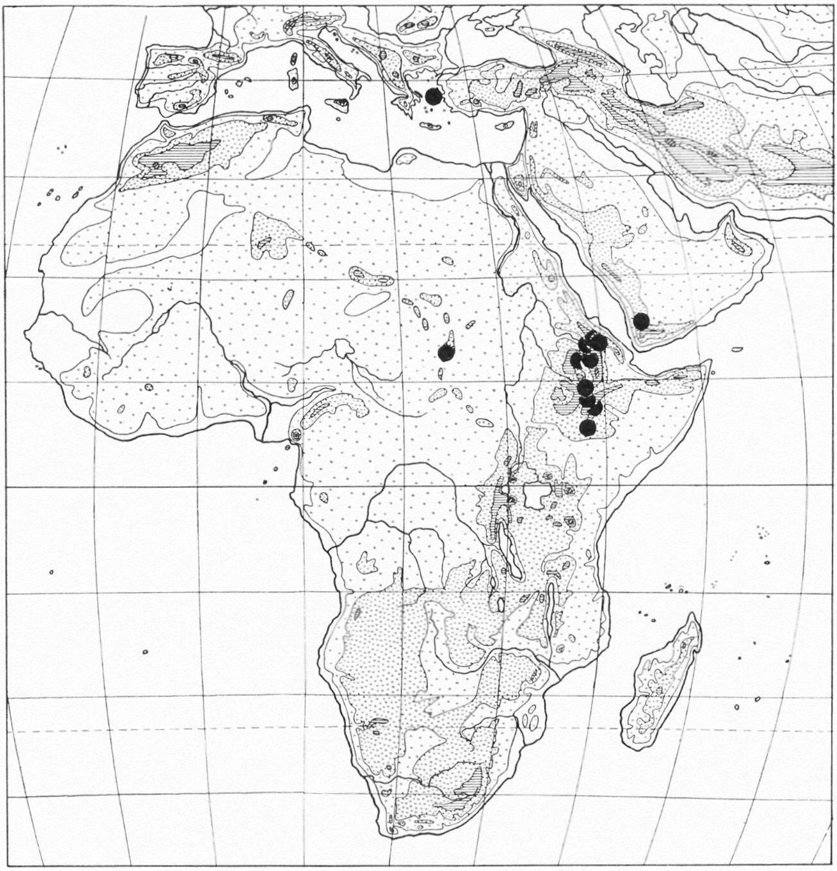

Fig. 5. The distribution of *Pteris dentata* ssp. *dentata*.

Pteris tremula is native in S.E. and E. Australia, Tasmania, Norfolk Island, New Zealand, Kermadec Island, and Fiji. In this area it is regarded as a polymorphic species (Hooker 1852 p. 176, Dobbie 1952 p. 180). Trealease (1897 p. 171) and Sim (1915 p. 256) reported it as an escape from cultivation in the Azores and South Africa, respectively. The small herbarium material examined by me of non-cultivated specimens (determined to *P. arguta*) from the Canary Islands, the Azores, and Portugal is very uniform, and coincides well with the photograph of a New Zealand specimen in Dobbie (1952 p. 181). To what extent *P. tremula* is now naturalized in Macaronesia needs to be investigated.

In this paper *Pteris dentata* has been subdivided into two geographically vicarious subspecies. Old records for the species from India,

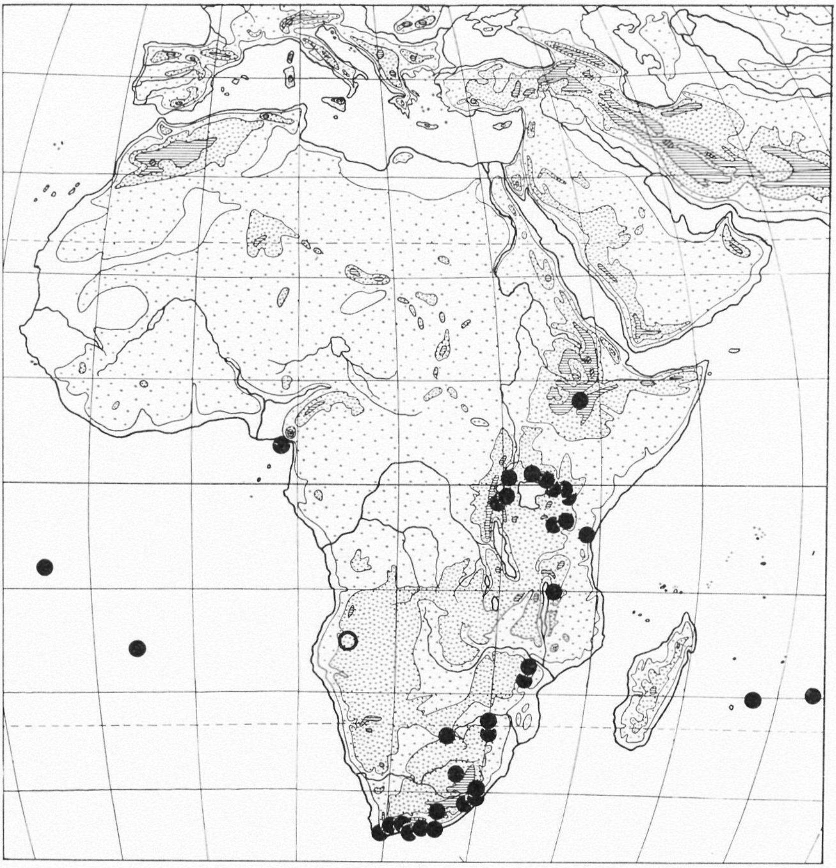

Fig. 6. The distribution of *Pteris dentata* ssp. *flabellata* (open ring indicates a locality with specimens intermediate between ssp. *flabellata* and ssp. *dentata*). Except in localities indicated on the map the species has been recorded for Madagascar and Cape Verde Islands. From these areas, however, I have not seen specimens.

the West Indies, and Macaronesia have not been verified and are probably due to confusion with other species.

P. dentata ssp. *dentata* (fig. 5) is apparently rather common in the high mountains of Yemen and Erithrea, as well as in parts of Ethiopia. The scanty material seen from the Marra Mountains in Sudan is also best referred to this subspecies.

The newly discovered localities in the Aegean are situated c. 2700 km from the nearest known one in Africa. They are located in the westernmost part of the island of Ikaria, in an area with siliceous bedrock (mainly hard schists). The species grows along small streams with perpetual water flow, shaded by plane and olive trees. The localities have a position well protected against northern winds, on the lower parts of a strongly sloping and partly vertical declivity, which is c. 1000 m high, exposed to the south, and facing the sea. This type of locality is surely unique within the Aegean. The preserved material of *P. dentata* cultivated in botanical gardens in Europe wholly belongs to ssp. *flabellata* (the species, however, is hardly cultivated in Greece). Therefore it is no doubt that *P. dentata* ssp. *dentata* is spontaneous in Ikaria, an island which is very isolated. This is especially true for the western part, which is difficult to reach and poorly inhabitated (only with a few small and poor villages). Because of the isolation, the island has formerly been visited only by two botanists Forsyth Major (1887) and Rechinger (1932, 1934). These botanists have only been able to reach the central and eastern parts of the 45 km long island.

The localities in the Aegean may be the result of a successful long-distance migration to a locality especially suitable for this subtropical plant. The possibility cannot, however, be overlooked that the localities in the Aegean are outposts of a relic area for the species in Asia Minor, not yet detected, as habitats similar to those of Ikaria probably exist along the south-western and southern coasts of Turkey.

In this connection Mazziari's old record of *P. arguta* (cf. Halacsy 1904 p. 469) from Kerkira (Corfu) in western Greece may be worth mentioning. This record has generally been regarded as incorrect and apparently no preserved material exists. However, there is still the possibility that the actual fern has been incorrectly determined and instead is *P. dentata*.

Several other examples exist, where mainly South-African species or genera are represented in the Mediterranean, in a way which gives an impression of former connections. Such examples are *Pteris cretica* L. (not in Crete), *Triglochin bulbosum* L., *Pelargonium, Mesembryanthemum,* and *Romulea.*

P. dentata ssp. *flabellata* is common in humid parts of South Africa at low altitudes, and in the Central and East African Mountains from North Rhodesia to Ethiopia at altitudes from 1000—3000 m (fig. 6). Besides it has been collected in western Angola in a form which in many respects is intermediate between the two subspecies. Outside this area I have seen specimens from Mauritius, Rodrigues, St. Helena, Ascension, and Fernando Po. *P. dentata* has also been recorded for

Madagascar and Cap Verde Islands. The material examined by me from Reunion determined to *P. dentata* is not that species but *P. biaurita* L.

Moreover, it may be worth mentioning that a minor part of the material from South Africa and St. Helena and the whole material seen from Ascension has smaller fronds and more deeply serrate margin of the segments than the rest of ssp. *flabellata*. This morphologically sometimes rather striking form has by some authors been treated as a distinct taxon (*P. ascensionis* Sw.).

Taxonomy

The taxa treated have the following characteristics in common: narrowly deltoid, 0.5—1.5 m high fronds; pinnatifid or partly further subdivided pinnae, in acute angles to the rhachis; segments in acute angles to the midrib, decurrent, often somewhat curved, with a small prickle-like scale at the base of the upper side of the midrib and free veins, which are once forked, except for the lowermost ones, which may be further forked and the apical ones which are undivided; sporangia with 16—24 indurated cells in the annulus; spores ± triangular in polar view, with sculptured surface and a distinct equatorial ridge.

Key to the Taxa

1. Only in the lowermost pair of pinnae 1—3 of the basal segments directed downwards transformed into pinnatifid pinnulae. Segments ± glossy, coriaceous, dark green. Pseudoindusia 1—1.5 mm broad, persistent. Sori restricted to the basal $^{1}/_{3}$ $^{2}/_{3}$ of the margin of the segments. Spores muricate, 42—48 μ, equatorial ridge c. 5 μ. . . . . *P. arguta*
2. At least several segments of the basal pairs of pinnae transformed into pinnatifid pinnulae (excepting very small blades). Segments mat, subcoriaceous to herbaceous, greyish green to green. Pseudoindusia 0.3—0.5 mm brod, ± ephemeral. Sori not rarely covering the whole margin of the segments (excepting the apices and the sinuses). Spores papillose to reticulate or with free ridges, 29—46 μ, equatorial ridge 1—3 μ.
   A. Basal pair of segments in the pinnae (excepting the uppermost, small ones) transformed into pinnatifid pinnulae. Segments with rounded apices, and at least most of them somewhat contracted towards the base. Pseudoindusia ± subcontinuous. Spores 42—46 μ, on the distal side with confluent ridges forming a network. . . . . *P. tremula*
   B. Segments transformed to pinnatifid pinnulae only in the basal part of the blade. If pairs of pinnulae occur, those directed upwards always much smaller. Segments ± acute usually not contracted towards the base. Pseudoindusia wholly continuous. Spores 29—42 μ, papillose or with free ridges.

a. Margin of segments (excluding fertile parts) crenate to denticulate (fig. 1 H). Spores 38—42 μ, with prominent low ridges at least on the distal side. *P. dentata* ssp. *dentata*

b. Margin of segments (excluding fertile parts) serrate to serrulate, with ± hooked teeth (fig. 1 F, G). Spores 29—36 μ, with high papillae. *P. dentata* ssp. *flabellata*

Pteris arguta Aiton 1789 p. 458.

Orig. coll. Madeira 1772 Masson (S, syntype).

The species is not very variable. The segments may be short and deltoid or moderately long and ± linear. The variation in spore size and spore sculpture is small.

I can see no reason to regard *P. arguta* as closely related to *P. dentata*. Instead it may be compared with *P. longipinnata* Wall (cf. Hooker 1852 p. 179). It has, e.g., the shape and size of segments, type of pseudoindusia, shape and sculpture of spores in common with this species.

Distribution. Canary Islands, Madeira, Azores, Portugal (Estremadura), Morrocco (Tanger).

Pteris tremula R. Brown 1810 p. 806.

Orig. coll. S.E. Australia, N.S. Wales, Port Jackson 1802—1805 R. Brown, (LD, syntype).

The species is variable in vegetative characters. Especially material from Norfolk Island is deviating. However, in the material examined spore sculpture and spore size are rather constant. By Hooker (1852 p. 175) and Christ (1897 p. 168) *P. tremula* is regarded as closely related to *P. chilensis* Desv. from humid parts of Chile.

The Macaronesian material is uniform and similar to material from New Zealand.

Distribution. S.E. and E. Australia, Tasmania, Norfolk Island, New Zealand, Kermadec Island, Fiji (according to Dobbie 1952, Harris 1955). Escaped from cultivation in South Africa and Macaronesia.

Pteris dentata Forskål 1775 p. 186 and CXXIV.

Orig. coll. Yemen, environments of Hadie 1763 (preserved specimens lost, if ever existing). — Neotype: Yemen, Menacha 2300 m. s.m. 1889 Schweinfurth 1402 (C).

ssp. *dentata*.

Specimens showing transitions to ssp. *flabellata* occur in Ethiopia (with herbaceous, green, broad, and rather short segments).

Distribution. Yemen, Erithrea, Ethiopia, Sudan (Marra Mts), Greece (Ikaria).

ssp. *flabellata* (Thunb.) stat. nov.

Pteris flabellata Thunberg 1800 p. 172. — Orig. coll. South Africa. Cape Province, between Taffelberg and Leuwekopp 1772—1775 Thunberg (UPS, lectotype).

Ssp. *flabellata* is a relatively variable taxon. A somewhat deviating type (with small fronds and deeply serrate segments) occurs on Ascension and rarely also on St. Helena and in South Africa (*P. ascensionis* Sw.). The taxonomic value of this type is uncertain. Specimens forming a transition to ssp. *dentata* have been collected in Angola. They have subcoriaceous, greyish green segments and spores with low ridges. Whether this type is a real intermediate between the two subspecies or whether it represents a third taxon in the group cannot be decided on the material available.

Distribution. South Africa, Rhodesia, Angola, Ruanda Urundi, Tanganyika, Kenya, Uganda, Ethiopia (Arussi), Fernando Po, Ascension, St. Helena, Mauritius, Rodrigues (*P. dentata* has also been recorded for Cap Verde Islands, Madagascar, and Reunion, but from these areas I have seen no material).

Appendix

Nomenclature

The nomenclature within this group of *Pteris* has not previously been satisfactorily treated. As far as I know the type material has not been discussed.

The name *arguta* was established by Aiton as a substitute for *P. serrulata* Forsk., a later homonym of *P. serrulata* L. (*P. serrulata* Forsk. is probably a superfluous name for *P. dentata* Forsk., but this can hardly be proved as no type material exists, cf. Christensen 1922 p. 31). Aiton gave the distribution for his new species "Arabia, Madeira, and the Cape of Good Hope". In the description he refers especially to Francis Masson, who introduced the species in England. I therefore find it permissible to include a specimen collected by Masson in Madeira in the type material, as this seems to be the best way of preserving present usage of the name.

Pteris tremula was described by R. Brown. On a sheet in the herbarium of Lund of *P. tremula* (N. Holl. Sieber, Flora Mixta 251) there is a fertile fragment which according to an annotation (sp. origin.) in the handwriting of C. A. Agardh is part of the type material. This fragment is regarded as a syntype of *P. tremula*.

Pteris dentata Forsk. has during the whole 19th century been called *P. flabellata* Thunb., a name based on material from South Africa. However, Christensen in Index Filicum (1906 p. 596) and later on Sim (1915 p. 255) used the older name *P. dentata* Forsk., based on material from Yemen. In Forskål's herbarium in Copenhagen no specimens of *P. dentata* exist or have probably ever existed (cf. Christensen 1922 p. 31). Christensen (l.c.) later doubted his identification of *P. dentata* with *P. flabellata*. However, the name has been generally used for a considerable time and it would be inconvenient to reject it as a nomen dubium. A neotype has therefore been chosen in material collected in the neighbourhood of the type locality.

As the type of *P. flabellata* Thunb. has been designated one of the two specimens of this taxon in Thunberg's herbarium in Uppsala.

Material Used for Drawings

Fig. 1. A. Madeira 1879 Buchanan (E) — B. Canary Islands. Teneriffa, Orotava 1921 Burchard (S) — C. Greece. Ikaria, Ag. Nikolaos 1958 Runemark and Snogerup (LD) — D. Canary Islands. La Palma, Barranco del Rio 1901 Bornmüller (LD) — E. Canary Islands. Teneriffa, Orotava 1921 Burchard (S) — F, G. South Africa, Cape Province, Table Mt. 1908 Dümmer (E) — H. South Africa. Cape Province, Katberg Hutton (C). — Fig. 2. A. Madeira. São Antonio da Serra s. coll. (K) — B. Canary Islands. Teneriffa, Orotava 1921 Burchard (S) — C. Greece. Ikaria, Ag. Nikolaos 1958 Runemark and Snogerup (LD) — D. Ethiopia. Galla e Sidama. Meccia, Bosco di Gaggi 1937 Giordano (FI) — E. Kenya. Mt. Kenya, Kathita River 1949 Schelpe (BM) — F. Ascension 1876 Moseley (E).

Revised Herbarium Material

I am most indebted to the heads and curators of the following institutes, which have placed herbarium material at my disposal.

Botanisches Museum, Berlin-Dahlem (B), British Museum (Natural History), London (BM), Botanisk Museum, Copenhagen (C), Botanical Institute of the University of Coimbra (COI), Royal Botanic Garden, Edinburgh (E), Herbarium Universitatis Florentinae, Firenze (FI), Conservatoire et Jardin botaniques, Genève (G), Royal Botanic Gardens, Kew (K), Universitetets Botaniska Museum, Lund (LD), Instituto Superior de Agronómia, Lisboa (LISI), Institute of Botany, Faculty of Science, Lisboa (LISU), Instituto "Antonio José Cavanilles", Madrid (MA), Naturhistoriska Riksmuseum, Stockholm (S), Institutionen för Systematisk Botanik, Uppsala (UPS).

Pteris dentata ssp. *dentata*

Greece. Ikaria, SW-part, around Ag. Nikolaos 50—300 m 1958 Runemark and Snogerup 6139, 6239, 11250, 12581, 12649 (LD)

Yemen. Menacha: the well Mechader el Kahil 2300 m 1889 Schweinfurth 1402 (B, C), Schiham near Kahil 2200—2500 m 1889 Schweinfurth 1400 (B); Wadi Nahemi, Attara, Jebel Harrasa 1800 m 1889 Schweinfurth 1731 (B, K); Ussil, Wadi Tehm 1300 m 1889 Schweinfurth 1337 (B)

Ethiopia. 1853 Schimper 280 (FI). — Eritrea. Acchelè-Guzai: Adi Caieh 2200 m 1915 s. coll. (FI), Soira, Goló 2800 m 1902 Pappi (FI) 1905 Dainelli and Marinelli (FI), Embalocà 1905 Dainelli and Marinelli (FI); Assaorta, Bosco di Caribozzo, Cohaito 2700 m 1902 Pappi 5207 (FI); Scimenzana, Guna-Guna 2200 m 1902 Pappi (FI); — Hamasen: Enda Abbo, Garawoldi (Dorfu) 1800 m 1915 Baldrati (FI), Bet-Garghis, Makalo, S. Giorgo 1902 Pappi (FI);

Tigrai, Adua 1838 Schimper 1156 (FI, S). — Amhara. Tembien Solazzo (FI). — Semien. Lumanino 1909 Chiovenda (FI), Ambiquo-Mai Sciahà 2950 m 1937 Pichi-Sermolli 1977 (FI). — Shoa. Mulu Sayu 2400 m 1952 Curle and Schelpe 31 (FI), Entotto 1896 Traversi (FI), "Limbossa" 2300 m 1909 s. coll. (FI), mt. Jerer 1916 Buscalioni 1913 (FI). — Galla e Sidama. Meccia, Bosco di Gaggi 2600 m 1937 Giordano 1895 (FI), Badditu, Keli, E-foot of Amaro Mts 1600 m 1953 Gillet 14877 (K)

Sudan. Darfur Province. Marra Mts: between Jebel Uo and Nyuringya 2700—3000 m 1934 Dandy 104 (BM), Miranya 2000 m 1921 Lynes (K)

Pteris dentata ssp. *flabellata*

Ethiopia. Arussi. Shashamanné, Soyuma 1700 m 1954 Mooney 5716 (FI)

Kenya. Mt Kenya: 3000 m 1922 Fries (UPS), West Kenya Forest St. 2350 m 1922 Fries (S, UPS), Nanyuki-Chagoria Track 2700 m 1943 Meinertzhagen 105 (K), Lower Sagana Falls 2700 m 1949 Schelpe 2804 (BM), Kathita River 3000 m 1949 Schelpe 2599 (BM); Nairobi distr.: Thika Road 2600 m 1950 Verdcourt 366 (K), Maruba Forest 1600 m 1949 Schelpe 2375 (BM); Aberdare Mts: Kinangop 2900 m 1934 Taylor 3887 (BM), SW-Aberdare Forests, Najabini 1500 m Gardner 1264 (K), W-part of Nyeri Track 3070 m 1948 Hedberg (S); Mt Elgon, eastern slope: 1920 Lindblom (S), above Japata 2100 m 1948 Hedberg (S)

Tanganyika. Mt Meru: 1903 Fickert (S) 1922 Fries (UPS), Thoura Forest 2000 m 1934 Longfield (BM); Kilimanjaro: 1884 Johnston (FI), Kihosho 2200 m 1907 Daubenberger 56 (E, K, S), Lyamungo 1300 m 1932 Greenway 3081 (K); Usambara Mts: E of Magamba 1650 m 1953 Drummond and Hemsley 2829 (K, UPS), Maschaua 1893 Holst 8735 (K); Nyasa Highland, Kyimbila Station 1350 m 1912 Stolz 771 (LD)

Uganda. Kigezi: Sabinio 2600 m 1934 Taylor 2095 (BM), Rubaya 2000 m 1945 Thomas 4255 (FI); Toro: Ruwensori 2000 m Dogget (K) 1940 Eggeling 4016 (K), Kibale Forest 1500 m Thomas 2265 (K); Mpanga Forest 1100 m 1935 Taylor 3234 (BM); Busoga, 14 miles NE of Jinja 1400 m 1952 Wood 458 (BM); "Mariba Forest" 1200 m Loveridge 14 (K)

Congo. Kivu: Mushuhangabo 2000 m 1930 Burtt 3157 (K), between Buronga and Kikeri 1937 Louis 5151 (BM), between Kilremba and Mikeno 1937 Lebrun 7182 (BM), "Nyamlagyza" 2000 m 1944 Germain 3175 (BM)

Fernando Po. 2200 m 1860—61 Mann (K), Moka 1200 m 1951 Adams 1048 (BM) 1933 Exell 839 (BM), Pico de Santa Isabel 1947 Guinea 2959 (BM, G)

S. Rhodesia. Umtali: Imbesa Forest Estate 1100 m 1956 Chase 6240 (BM), Vumba, below Cripps' Grid 1948 Chase 1107 (BM), Stapleford Forest Res. 1953 Chase 5168 (BM), S-slope of Lumamatshira Mts 1949 Chase 3315 (BM); Melsetter, Belmont Farm 1950 Chase 3087 (BM)

Transvaal. s. coll. (FI); Magaliesberg 1845 Zeyher (BM); Selati 1000 m Junod 4053 (K); Zoutpansberg 1300 m 1894 Schlechter 4600 (BM, COI, K)

Orange Free State. 1863 Cooper 1055 (BM).

Natal. s. coll. (E) Buchanan (E) Zeyher (FI); Howick, bottom of Shelter Falls 1941 Rycroft 325 (BM); Mooi River, Bray Hill 1902 Johnston 979 (E); Van Reenenpass Rehmann 7216 (S)

Cape Province. "Cape Bon Spei" s. coll. (C, E, LD, UPS) Harvey (E) Buchanan (E) Sieber 9 (BM, C, E, K, S); Cape distr.: Bowie (BM), between Taffelberg and Leuwekopp Thunberg (UPS), Chapman Bay 1852 Mc Gillivray (K), Devil's Peak 1897 Dod 2370 (K) 300 m 1838 Drège (BM, K, S), Table Mt. 150 and 300 m Dümmer 447, 697 (E) Ecklon and Zeyher (E, LD), Karbonkelberg 600 m 1938 Levyns 6589 (BM), Tulbagskloof Ecklon and Zeyher (UPS), Katrivier above Philipstown 1000—1300 m Ecklon and Zeyher (LD); Worcester distr.: 1860 Cooper 1602 (BM) Zwellendam Ecklon and Zeyher (S), Stellenbosch, Jonkars Hook 500 m 1941 Adamson (BM); "Kaffraria" 1860 Cooper 1055 (BM); Knysna: 1858 Trimen (BM) s. coll. (FI), N of Plattenberg Bay 1947 Rodin 1182 (E, G); Humansdorp: Tzitzikama Forest 250 m 1953 Schelpe 4376 (BM) 1894 Schlechter 5951 (BM, G), Blauuwkrantz Pass 100 m 1953 Schelpe 4343 (BM); Queenstown, Katberg Hutton (C); Uitenhage: Zuureberg 700—1000 m Ecklon and Zeyher (S), Kragakamma Harvey (FI); Amatola Forests Sim (E); Somerset East, Boschberg 1877 Mc Owan (FI, G, UPS); Griqualand East, Omsamcaba 250 m 1838 Drège (BM, K)

Ascension. s. coll. (LD) Sparrman (S) d'Urville (E) 700 m Gordon (E) Mc Curvan (K) 1779 Forster (S) 1876 Moseley (E, K) 1813 Bory (E)

St. Helena. 1832 s. coll. (E) 1850 s. coll. (K) Houghton (K, UPS) Anderson (S) Braun (S) 1856 Perrotet (E) Cuming 425, 426, 1041 (E, FI, LISU, K, UPS) 700 m 1953 Schelpe 3736 (BM) 1930 Mortensen 429, 432 (C), Swanley Valley 1809 Burchell (K), Busch Rosemary 1901 Just (S)

Mauritius. s. coll. (FI, LD) Mc Gregor (BM) Neville (K) Gröndahl (S).

Rodrigues. 1859 Duncan (BM) 1874 Balfour (K), Cascade Pigeon 200 m 1924 Corbett (K)

Pteris arguta

Portugal. Brotero (C). — Estremadura, Serra de Sintra 1846 Welwitsch (LISU) 1852 Welwitsch 466 (E, G, FI) 1798 Schousboe (C, K) 1880 da Cunha (LISU)

Azores. s. coll. (LD) 1868 Drouet (BM). — São Miguel: 1845—46 Hunt 337 (BM, C, K), Feteiras 1903 Carreiro 588 B (COI), Lameiro 1898 Carreiro 588 (COI); São Jorge: 1929 Warburg and Tutin (K), S:ta Antonio 1937 Palhinha (LISU) 1938 da Cunha (LISU), Pico des Monteiros 1938 da Cunha (LISU); Pico 1842 Watson (E, FI) Hochstetter 184 (BM) 1937 Prainha (LISU); Terceira: 1937 Palhinha (LISU): Angra do Heroismo s. coll. (COI)

Madeira. s. coll. (BM, C, COI, E, FI, LISU, K, LD) Cavanilles (S) Dickson (S) Fritze (S) Voigtlaender-Tetzner (S) Alexander (E) Ross (E) Sieber (BM) Welwitsch (LISU) 1844 Mc Iravan (E) 1852 Mc Gillivray 115 (K) 1856 Mason (E) 1856 Young (E) 1879 Buchanan (E) 1829 Lowe (E), Ribeiro Frio 1838 s. coll. (LISU) Lemanne (K) 1901 Vahl (C) 800 m 1878 Thiebaut 2310 (FI, K) 600 m 1880 Fritze (LD, FI) 900 m 1900 Bornmüller 1429 (LD, S) 1100 m 1885 Lindman (S, UPS), São Joano Holl (LD), Melhada Velha 1865 Mandon 297 (BM, C, FI, K, S), Caldeirãs Verde 1941 Carvalho (LISI) 1949 Romariz (LISU), São Antonio da Serra s. coll. (K), Ribeiro Santa Luzia 1880 Fritze (FI) 1906 Carvalho (S), Ribeiro da Touvos 1877 Hildebrand (S), Gran Curral 1885 Lindman (S, UPS) 1100 m 1900 Bornmüller 1427 (LD, S), Machico, Portella 400 m 1900 Bornmüller 1428 (S), Ribeiro da Porco 1200 m 1929 Cyrén (UPS), Ribeiro da Passo 1952 Een and Persson (S), "Lucimadas" 1954 da Gama (COI), Fayal s. coll. (LISU), Rabacal s. coll. (LISU), Levada do Furado 1951 Romariz (LISU)

Canary Islands. s. coll. (E, FI, K) Smith (C) 1848 Webb (E), "Tarifa" 1897 Caster-Cook (UPS). — Gran Canaria: S. Mateo 1892 Murray (C), El Cumbre 1861 s. coll. (K), Tenteniguada 1856 Bolle (BM), Firgas Bañas 1912 Rosendahl (S). — Gomera. Valle Hernioso 1100 m 1924 Czeczott 290 (K). — La Palma. Barranco del Frio 1901 Bornmüller 3100 (UPS), Los Tiles 400 m 1906 Pitard (S). — Tenerife. Blauer (FI) Broussonet (BM, S) Lindley (K) 1912 Rosendahl (S), La Orotava, Moutijo 500—600 m 1921 Burchard (E), Icod 1884 Christ (FI) 1908 Schröter (S), Santa Cruz, Val Bufadero 1887 Frazer (E), Guimar 1845 Bourgeau 161 (BM, E, FI, K) 1913 Rosendahl (S), Barranco Ruiz 1884 Christ (FI, S), Realejo Alto 1905 Burchard (K) 1921 Börgersen (C), Montes de Anaga, Vueltas de Taganana 500 m 1933 Asplund (S), Las Mercedes 1855 Bourgeau 1550 (C, E, FI, S, UPS)

Tanger. Aglà 1927 Jahandiez 394 (E), Djebel Kebir 1798 Schousboe (BM, C, G, K, S)

Pteris tremula

(Macaronesian localities)

Portugal. Estremadura. Serra de Sintra 1880 Mendiaz (LISU)

Azores. São Miguel, Ponta Delgada 1894 Trealease (K) 1896 Paulsen (C)

Canary Islands. Tenerife. Orotava, Barranco de Moutijo 300—600 m Burchard (S)

Acknowledgement

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Summary

Pteris dentata Forsk. is recorded for the first time in the Mediterranean (Greece, Ikaria). The nearest known locality is situated in Sudan (Marra Mts).

Pteris dentata is subdivided into two geographically vicarious subspecies, ssp. *dentata* and ssp. *flabellata* (Thunb.) stat. nov.

The differences between *P. dentata, P. arguta* Ait., and *P. tremula* R. Br. are analyzed.

P. arguta is not regarded as closely related to *P. dentata,* but attention is called to similarities between *P. arguta* (Macaronesia) and *P. longipinnata* Wall. (East Asia).

Maps for the distribution of *P. dentata* and *P. arguta* have been prepared. The subspontaneous occurrence of *P. tremula* in Macaronesia is discussed.

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Contribution to the Cytology of the Endemic Canarian Element

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Introduction

The flora of the Atlantic Islands is rapidly disappearing by man's more and more intensive methods for cultivating the land. Acre after acre of the lower zone of the Canary Islands is taken in for banana plantations and tomato fields; large areas in the nebular zone are today potato fields and vast areas in the high mountains are rapidly being transformed to conifer plantations. Several of the endemic species are in great danger of becoming extinct, some are already available only in botanical gardens, e.g. *Lotus peliorrhynchus* and probably two of the tree endemic species of *Dorychnium*. Therefore, it is high time to study these relict taxa, which may be regarded as ancestors of several members of the European and African flora, and so most important for our understanding of evolution and migration routes of several plant groups.

In the author's first study of the cytology of the Canarian flowering plants (Larsen 1960) the endemic element revealed several problems which invites further studies. Thus it was shown that the degree of polyploidy of this group is extremely low, the calculation undertaken on the basis of a scrutiny of approximately one tenth of the endemisms. In order to supply further cytological data, seed samples kindly sent through the Botanical Garden in Orotava, Tenerife, have been sown in Copenhagen, and several endemic flowering plants are at present grown in the experimental fields in summer and in hibernation houses in winter.

The methods for cultivation and the cytological technique are the same as described in the author's first work quoted above.

Species studied

Polycarpaea carnosa Chr. Sm. var. ***carnosa***, 2n=18, Fig. 1, No. 254. Tenerife: Valle de Masca, alt. 200 m.

This species is very rare on the islands; it is found in two varieties, the typical one and var. *spathulata* Svent.; in the latter variety Larsen (1960) counted 2n=18, i.e. the same number as found in the var. *carnosa*; the chromosome number is here reported for the first time. The chromosomes are of the same general size and shape. When SAT-chromosomes are not seen in the slides of var. *carnosa,* it may be due to the fixation.

The species is diploid.

Silene bourgaei Webb, 2n=24, Fig. 2, No. 285. Gomera: Roquillo.

Six endemic species of *Silene* are known from the Canary Islands, two are now studied cytologically, viz. *S. nocteolens* Webb & Berth. (Larsen 1960) and the present species. There are great resemblances between the chromosomes of these two species.

The species is diploid.

Rumex lunaria L., n=18, Fig. 3, No. 146. Tenerife: Buenavista.

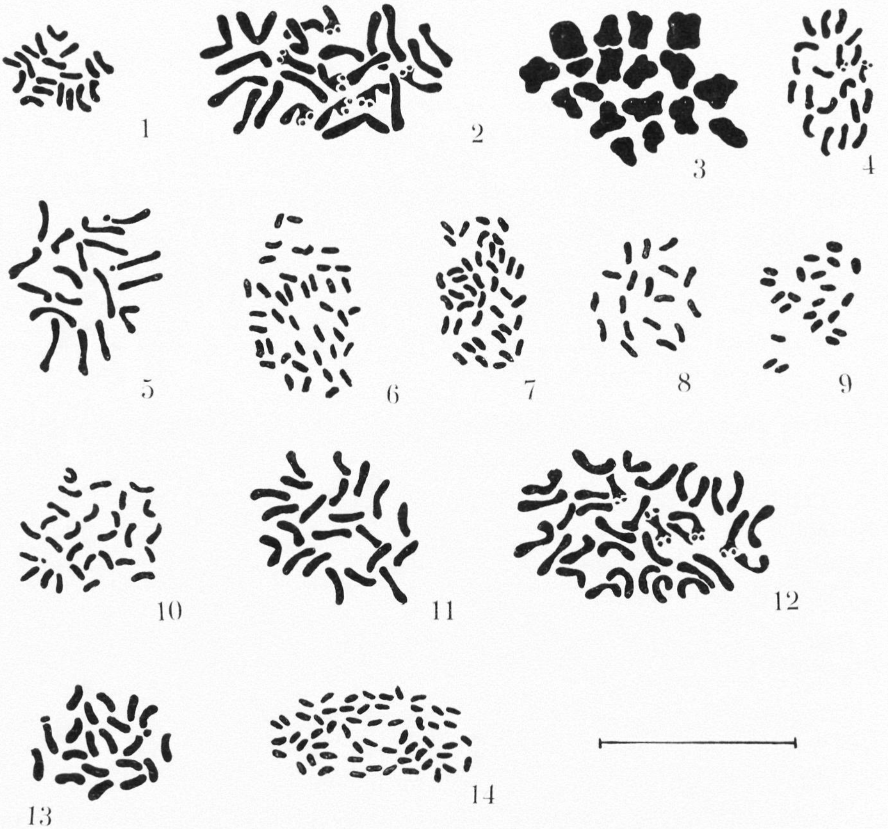
This is the same strain as dealt with in the author's earlier work. Previously only root tip mitoses were studied and in these it is often very difficult to count the chromosomes. The culture, however, still thrives excellently and flowers every spring in abundance. Flower buds were therefore fixed and the meiosis in the pollen mother cells studied. This proved to be quite normal, and in all anthers observed 18 bivalents were found in the cells.

Rumex maderensis Lowe, 2n=20, Fig. 4, No. 282. Tenerife: Agua Mansa.

This species belongs to quite another group than *R. lunaria,* as also immediately appears from the cytological pattern. This species belongs to a 10-series with small isomorphic chromosomes with median or submedian kinetochore. It may be regarded as a diploid while *R. lunaria* is a tetraploid. These two species are the only endemic *Polygonaceae* on the islands; *R. maderensis,* as the name tells, is also found on the island of Madeira.

Beta patellaris Moq., 2n=18, Fig. 5, No. 283. Tenerife: Puerto de la Cruz.

The species is found to be diploid, which is in accordance with the results of Bleier (1930). Strictly speaking, the species is not an



Figs. 1—2 and 4—14: metaphase plates from root-tips. Fig. 3: 1. metaphase from PMC. — Fig. 1: *Polycarpaea carnosa* var. *carnosa*; 2: *Silene bourgaei*; 3: *Rumex lunaria*; 4: *Rumex maderensis*; 5: *Beta patellaris*; 6: *Hypericum canariense*; 7: *Hypericum grandiflorum*; 8: *Hypericum reflexum*; 9: *Forskahlea angustifolia*; 10: *Bencomia brachystachya*; 11: *Melanoselinum decipiens*; 12: *Canarina campanula*; 13: *Allagopapus dicotomus*; 14: *Digitalis isabellina*. — The scale is 10 μ.

endemism, as it is not only widespread over the Canary Islands, but also found on Madeira and in the littoral zone of the neighbouring African coast. Lems (1960) treats the species as a therophyte. Grown under the conditions given in Copenhagen it behaves like a perennial. The life form of the species ought to be studied more closely.

Hypericum canariense L., 2n=40, Fig. 6, No. 208. Tenerife: Barranco Gercad outside Santa Cruz, alt. ca. 100 m; No. 288. Tenerife: Orotava.

Both strains showed the same chromosome number. The chromosomes are all of the same size and shape. The species is regarded a decaploid (see below).

Hypericum grandiflorum Choisy, 2n=40, Fig. 7, No. 289, Tenerife: Agua Mansa.

The metaphase plates of this species cannot be distinguished from the preceding one.

Hypericum reflexum L. fil., 2n=18, Fig. 8, No. 290. Tenerife: Guimar.

The 18 somatic chromosomes of this species are all of same size and shape and considerable larger than the chromosomes of the two preceding *Hypericum* species. *H. reflexum* may be a hexaploid.

With the exception of the rare *Hypericum perforatum* L. and *H. humifusum* L., which have only been found once each, the remaining five species of the family *Hypericaceae* all belong to the endemic element. Pitard & Proust (1908) deal with three genera, viz. *Hypericum* Tourn., *Webbia* Spach, and *Androsaemum* All. The three *Hypericum* species are *H. coadunatum* Chr. Sm., *H. glandulosum* Ait., and *H. reflexum* L. fil. The two first mentioned species are cytologically unknown. According to the considerations of Sugiura (1944) the number 2n=18 may be regarded as a hexaploid of a 3-series in order to explain the evolution of the group. The explanation seems reasonable even if the diploid level has not been found; further studies ought to be undertaken.

There seems to be little reason to maintain the genus *Webbia,* the only species *W. canariensis* Webb & Berth., synonym of *Hypericum canariense* L., is widespread over the Canary Islands and also found on Madeira. The chromosome number 40 is a multiple of the other basic number in the genus, x=4.

Even the genus *Androsaemum,* whose fruits are berries, ought to be given subgeneric rank, as from an evolutionary point of view it seems to be very little different from *Hypericum* sens. str. Only one species is found on the Canary Islands, *A. webbianum* Spach, synonym of *H. grandiflorum* Choisy. Like the preceding one this is a widespread species, but rather uniform all over the islands, while *H. canariense* shows considerable variation. Like most other species belonging to the *Androsaemum*-group it is a decaploid with the basic number 4.

Concluding we may say that the endemic *Hypericum* species fit very well into the pattern formed by the Mediterranean and North European species.

Forskahlea angustifolia Retz., 2n=22, Fig. 9, No. 281. Tenerife: Guimar.

The chromosomes are small rod-shaped bodies, all of the same size and shape. The number is the same as found by Reese (1957) in the North African species *F. tenacissima.* This author counted the number in PMC's and found 11 bivalents. I may emphasize that the counting of the root-tip metaphases in my material has been rather difficult in smear preparations as well as in ordinary Nawashin fixations treated according to the paraffin method. In some plates I have been in doubt whether the chromosome number was 24 or 22, but in the best plates I found 22 as shown in the drawing.

The species is diploid.

Bencomia brachystachya Svent., 2n=28, Fig. 10, No. 307. Botanical Garden, Orotava.

This species is a close relative of *B. caudata* (Ait.) Webb & Berth. While *B. caudata* is an inhabitant of the nebular zones of Tenerife, Palma, and Hierro, the present species is found on drier localities on Gran Canaria. It has the same chromosome number as *B. caudata* (cp. Larsen 1956) and crossing experiments ought to be tried.

The species is tetraploid.

Melanoselinum decipiens (Schrad.) Hffm., 2n=22, Fig. 11, Botanical Garden, Copenhagen.

This species is not endemic to the Canary Islands, but only found on Madeira, where it occurs together with a near relative, *M. edulis* (Lowe) Drd. As none of the two species of this genus have been studied cytologically before, I took the opportunity to include this material in the survey. The number 2n=22 has been counted in several good metaphase plates.

The species is diploid.

Canarina campanula L., 2n=34, Fig. 12, No. 312. Botanical Garden, Orotava.

The genus *Canarina* L. has recently been studied by Hedberg (1961), who found the basic number to be 17 and all three species within the genus to be diploids. A single chimaera was found in material from the greenhouses in the Botanic Gardens, Kew; this showed some root tips with the tetraploid number 68; five other counts of different origin gave the number 2n=34, which is further corroborated by the present find.

Allagopappus dicotomus (L. fil.) Cass., 2n=20, Fig. 13, No. 300. Tenerife: Guimar.

This genus, not previously studied cytologically, is monotypic if *A. viscosissimus* Bolle is regarded as a variety only of the present species. It belongs to the group *Inuleae - Inulinae* in which 20 is a common chromosome number (cp. e.g. *Inula, Pulicaria,* and *Buphthalmum*).

The species is tetraploid.

Digitalis isabellina Linding, 2n=56, Fig. 14, No. 310. Botanical Garden, Orotava.

The chromosomes are all of the same size, small rod-shaped bodies, easily countable in the root-tip metaphases.

The genus *Digitalis* L. has recently been dealt with taxonomically by Werner (1960), who maintains the viewpoint of a separate genus *Isoplexis* including 3 species, two of which are Canarian endemisms. Both of them have now been studied cytologically, as Haase-Bessel (1931) has studied *D. canariensis* L., in which he found 2n=56. Cytologically the genus *Digitalis* is unique within the *Scrophulariaceae* in having the secondary basic chromosome number $x_2=28$. The common somatic numbers are 2n=56 and 112. The two species of the *Isoplexis* group fit well into this series. Thus the cytological data show *Isoplexis* and *Digitalis* to be one evolutionary unit; the old viewpoint of Linné of regarding the woody species as also belonging to the genus *Digitalis* is here once more supported.

As the basic number is 28 the species may be regarded as diploid.

Summary

As a link in a study on the cytology of the endemic Canarian element the chromosome numbers of 14 endemisms are here reported. Only two of these have previously been dealt with by cytologists.

This scrutiny is being continued and it is the authors intention from time to time to report his results until a final conclusion can be formed.

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Notes on South African Hepaticae VII

By Sigfrid Arnell

Riksmuseum, Paleobot. Division, Stockholm

Cephaloziella triplicata S. Arnell nov. spec.

Cephaloziella Kiaerii S. Arnell, Bot. Not. 1952 p. 319.

Monoica, pusilla, muscis consociata. Caulis ad 2 cm. longus. Folia ad $^1/_3$—$^1/_2$ bilobata, lobis triangularibus acutis, sinibus acutis. Cellulae marginales 10—20 μ, mediae 20—30 μ, trigonis nullis. Cuticula levis vel papillosa. Amphigastria minima vel nulla. Folia floralia caulinis multo majora, bilobata, dentata. Perianthia triplicata, ore parum contracto, ciliata. Androecia subfloralia, bracteis ad 10-jugis. Propagula globosa—ellipsoidea, unicellularia.

For description in English and picture see Bot. Not. 1952 p. 319—320. *Cephaloziella Kiaerii* (Aust.) S. Arnell is dioicous, has smaller leaf-cells, only 8—10 μ large, smaller leaves which are almost as long as broad and perianth generally 5-plicate. *C. triplicata* is collected in several places in Cape Peninsula (Constantia Nek, Kirstenbosch and between Kirstenbosch and Constantia Nek on a wet rock, type specimen no. 128, Paleobotanical Department, Riksmuseum, Stockholm).

Hyalolepidozia S. Arnell nov. genus.

Vegetative branches both from the axils of leaves and amphigastria, stem with cortex of 6 rows of large, pellucid, rather thin-walled cells, forming a distinct hyalodermis around the numerous smaller inner cells, arranged in about 10 outer rows and four inner rows; female bracts shortly bilobed; perianth cylindrical, mouth wide, crenulated—irregularly and shortly dentate. Leaves bilobed to $^1/_2$, lobes lanceolate, broad.

Only species: *Hyalolepidozia bicuspidata* (Mass.) S. Arnell nov. comb. *Lepidozia bicuspidata* Massalongo, N. Giorn. bot. ital. Vol. 17 p. 239.

Genus *Lepidozia* has the leaves 3—4-lobed and the cortical cells of the stem thick-walled and numerous.

Simia S. Arnell nov. genus.

Differs from *Cephaloziella* in following features: Seta with a mid-string of narrow cells, surrounded by four rows of large, thin-walled cells. (In *Cephaloziella* the seta consists of 4 rows thin-walled cells.) Perianth with wide, generally smooth-margined mouth. (In *Cephaloziella* the mouth of the perianth is constricted and the margin generally dentate.)

Only species: *Simia atroviridis* (Sim) S. Arnell nov. comb. *Cephalozia atroviridis* Sim, Transactions Royal Soc. S. Afr. XV p. 84 (1926). *Cephaloziella atroviridis* (Sim) S. Arnell, Bot. Not. 1952 p. 309.

Microlepidozia Jörgensen (Bergens Mus. Skr. Nr. 16 p. 303, 1934) is now generally accepted as a distinct genus, well separated from genus *Lepidozia*. Two species belonging to this genus occur in S. Africa, *Lepidozia tabularis* Stephani (in Spec. Hep. III p. 560, 1909) and *Lepidozia succulenta* Sim (Trans. Royal Soc. S. Afr. XV p. 90, 1926). The names should be:

Microlepidozia tabularis (St.) S. Arnell nov. comb. and
Microlepidozia succulenta (Sim) S. Arnell nov. comb.

The genus ***Bazzania*** is also generally accepted and the species earlier placed in the genus *Mastigobryum* must be transferred to *Bazzania*:

Mastigobryum pulvinatum Stephani (Hedw. 1891 p. 267) must be *Bazzania pulvinata* (St.) S. Arnell nov. comb.

Mastigobryum Molleri Stephani (in Engler, Bot. Jahrb. Vol. 8 p. 84 and Spec. Hep. III p. 453, 1908) must be *Bazzania Molleri* (St.) S. Arnell nov. comb.

Plagiochila lunata S. Arnell nov. spec.

Cape Province; Ceres Division, Hansiesberg, kloof on W. slopes, on cliffs, S. aspect. 4,500 ft. E. Esterhuysen 25,692, type specimen in The Bolus Herbarium, Cape Town. Table Mt., Silverstream Ravine, along cracks in roof of overhang, 3,000 ft. E. Esterhuysen 25,104. Table Mt., The Saddle, 2,200 ft, T. R. Sim 9814, National Herbarium, Pretoria 2629. Ditto, Intake Woodheads Tunnel, T. R. Sim 9812, National Herbarium, Pretoria 2613.

Sterilis, minor, pallide viridis—pallide brunnea. Caulis ad 4 cm longus, pallide viridis—pallide brunneus. Folia caulina 0.5—0.8 mm longa, 0.2—0.5 mm lata, remota, sub angulo 45—80° patula, e basi cuneato-angustata obovata—ovata, apice truncata vel lunata, 2—3-dentata, margine antico ar-

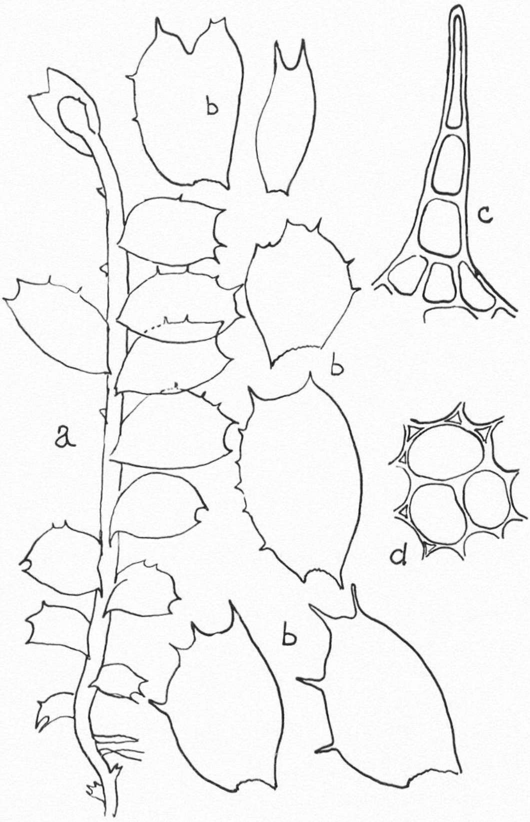

Fig. 1. *Plagiochila lunata* S. Arnell. a. Shoot in ventral view. b. Leaves. c. Apical tooth of a leaf. d. Cells from the centre of a leaf.

cuato, integro, margine postico arcuato, 2—4-spinoso, spinis recte patulis, plerumque 3—4 cellulas longis. Cellulae marginales 12—14×18—20 μ, interiores 14—20×24—30 μ, trigonis ± nodosis.

Sterile, small, shoots up to 2 cm long. Stem sparsely or not branched, pale—brownish green—pale brown, cortical cells about 20×50 μ, walls thin; rhizoids only at the base. Leaves distant, somewhat caducous, about 0.5—0.8 mm long, 0.2—0.5 mm broad, subplane—slightly concave, diverging in 45—80° from the stem, asymmetrically obovate—ovate, base narrow, shortly decurrent on the dorsal face, apex usually lunate, with two or three sharp teeth, lower margin slightly arched, entire, upper margin arched, usually sparsely dentate, teeth spinous, often 3—4 cells long, distal cell elongated. Marginal cells 12—14×18—20 μ, inner cells 14—20×24—30 μ, walls thin, trigones distinct—rather large, formed by the middle lamella, the intermediate layer usually coloured pale brown.

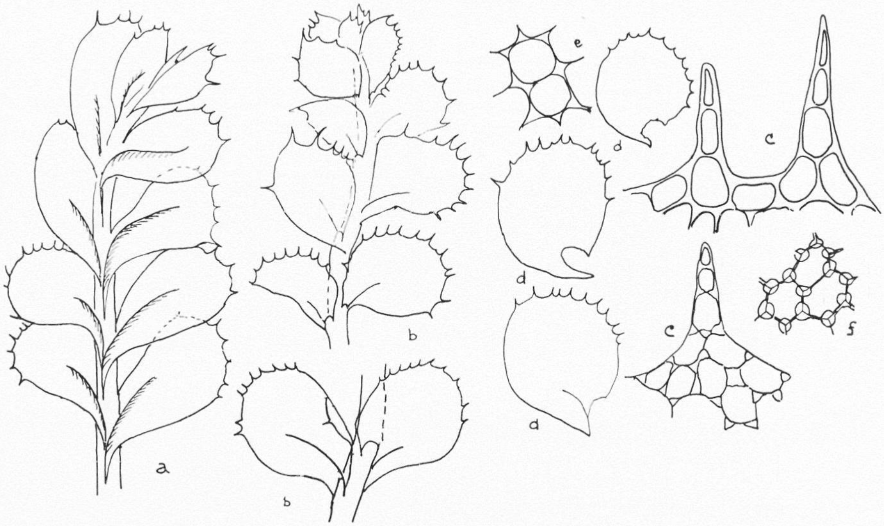

Fig. 2. *Plagiochila pseudo-attenuata* S. Arnell. a. Apex of a shoot in dorsal view. b. Apex of a shoot and leaves in ventral view. c. Marginal teeth from leaves. d. Leaves. e. Cells from the medium portion of a leaf. f. Cells from the medium portion of a leaf, exceptionally large trigones.

Resembles *P. Haumannii* Herz. from Ruwenzori, but the plant and especially the leaves are much smaller (in P.H. 1×2 mm) and the cells are smaller (in P.H. the apical cells of the leaves are 30×36 μ).

Plagiochila pseudo-attenuata S. Arnell nov. spec.

Sterilis minor fusco-olivacea, in rupibus dense pulvinata. Caulis ad 2 cm longus, pallide viride-brunneus, apice hamatim decurvo. Folia remotiuscula, decurvohomomalla—squarrose patula, in plano rotunda, margine infero decurvo, integro, margine supero spinoso-dentato, apice rotundato et spinoso-dentato. Cellulae marginales 14×14—16×20 μ, mediae 16×16—20×20 μ, basales ad 20×40 μ, parietibus tenuibus, trigonis magnis.

Sterile, small, ± rigid, dark olivaceous green, shoots up to 2 cm long, densely pulvinate, growing in crevices and on rocks. Stem about 120 μ in diameter, pale greenish brown. Leaves 0.75—0.9 mm long, patent and postically decurved, almost circular with dorsal margin slightly decurrent and incurved, entire; ventral margin with spinous teeth up to 4 cells long, shortly decurrent. Marginal cells 14×14—16×20 μ, interior cells 16×16—20×20 μ, basal cells up to 20×40 μ, trigones large, pale brown, formed by the intermediate layer, walls thin. Oil bodies small, 1—2 μ, homogeneous, 2—6 per cell.

Habitus of the plant somewhat resembling *Adelanthus uniformis,* also described as *Plagiochila attenuata* by Stephani. The shoots are, however, not attenuate towards the tops, and the leaf-cells are of a quite different appearance with thin walls and large trigones.

The plant is collected in Natal, Bergville Division, Injasuti area, Drakensberg. Ledge below head of kloof, S. aspect. On weathered rock face, in crevices and recesses, 10,000 ft. E. Esterhuysen 26106 (type specimen, The Bolus Herbarium, Cape Town). Steep rocky sides of Cowl Gully, S. aspect, 8,000 ft. E. Esterhuysen 26142.

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The Embryo Sac Development of Some Cotoneaster Species

By H. HJELMQVIST

(Meddelande från Lunds Botaniska Museum, Nr 163)

In her paper "Polyploidy and apomixis in Cotoneaster", published in 1954, Hally J. Sax arrived at the conclusion that a great number of *Cotoneaster* species bred true if propagated by seed and that they agreed with the maternal parent, whereas in certain cases a minor number of variants appeared in the progeny. These conditions were referred to a total or partial apomixis occurring in the triploid or tetraploid species of the genus, whereas the diploid ones, judging from the great variation of the offspring, were apparently amphimictic. Flinck and Hylmö (1962) also mention an instance of true breeding in *Cotoneaster,* observed in the cultures of *Cotoneaster* species which they have established in connection with a taxonomical revision of the genus; according to an oral communication from the authors several other species of their cultures show constancy in the offspring, indicating an apomictic reproduction. An investigation was on this account undertaken of the embryology of some *Cotoneaster* species, in order to determine whether and to what extent the embryo sac showed such a development as is usually found in apomictic plants, where it as a rule is formed without reduction division. If this is regularly the case, the development must be apomictic; otherwise the chromosome number would increase for each generation.

The species that were investigated were all cultivated in the Botanical Garden of Lund and most of them belong to the investigation material of Flinck and Hylmö and have been controlled by them as to the determination. However, two of the species included here do not belong to this material: *Cotoneaster bullata* and *C. racemosa* var. *soongorica.* Their identity has been controlled by the present writer.

Investigated species

	Number	Provenience	Origin, for spontaneous material	Chromosome number acc. to Sax 1954
Cotoneaster rosea Edgew.	9020	Frankf. a.M. 1937	—	3 n
— nitens Rehd. & Wils. . .	9015	Oslo 1943	—	3 n
— bullata Bois	—	Unknown	—	3 n
— obscura Rehd. & Wils.	9045	Pruhonice 1947	Kansu (Rock 13775)	—
— "obscura var. nova" . .	9051	Uppsala	Sikang (H. Smith 12805)	—
— acutifolia var. villosula Rehd. & Wils.	9016	Oslo 1943	—	4 n
— racemiflora var. soongorica Schneid.	9019	Alnarp 1947	—	—

The chromosome number determinations of Sax were made on material in the Arnold Arboretum. Of *C. obscura* and *racemiflora* other varieties than those investigated here have been determined as to chromosome number and for them (*C. obscura* var. *cornifolia* Rehd. & Wils. and *C. racemiflora* var. *Veitchi* Rehd. & Wils.) the triploid number is given.

The usual technique was employed: buds and flowers were fixed in the solution of Navashin-Karpechenko, embedded in paraffin and sectioned in longitudinal sections. Staining was made in iron-haematoxylin according to Heidenhain. — The fixations were made in the spring of 1959 and 1960.

General features in the embryology

All investigated species are characterized by a crassinucellate, bitegmic ovule and the occurrence of an obturator, as is the case also, for instance, in *Malus*. As usual in Rosaceae the nucellar epidermis is divided by periclinal walls into several cell layers and there is a pluricellular archesporium, from which parietal cells are cut off outwards. However, among the secondary archesporial cells which remain after the formation of the parietal cells as a rule only one, in a central position, develops into a megaspore mother cell (MMC), whereas the other generally divide into short cell rows, the "lateral rows". In contradistinction to the conditions in some other apomictic forms a micropylar canal is present in the fully developed ovule.

Cotoneaster rosea

In the earliest developmental stages of the ovule that were observed the integuments were only visible as low swellings and the epidermis was entirely 1-layered (Fig. 1 *a*). Here a MMC with early prophase in the nucleus was observed, lying beneath a single or double layer of parietal cells in the nucellar centre or slightly to the side thereof. The nucleus of this MMC might be in early prophase stages, up to pachytene or diplotene (Fig. 1 *b*), but such a late stage as diakinesis never occurred. The primary MMC always degenerates in an early stage: in ovules which are of about the same age as the one illustrated in Fig. 1 *b* it is not infrequent that it is present only as a degenerated, compressed remnant in the centre (Fig. 1 *c*). At this time of development, however, there are some cells with a dense cytoplasm and big nuclei (these drawn in the figure); these are initials of unreduced embryo sacs. In an exceptional case (Fig. 1 *d*) there was a not quite degenerated MMC in a somewhat more advanced stage, when the epidermis cells had begun to be divided by periclinal walls and the parietal cells formed up to 4 cell layers. However, it is clear that the MMC also in this case is going to degenerate — the cytoplasm is shrunken, somewhat vacuolized, and resembles that of the surrounding cells — and unreduced embryo sac initials (EI:s) are being formed beneath it.

The further development, however, is not quite simple, since besides the unreduced EI:s also secondary MMC:s appear which develop parallelly with the former. This is shown by Fig. 1 *e*, a later stage where the epidermis is 5- to 6-layered in the top and the inner integument almost reaches the top of the nucellus, while the outer surpasses it a little. Here such a secondary MMC with prophase in the nucleus is seen at the side of the long and narrow, now strongly compressed primary MMC. In Fig. 1 *f* — showing a nucellus in about the same

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Fig. 1. *Cotoneaster rosea. a* Nucellus in longitudinal section (l.s.) with a MMC in an early stage. *b*—*d* The same with MMC in prophase (*b* and *d*) and in degeneration (*c*) and in addition unreduced EI:s (the nuclei drawn, in *b* also the cytoplasm). *e* L.s. of nucellus (without epidermis cap) with degenerated primary MMC, a secondary MMC beside it with compressed nucleus and a vigorous unreduced embryo sac in another plane (its place marked below, to the left it is fully drawn). *f* Centre of nucellus with remnants of primary MMC, two secondary MMC:s above and at the side of it, and a group of EI:s beneath. *g* Cell group from the nucellar centre with a normal, reduced 1-nucleate embryo sac in the midst of it (degenerated triad cells above) and unreduced EI:s around it. — Enlargement in Fig. 1—7 about ×625.

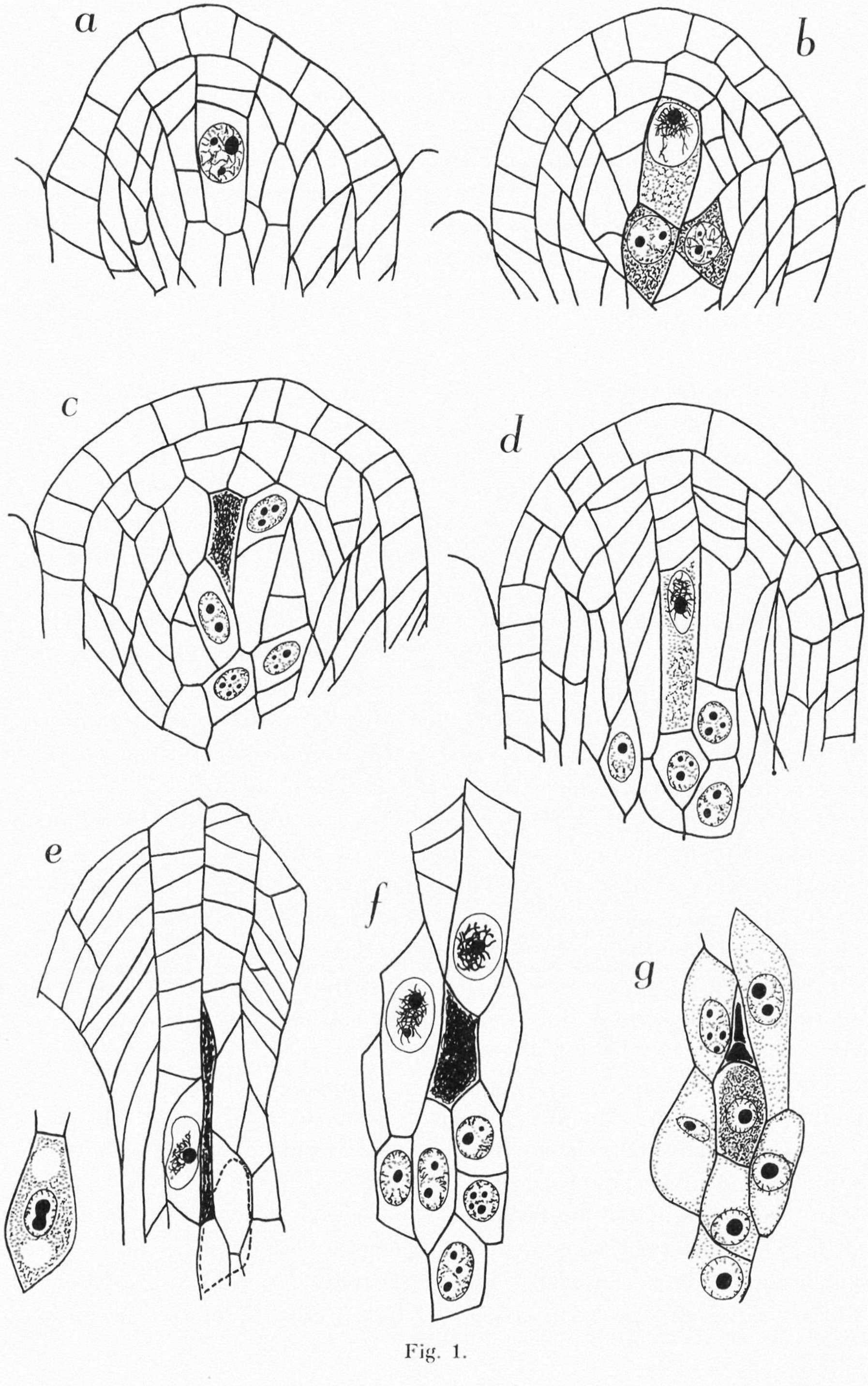

Fig. 1.

stage of development — two such secondary MMC:s are shown at the side of or above the degenerated primary one. In the former case the secondary MMC is just on the point of starting to degenerate (the cytoplasm is somewhat shrunken and the nucleus is a little irregular in shape) and a vigorous unreduced EI is growing out close to it (to the right in the figure), but in the latter case it is by no means sure that the unreduced EI:s will win in the competition, as the secondary MMC:s are here big and vigorous; the upper one is more advanced.

In a few cases it was also observed that this secondary MMC had divided and formed a triad, consisting of two megaspores and an undivided dyad cell. An instance of this is shown in Fig. 1 *g*, a late stage where both integuments have reached the top of the nucellus; a degenerated cell remnant, probably of the primary MMC, is visible in the adjacent section. In the centre of the nucellus there is here a group of cells that are going to grow out into embryo sacs; one of these, in the centre of the group, deviates in having a dense cytoplasm without vacuoles and a comparatively small nucleus, and above this cell are degenerated cell remnants, apparently of two cells, though the limit between them is indistinct. Obviously this is a triad, arisen through meiosis, with a basal megaspore that develops. The megaspores are in other Rosacean plants, for instance the partially apomictic *Malus Sieboldii,* of a similar appearance, deviating from the unreduced potential embryo sacs: the cytoplasm is not so vacuolized and the nucleus, having the reduced chromosome number, is smaller.

One more instance was observed where a similar triad had been formed; also in this case the cytoplasm of the basal cell was dense, without true vacuoles, and two degenerating cells were present above it. In both cases, however, there were unreduced 1-nucleate embryo sacs around the reduced ones, and as they appeared to be of about the same vigor, the course of development was uncertain; it might be supposed, however, that the reduced embryo sacs at least in solitary cases would win in the competition.

The later stages that were observed, 4- and 8-nucleate embryo sacs, could not be determined with certainty as to their origin; in these advanced stages there is no possibility of deciding whether there are some ousted megaspores or not.

In the investigated material of *Cotoneaster rosea,* thus, only two cases were observed when megaspores were formed. In 8 other cases secondary MMC:s occurred which appeared vigorous and capable of further development (as in Fig. 1 *f*). In 6 cases there were secondary

MMC:s which more or less certainly were going to degenerate and to be replaced by unreduced embryo sacs. Finally, in about 25 cases only unreduced potential embryo sacs occurred around the degenerated primary MMC. Thus in a total of about 30 cases the development judging from all appearances was apomictic, whereas in the remaining 10 (8+2) a possibility of amphimixis was present, though it certainly could not take place in all these cases, probably only in a few of them. The apomictic tendency in *C. rosea,* however, is not so pronounced as in several other species: in certain cases reduced embryo sacs are developed that apparently are capable of competition with the unreduced ones and an amphimictic reproduction may thus be supposed to sometimes occur. In agreement with this is the statement (Sax, 1954, p. 351) that the species is assumed to hybridize with *C. acuminata* Lindl. In connection with the weaker apomictic tendency is probably also the fact that the degeneration of the primary MMC in *C. rosea* is comparatively late, reminiscent to some extent of the conditions in *Alchemilla.*

Cotoneaster nitens

In *Cotoneaster nitens* the earlier development is of the same type as in several other species: in the centre of the nucellus there is a long, degenerated and compressed primary MMC, while a group of unreduced EI:s are developing in the proximity (Fig. 2 *a*). Those cells that develop into unreduced embryo sacs often belong to the lateral rows and have thus arisen through division of secondary archesporial cells; however, also more deeply situated cells of the nucellus may develop in this way, i.e., cells that do not belong to the original archesporium. Among the unreduced embryo sacs one is often more vigorous and dominating, as shown in Fig. 2 *b*; in other cases several unreduced EI:s develop parallelly.

In some cases, however, secondary MMC:s may appear, as shown in Fig. 2 *c,* where even two such secondary MMC:s have been formed. The primary MMC is highly degenerated and is visible in the figure to the left as a narrow stripe in the nucellar centre; alongside of this unreduced EI:s have developed from the lateral rows. Furthermore there are two MMC:s of which at least one, probably both, likewise derive their origin from a lateral row. Especially one of these is big and vigorous and it is possible that it could have given rise to a reduced embryo sac and that the development would have been amphimictic. However, it is not possible to decide with certainty which course of

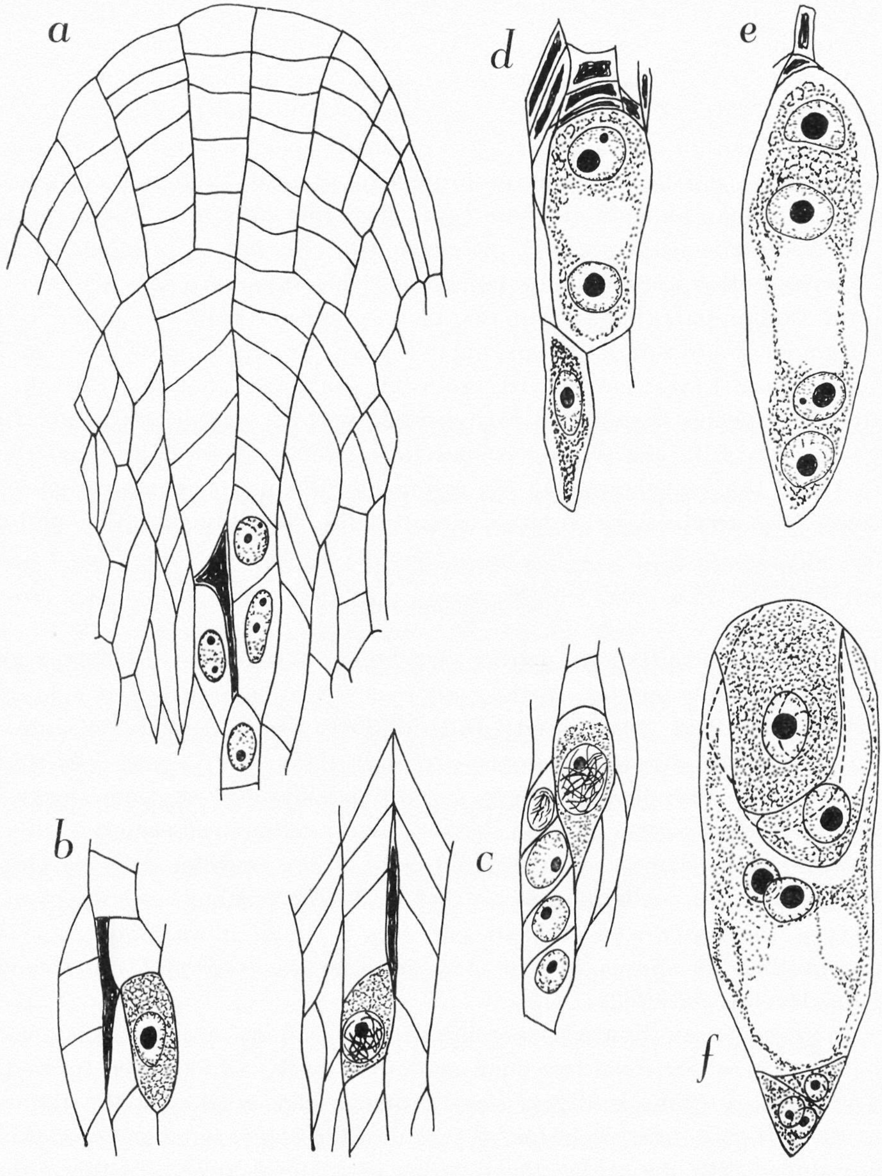

Fig. 2. *Cotoneaster nitens*. *a* L.s. of nucellus with degenerated MMC and unreduced EI:s. *b* A vigorous EI in the proximity of the reduced primary MMC. *c* Two consecutive sections of the same nucellus, with two secondary MMC:s and a row of unreduced EI:s, the primary MMC strongly disintegrated. *d* 2-nucleate embryo sac, a small 1-nucleate below. *e* 4-nucleate embryo sac. *f* Mature embryo sac.

development would have taken place. — In another case the primary MMC had degenerated as usual and around as well as beneath it unreduced EI:s were in development. In addition there occurred a secondary MMC with meiotic prophase in the nucleus. This cell was bigger and more vigorous than the unreduced EI:s and thus it is probable that it would give rise to a normal, reduced embryo sac. — A third instance was also observed; here a secondary MMC was also present, where the nucleus was in meiotic prophase. In this case the unreduced EI:s were not specially vigorous, and therefore it is not impossible that a reduced embryo sac would have some chances of winning in the competition.

Some late stages of the embryo sac development are shown in Fig. 2 *d*—*f*. In these cases it is hardly more possible to say, whether the embryo sac has developed normally or without meiosis, as by its growth those cells have been ousted that were lying above it and the possibly present megaspores are very difficult to observe. It appears however, as if the 2-nucleate embryo sac (Fig. 2 *d*) did not have any suppressed megaspores above it, but only some compressed parietal cells; probably at least this embryo sac is unreduced. Obliquely beneath it there is also a 1-nucleate unreduced embryo sac which has been ousted in the competition. The 4-nucleate embryo sac (Fig. 2 *e*) has also such an undeveloped cell obliquely beneath it; in this case it is, judging from the appearance of the nucleus, a secondary MMC that has lagged behind in the competition. The mature embryo sac (Fig. 2 *f*), finally, is conspicuous by its unusually large synergids, whereas the antipodals are quite small. In an embryo sac of a still later stage, where both synergids were degenerated, it was observed that the polar nuclei had fused into a secondary nucleus, which just had been formed, as it was still somewhat lobated and had two big nucleoli. No traces of pollen tube were discernible.

When cultivating *Cotoneaster nitens* Flinck and Hylmö (1962) have found true breeding and agreement with the maternal plant in the progeny (about 500 seedlings); thus they consider the species totally apomictic. Sax (1954, p. 353), on the other hand, has observed a certain percentage of deviating plants: among 26 seedlings there were 3 variants which differed both from the maternal plant and among themselves. The embryological observations show that a development of unreduced embryo sacs and consequently an apomictic reproduction is by far most common. In *C. nitens* thus 16 cases were observed where this development could be stated with rather great certainty, against 3 where an occurrence of secondary MMC:s made a development of reduced embryo sacs conceivable. However, no instance of a meiosis or a developed tetrad or triad was observed and thus it cannot with certainty be asserted that amphimixis occurs; the only thing that can be said is that because comparatively vigorous secondary MMC:s occur, so it is not impossible that the development in exceptional cases may be amphimictic; if so, however, this development certainly is very rare.

Cotoneaster bullata

In *Cotoneaster bullata* the primary MMC degenerates in such an early stage that the meiosis scarcely has begun. In the stage illustrated in Fig. 3 *a,* where the integuments just have begun to grow out, — the outer one is only visible as a low swelling — and the nucellus is about equally broad as it is high, with 1-layered epidermis, it is possible to see a MMC that has not yet degenerated. Here is a large cell, with two parietal cells above it, that undoubtedly is going to be a MMC, even though the meiosis is scarcely initiated. In its size, as well as in the big size of the nucleus and nucleolus, it clearly deviates from the surrounding cells. Some of these, however, have comparatively big nuclei, thus showing that they are potential embryo sac initials. In as early a stage as that one illustrated in Fig. 3 *b,* — almost as early as the above-mentioned one — the cell in question is degenerated and two cells with big nuclei at the side of it start to develop into unreduced embryo sacs.

In later stages, when the nucellus has increased in length and the epidermis consists of two or more cell layers, this primary MMC is visible as a degenerated, more or less compressed cell or cell remnant in the centre of the nucellus (Fig. 3 *c*—*e*), and in its place other cells develop without meiosis into embryo sacs. These unreduced embryo sacs here are comparatively few in number, often long and rich in cytoplasm. They may develop from cells with varying position. Not rarely they are formed above the degenerated cell, from a cell that must be regarded as a parietal cell (Fig. 3 *c*); sometimes two such cells develop above the primary MMC, but in one of the cases where this was observed the upper cell was obviously going to degenerate. In other numerous cases the unreduced embryo sacs are developed at the side of the primary MMC in the "lateral rows", originating from secondary archesporial cells (Fig. 3 *b, d*—*e*). On this occasion

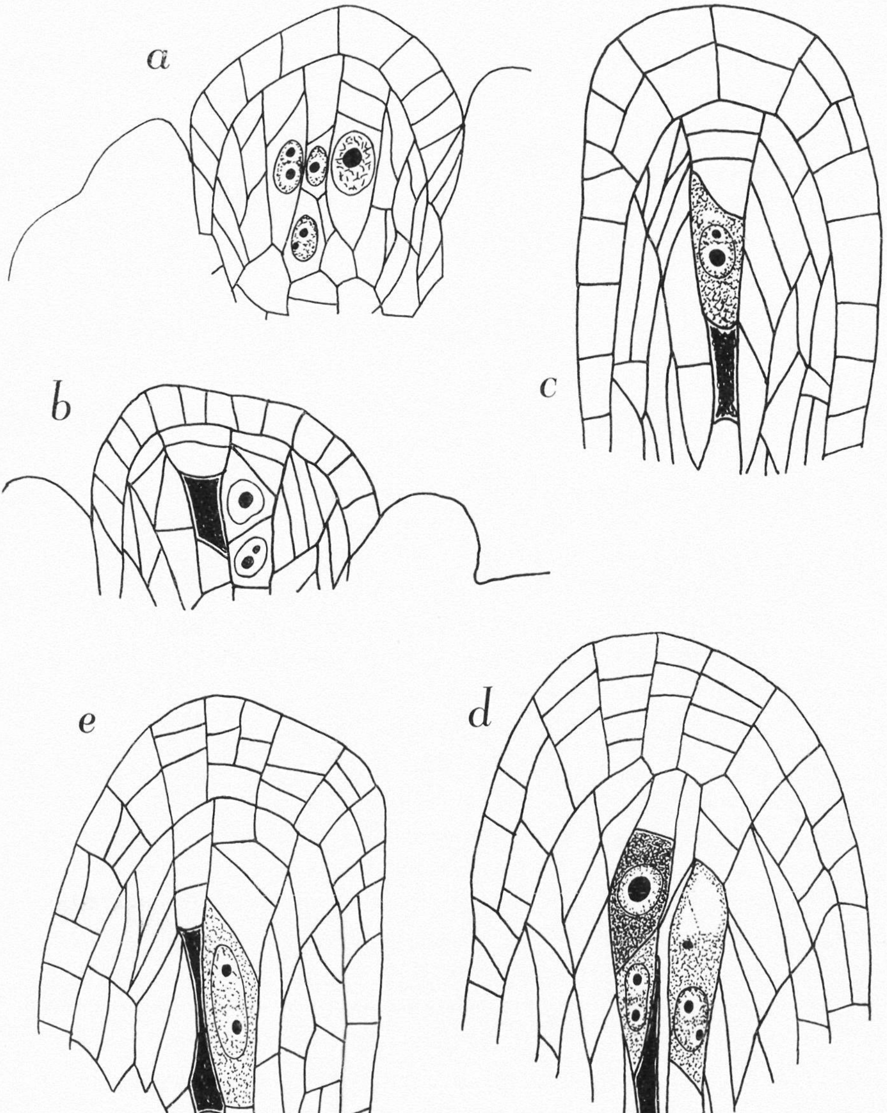

Fig. 3. *Cotoneaster bullata*. *a* Young ovule in l.s. with MMC in an early stage and three potential EI:s. *b* Young ovule with degenerated MMC, two potential EI:s visible. *c—e* Later stages, the primary MMC disintegrated, one or a few EI:s growing out (the cell contents drawn).

they may develop either directly from the secondary archesporial cells, without any division of these (Fig. 3 *e*), or from the "daughter cells", in which these have been divided (Fig. 3 *b*). The former case, which when it occurs in the genus *Rubus* has been regarded as a reduction phenomenon (Christen 1950), is apparently more uncommon than the latter.

In isolated cases secondary MMC:s may appear in later stages. These are rare, however, and it appears as if these MMC:s or their derivatives had no chances of winning in the competition. In a few cases thus cells were visible that were beginning to degenerate, but which, judging from the appearance of the nucleus, certainly or probably were secondary MMC:s. In another case there was a conspicuous secondary MMC in a lateral row; the nucleus was in prophase, but it was compressed from the sides and there was no doubt that it was going to degenerate. One instance only was stated of a secondary MMC that showed no signs of degeneration; it was situated uppermost in a lateral row, with the nucleus also here in prophase. Immediately beneath it in the same row there was, however, a cell with large nucleus — larger than that of the MMC — which certainly would develop into an unreduced embryo sac and oust the MMC above it or — if a division of the cell should take place — its daughter cells.

No division of the secondary MMC:s has thus been observed and it is doubtful whether megaspores are ever formed. In comparison with the few mentioned instances of secondary MMC:s those cases were numerous where only unreduced embryo sacs were developing, instead of the degenerated primary MMC. This was observed in some 30 cases. The embryological observations thus indicate a pronounced apomixis; in the rare cases when secondary MMC:s appear they never seem to be able to vindicate themselves in the competition and there are no indications that an amphimictic development may occur.

The further development of the embryo sac proceeds in the usual way. In the mature embryo sac the polar nuclei at first lie at great distance from each other, later on they are in close proximity, but no fusion was observed. The polar nuclei as well as the nucleus of the egg cell may have two nucleoli, a condition that may have some connection with the high chromosome number of the unreduced embryo sac (cf. Håkansson, 1946, p. 54).

In the sowing experiments of Sax (l.c.) with *C. bullata* the total number of seedlings proved to agree with the maternal plant. Even if the number of plants was comparatively small (14 of *C. bullata*, 34 of *C. bullata* var. *floribunda*) the results obtained do not in any case contradict the conception that the species is more or less completely apomictic.

Cotoneaster obscura

In the earliest observed stages of *Cotoneaster obscura* (Fig. 4 *a*) a pluricellular archesporium is visible, about 3 or 4 cells in breadth, which outwards has cut off a layer of parietal cells. One of the secondary archesporial cells which is situated in the centre of the nucellus has a larger nucleus than the other and is developing into a MMC. However, this primary MMC also here always degenerates in an early stage and some of the surrounding cells grow out into unreduced embryo sacs (Fig. 4 *b*). In a degenerated MMC where the cytoplasm was highly disintegrated, lumping together and staining heavily, the nucleus was still visible, obviously in meiotic prophase, not so degenerated as the cytoplasm. It thus appears as if the degeneration began in the cytoplasm; the nucleus is in any case not the first to degenerate, as is usual in *Sorbus* (Liljefors 1953). The unreduced embryo sac initials that are formed after the degeneration of the primary MMC are here, in similarity with *C. bullata* but in contradistinction to other species, comparatively few but often unusually long and with a dense cytoplasm (Fig. 4 *b*—*c*). In some cases such an initial has no doubt arisen directly from a secondary archesporial cell; in other cases, however, it is quite clear that the secondary archesporial cell has first divided and the initials have been formed from its daughter cells. In the case reproduced in Fig. 4 *b*, thus, the larger secondary EI, to the right in the figure, has doubtless been formed through a division of a secondary archesporial cell into two (the second daughter cell is immediately above), whereas the other (to the left in the figure) has certainly arisen from an undivided secondary archesporial cell. Only few late stages of embryo sac development were observed; i.a. a 2-nucleate embryo sac was seen, which had arisen from a parietal cell above the primary MMC and quite certainly was unreduced.

As in other species, there are also here in later stages secondary MMC:s. In the investigated material, however, such cells were observed only in few cases, exactly in four cases, all in meiotic prophase. For comparison it may be mentioned that in about 20 cases unreduced EI:s were seen to arise in the neighbourhood of the degenerated primary

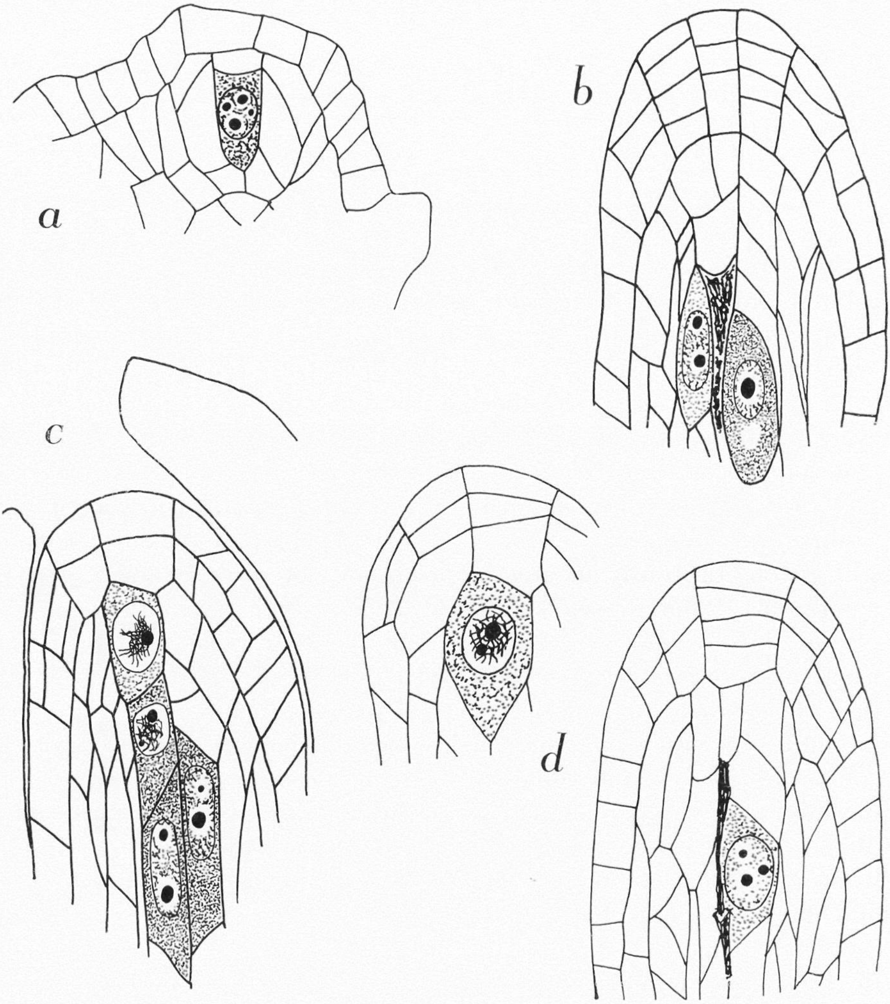

Fig. 4. *Cotoneaster obscura. a* Very young ovule in l.s. with central cell that develops into MMC. *b* Later stage with the MMC degenerated and two EI:s at the sides of it. *c* Nucellus with two EI:s and two secondary MMC:s above one of them. *d* Two subsequent sections of the same nucellus with remnants of the primary MMC, one secondary MMC (to the left) and one EI (to the right). —

MMC, but secondary MMC:s were absent. The instance reproduced in Fig. 4 *c* shows two secondary MMC:s, the one above the other, at least the upper one arisen from a parietal cell. The latter here seems vital, but as two large and vigorous unreduced EI:s are present lower down, it probably has no chance in the competition with them. — In one case the MMC was compressed, the nucleus was small and no doubt it was going to degenerate and to be replaced by an unreduced embryo sac. — In a third case such a MMC had been formed from a parietal cell in the nucellar centre; however, the nuclei of the unreduced EI:s were here at least as large as the nucleus of this MMC, and presumably they thus would win in the competition. — The sole case where possibly the secondary MMC might be capable of competition is the one that is illustrated in Fig. 4 *d*: here the MMC, which here also has been formed from a parietal cell, is larger than the EI competing with it; their nuclei are about equally large. However, it must be pointed out that not until the MMC has passed through two divisions (the meiotic divisions) is the cell formed, the megaspore, that is the real competitor of the unreduced EI, and thus the chances are also here very small. It should also be emphasized that no division has ever been observed of some MMC, as a matter of fact no later stage than the early prophase. Also this species is thus certainly a pronounced apomict, and it is doubtful whether any amphimictic reproduction ever occurs.

"Cotoneaster obscura var. nova"

An investigation was further undertaken of a *Cotoneaster* that had been brought home from China by Dr. H. Smith under the designation *Cotoneaster obscura* var. nova (H. Smith No. 12805). According to Dr. Hylmö, who has observed the form in cultivation during a longer period, it is a microspecies of its own, which is very close to *C. obscura* but clearly distinct from it; it has proved to breed true on seed reproduction for three generations.

As in *C. obscura* and many other species the primary MMC here degenerates in an early stage. The only case when a primary MMC could be observed that had not yet degenerated was the one illustrated in Fig. 5 *a,* an early stage, where the epidermis on the whole was 1-layered and the integuments were visible as two low swellings. The MMC nucleus here was in meiotic prophase, but the cytoplasm as well as the nucleus were irregularly shrunken, evidently going to degenerate. In the ovule reproduced in Fig. 5 *b,* which was about of the same age — the integuments were here also seen as two low swellings and the epidermis was 1-layered — the primary MMC was quite degenerated, but at the side of it a big-nucleate cell was perceivable that had cut off a cell upwards and no doubt was a potential EI. Other cells in the vicinity had also comparatively big nuclei and had presumably

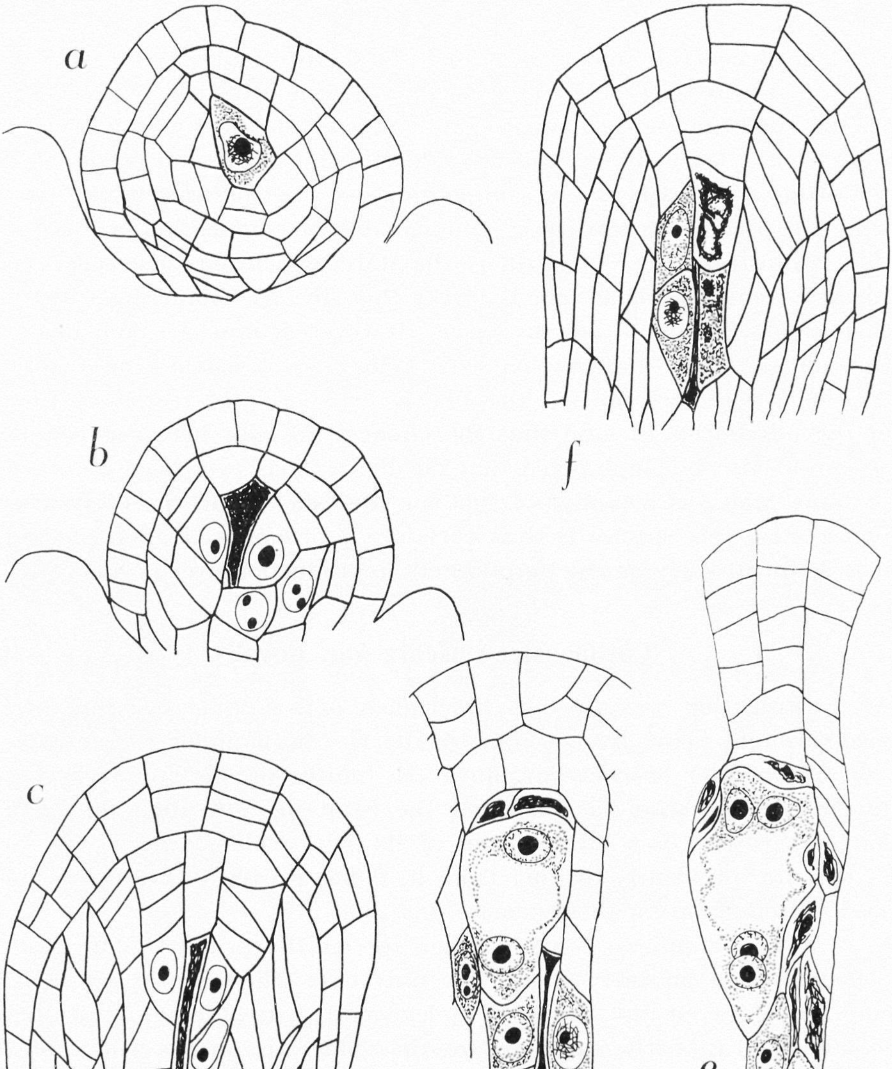

Fig. 5. "*Cotoneaster obscura* var. nova". *a* Quite young nucellus with MMC in the centre. *b* The MMC degenerated, unreduced EI:s begin to develop. *c* The same, a little later stage. *d* 2-nucleate embryo sac; obliquely beneath it the compressed primary MMC, surrounded by some 1-nucleate unreduced embryo sacs and (to the right) a secondary MMC. *e* 4-nucleate embryo sac and below two 1-nucleate embryo sacs that will be supplanted. *f* The primary MMC visible as a dark stripe in the centre, at the left of it a secondary MMC and, above, an EI.

the same potentiality, though in this early stage it was not so decidedly conspicuous. Numerous other cases (about 35) were observed where the primary MMC had degenerated and other cells in the neighbourhood began to grow out into EI:s. Often these were quite numerous: in the case shown in Fig. 5 *c* five such EI:s are visible in the figure, but in addition there were some more in other planes, so that the total number probably was about ten. In comparison with *C. obscura* s. str. the unreduced EI:s here thus are of greater number but of a more rounded shape, not so elongate; probably they always arise here from daughter cells of the secondary archesporial cells.

In Fig. 5 *d* a 2-nucleate embryo sac is visible that has grown out at the side of the now much compressed primary MMC; in spite of the advanced stage it can be stated with rather great certainty that it is unreduced. At least five 1-nucleate EI:s are present that are going to be suppressed (four of them visible in the figure). A 4-nucleate embryo sac is shown in Fig. 5 *e*; in this late stage it is not possible with respect to the embryo sac or the surrounding cells to make any conclusion about its mode of origin. However, here it is visible that two 1-nucleate embryo sacs have increased in size and have been vacuolized; one additional is present in another plane. The competing embryo sacs thus may continue their development to a certain extent before being suppressed by the winning one.

The mature embryo sac was observed in this species in several cases. Also in older embryo sacs the two polar nuclei lay beside each other without having fused; they were close to each other, but there was a distinct limit between them. In one case four polar nuclei were observed; three of them were large, with big nucleoli, and lay close to each other, the fourth was smaller and was situated between the former group and the base of the embryo sac. In *Alchemilla* an abnormal increase in number of polar nuclei is not uncommon (Murbeck, 1902); it is caused by a change of synergids or antipodals into polar nuclei. In this case the two synergids were present and the two supernumerary polar nuclei thus certainly are transformed antipodals; the smaller one is with respect to size and position perhaps to be regarded as a transition between antipodal and polar nucleus.

An occurrence of secondary MMC:s is here rare and probably never results in a development of reduced embryo sacs. In the few cases where such secondary MMC:s were observed they obviously were going to degenerate. In one or two instances it was as a matter of fact difficult to say whether these cells were MMC:s or not, owing to the beginning degeneration. In another case (Fig. 5 *d*) there was an obvious secondary MMC at the side of the remnants of the primary one, but here it was undoubtedly going to degenerate: it showed signs of disintegration and among the competing embryo sacs one had already reached the 2-nucleate stage. In Fig. 5 *f* also a secondary MMC is shown, in the same lateral row as an unreduced embryo sac. The general appearance here also decidedly indicates a beginning degeneration.

The embryological observations thus clearly speak in favour of a pronounced apomixis in this microspecies, in agreement with the result of the genetical experiments.

Cotoneaster acutifolia var. villosula

As early as in the youngest stage observed (Fig. 6 *a*), when the epidermis was still mainly 1-layered and only exceptionally showed periclinal walls, the primary MMC was quite degenerated. In this early stage it was hardly yet possible to discern some potential EI:s, but in a slightly later stage, when the epidermis is 2- or partly 3-layered, such could be observed. Fig. 6 *b* shows an instance of this: beside the degenerated primary MMC a large EI is visible and one more — with the nucleus somewhat smaller and not quite as vigorous as in the former — is situated beneath it; two additional ones seem to be present in adjacent sections. The same position as in this case, viz. that the unreduced EI:s are formed in a small group beside or beneath the degenerated primary MMC, is the usually occurring condition. In the cases where they arise from the lateral rows they at least generally originate through division of the secondary archesporial cells and not from whole such cells. A mature embryo sac is shown in Fig. 6 *d*. The polar nuclei have two nucleoli; the richness of nucleolar substance could of course be regarded as indicating that the embryo sac is unreduced; it is, however, not possible to say anything with certainty about the formation of the embryo sac when it is at such a late stage.

Stages similar to the one drawn in Fig. 6 *b* were observed in some 50 cases, thus nucelli where unreduced EI:s developed beside the degenerated primary MMC, whereas secondary MMC:s were absent, the development thus from all appearances being apomictic. In some other cases, however, secondarily appearing MMC:s were here also observed among the unreduced EI:s; they could be one or sometimes two in number. This was observed in 9 cases, although in 6 of them these secondary MMC:s were already degenerated, going to degenerate or

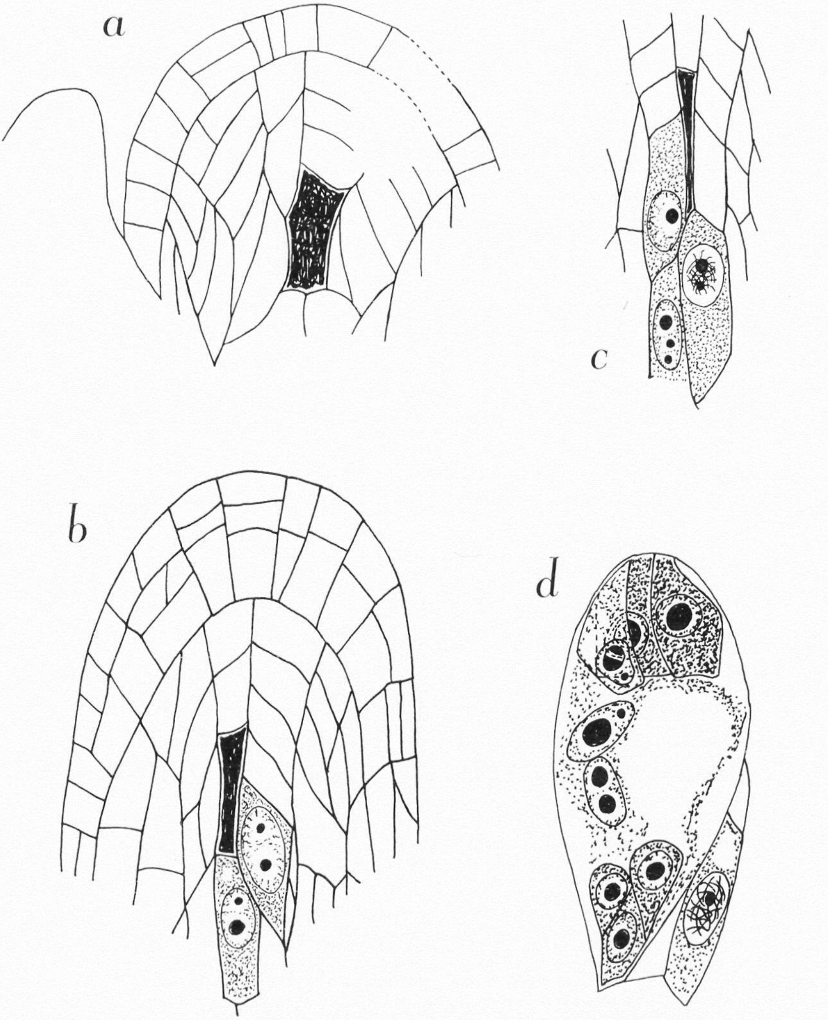

Fig. 6. *Cotoneaster acutifolia* var. *villosula*. *a* L.s. of nucellus in early stage, the MMC already degenerated. *b* Later stage, the MMC degenerated and compressed, two unreduced embryo sac initials visible. *c* Degenerated and strongly compressed primary MMC, beneath it a secondary MMC, in addition two unreduced EI:s. *d* Mature embryo sac, with a secondary MMC at the side, going to degenerate.

clearly inferior to the EI:s; in a 7th case, where two MMC:s were present, one above the other, they were not especially vigorous and would probably also degenerate without division. Only in the two remaining cases did the secondary MMC:s appear more vital, about equal to the unreduced EI:s or even a little more vigorous (see Fig. 6 *c*). Even if a division and megaspore formation in these cases were imaginable, the chances are very small that the reduced embryo sacs would win in the competition, as two division steps (the two meiotic divisions) are necessary for a formation of the reduced embryo sac, while the unreduced ones are already present and show a rather vigorous development.

Sax (1954) states that *C. acutifolia* var. *villosula* in her cultures has shown a not inconsiderable segregation after seed propagation, which she puts in connection with the fact that the species is tetraploid and not triploid. The plant of var. *villosula* that has been investigated by the present writer is, however, pronouncedly apomictic, quite as much as any other species that has been investigated, and if any amphimixis really occurs, it must be very rare. It must on this account be assumed that Sax has studied another form than that investigated here, perhaps another chromosome race of the variety; even if it is difficult to count the chromosome number in flower buds it appears as if the number in the present material were about the triploid one. A confirmation of the apomictic behavior of the here cultivated var. *villosula* may be taken from the fact that Flinck and Hylmö (according to an oral communication) have found a complete agreement between plants of the form obtained from different sources and further also that in their cultures the seedlings of the variety (16 plants) show a great uniformity.

Cotoneaster racemiflora var. soongorica

Cotoneaster racemiflora var. *soongorica* behaves on the whole as the preceding species group, but in spite of this it presents to some extent another picture of some details. As in other species the primary MMC degenerates without reaching any later stage than the prophase, but while this degeneration in other species takes place early, when the meiosis scarcely has begun, it occurs here somewhat later. A well-developed MMC is visible not only in the stage that is shown in Fig. 7 *a*, where the epidermis consists of 1—2 layers, but it may retain about the same appearance even when the epidermis has been divided into two or partly three layers, although its duration may vary in different cases. When the degeneration begins the cytoplasm is contracted and uneven and the nuclear outline is diffuse, while the chromosomes and the nucleolus of the nucleus appear intact in the first degenerating stage. However, in later stages as the one shown in Fig. 7 *b*, where

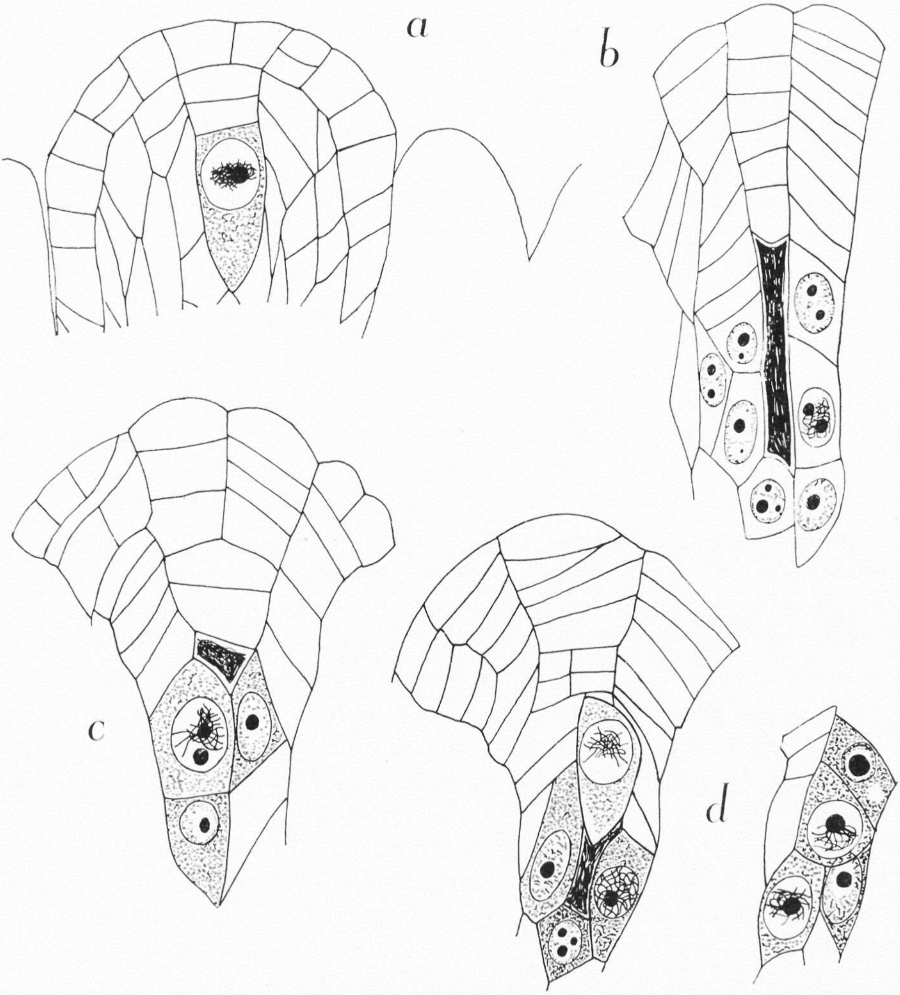

Fig. 7. *Cotoneaster racemiflora* var. *soongorica*. *a* Young ovule in l.s. with central MMC. *b* The primary MMC is degenerated, a group of EI:s develops around it, as well as a secondary MMC (to the right). *c* A vigorous secondary MMC has developed, as well as some EI:s, two of which are visible. *d* Two consecutive sections showing a degenerating primary MMC surrounded by three secondary MMC:s (one of them, the uppermost one, visible in both sections) and some unreduced embryo sacs. — The epidermis cap is not drawn in Fig. 7 *b*—*d*.

the epidermis (not drawn in the figure, like in *c* and *d*) is 5—6-layered in the top, the primary MMC is always degenerated. As in other species there are here around the degenerated MMC cells with big nuclei and nucleoli, also comparatively rich in cytoplasm, which are initials of unreduced embryo sacs. They may be rather numerous; besides the six initials indicated in Fig. 7 *b* at least one more seems to be present in another plane. In addition there are also secondary MMC:s which here seem to play a comparatively great role. In Fig. 7 *b* such a MMC is visible beside the degenerated primary one in a lateral row; in this case, however, it certainly is going to degenerate. In Fig. 7 *d* it is seen that several such secondary MMC:s may occur and that they may be more vigorously developed. Three such cells are visible in the two sections (one of them is divided between the sections) and even if one of them is degenerating, the other two are vital and especially one of them — apparently formed from a parietal cell — is big and vigorous. Also in Fig. 7 *c* a secondary MMC is seen, here arisen from a cell in a lateral row, which is large and vigorous, larger than the EI:s in its proximity; the primary MMC is partly hidden but a part of it is visible. In another case a secondary MMC was observed that obviously was formed by an undivided secondary archesporial cell, since the upper and lower delimitation of it approximately agreed with the primary MMC. Secondary MMC:s were observed in some ten cases, whereas in about twenty cases only unreduced EI:s or embryo sacs were present. No division of the secondary MMC:s and no reduced embryo sacs were ever observed in this material and thus it is doubtful whether such reduced embryo sacs occur and in such a case whether they are capable of competition. Vigorous unreduced embryo sac initials occur and even if these in some cases — as illustrated in Fig. 7 *c* — appear somewhat inferior to a secondary MMC, the conditions are, of course, different when after a possible division of this a reduced embryo sac has arisen, which stage is the one that should be taken into consideration for comparison. However, it is incontestable that the secondary MMC:s in *C. racemiflora* var. *soongorica* on the one hand are more vigorous, on the other of a greater frequency than in many other species; the apomictic tendency on this account (and also with regard to the later degeneration of the primary MMC) does not appear quite as pronounced here and it is perhaps conceivable that reduced embryo sacs occasionally could be formed and the reproduction be amphimictic.

The experimental investigations that have been made by Sax (l.c.) as regards *C. racemiflora* have however not shown any segregation in the F_1-generation, but all seedlings have agreed with the maternal plant. However, it was only *C. racemiflora* var. *veitchii* that was investigated, whereas var. *soongorica* was not included in the material.

Discussion

A survey of the *Cotoneaster* species investigated shows that they have a pronounced apomictic tendency. A characteristic common to them all is that the primary MMC degenerates in an early stage and that unreduced embryo sac initials develop in its place. Simultaneously with these, however, also secondary MMC:s arise, observed in all investigated forms, though often comparatively rare. As a rule also these MMC:s degenerate and only in one species (*C. rosea*) has a development into megaspores been observed. The basal megaspores here was apparently about as vital as the unreduced embryo sacs in the neighbourhood and thus it is probable that normal, reduced embryo sacs sometimes are formed. In two other cases, in *C. nitens* and *C. racemiflora* var. *soongorica,* it is perhaps also possible that in exceptional cases reduced embryo sacs may develop; to be sure, no division of the secondary MMC:s was ever observed, but they appeared so large and vigorous that a further development did not appear quite inconceivable. Inasmuch as a regular formation of unreduced embryo sacs presupposes an apomictic development, it may be said summarily that the investigated species are by far predominantly apomictic; only one of them, *C. rosea,* is probably occasionally amphimictic, while this may possibly be true also of two others, *C. nitens* and *C. racemiflora* var. *soongorica.* Of course, it cannot either be quite excluded that in exceptional instances also in other species a reduced embryo sac may be formed and a normal amphimictic development may take place.

If the development in *Cotoneaster* is compared with other genera in Rosaceae where apomixis to a varying extent is stated certain general similarities are found, but also some deviations in the details.

In Alchemilla (Murbeck, 1901) a primary, more or less central ('axial') MMC is formed which shows meiotic prophase in the nucleus and persists for a very long time, before it degenerates; even when the epidermis cap is 7—8-layered in the top it has about the same appearance and the secondary MMC:s which sometimes arise from parietal cells or lateral rows develop almost as early as the primary one and degenerate about at the same time as that. The unreduced EI:s here never originate directly from secondary archesporial cells, but from the daughter cells that have arisen through their division (which division by Murbeck was regarded as a tetrad division without chromosome reduction).

In the North-European *Alchemilla* species with their very pronounced apomixis no true micropyle is formed, whereas a such one may be observed in tropical species of the genus, where the development against apomixis obviously has not preceeded equally far (Hjelmqvist, 1956). The integuments are two in number; the polar nuclei fuse at least as a rule.

In the genus Aphanes, related to *Alchemilla,* there are both amphimictic and partially or totally apomictic species (Böös, 1917; Hjelmqvist, 1959 a). In *Aphanes arvensis* — partially apomictic — usually several MMC:s are present, one central and a few others, formed from parietal cells or lateral rows; one of these, the central one, passes through meiosis, forming a triad, while the remaining ones as a rule degenerate without dividing. The basal megaspore develops into embryo sac in competition with unreduced EI:s, originating from the lateral rows; generally the reduced embryo sac wins in the competition, sometimes it is ousted by an unreduced embryo sac. In two American species belonging to subg. *Lachemilla* (Böös, 1917) as a rule only one MMC is formed and this degenerates in the prophase and is substituted by unreduced embryo sacs formed by surrounding cells, as in *Alchemilla*; the apomixis is total.

In *Aphanes* only one integument is present, in *A. arvensis* the polar nuclei fuse (as in *Alchemilla*) and a micropylar canal is formed, while in the totally apomictic species of *Lachemilla* there is no micropylar opening and it is doubtful whether the polar nuclei fuse.

To Potentilla both amphimictic and more or less apomictic species belong. According to Håkansson (1946) contrary to the preceding genera there is no central dominating MMC, but already from the beginning there is a parallel occurrence of several MMC:s and the number may increase further through formation of accessory MMC:s outside the archesporium. Unreduced EI:s may be formed from secondary archesporial cells (rare) or other derivatives of the primary archesporium, or from cells lying beneath it. The development of reduced embryo sacs is uncommon in the partially apomictic species.

As in *Aphanes* there is only one integument. A micropylar canal is not developed and the polar nuclei do not fuse.

In the genus Malus the more or less apomictic *Malus hupehensis* (Dermen, 1936) and *M. Sieboldii* — the tetraploid form —, as well as a hybrid of this species (Hjelmqvist, 1957; 1959 b) agree in their general embryology with the preceding genera. As a rule only one MMC occurs and this generally passes through meiosis, a triad being formed, the basal cell of which may develop into an embryo sac. Unreduced embryo sacs with varying success compete with the MMC or its derivatives; they are formed from the daughter cells of the lateral rows, from parietal cells, or even from the epidermis; often, however, they originate from basal cells not belonging to the archesporial tissue. — There are two integuments, a micropyle is developed as well as an obturator, a secondary nucleus is formed in *Malus Sieboldii,* whereas its formation in *M. hupehensis* is delayed and possibly does not take place at all.

In Sorbus (Liljefors, 1953) there develops generally in the centre of the nucellus a primary MMC, while surrounding secondary archesporial cells as in *Alchemilla* divide into lateral rows of 2—4 cells. In the polyploid apomictic species the primary MMC sometimes degenerates in a very early stage, before any meiotic prophase is distinguishable in the nucleus. In other cases the degeneration is later, when the prophase has begun. The degeneration of the MMC usually begins in the nucleus; exceptionally (one species) in the cytoplasm, in similarity with *Alchemilla.* Unreduced embryo sacs develop in varying number and at different times; they generally come from lateral rows or parietal cells. Accessory MMC:s may occur (not observed in all species) in the lateral rows or in basal tissue, but they degenerate.

Some species are partially apomictic, for instance *S. hybrida.* Here the primary MMC may either degenerate in an early stage or form a tetrad; in this case also probably reduced embryo sacs are formed. In exceptional cases a division of accessory MMC:s is observed. The unreduced EI:s arise earlier or later and usually win in the competition.

There are two integuments and an obturator, as in *Malus*; the polar nuclei do not fuse.

Within the genus Rubus, sect. *Moriferi* of subg. *Eubatus,* there are according to Christen (1950) both reduced and unreduced embryo sacs in the polyploid species that have been investigated. As in *Alchemilla* there is a primary central MMC and additional ones also develop in varying number. These may originate from secondary archesporial cells, from the daughter cells of these cells, or from parietal cells; the primary as well as the secondary MMC:s may pass through meiosis. The unreduced embryo sacs may either have the same origin as the MMC, thus deriving their origin from generative cells, which by the author is denoted as diplospory, or originate from somatical cells, above all in the chalaza, which is called apospory; both modes of development may occur in the same species. In some species the secondary archesporial cells divide into daughter cells, in others they are generally or — in other species — practically always undivided, which means that the unreduced EI:s may arise directly from the secondary archesporial cells.

There is only one integument and in the mature embryo sac the polar nuclei — as far as studied — are close together but do not fuse.

A comparison of the different details in the development of *Cotoneaster* with the mentioned genera gives the following results.

In the general organization *Cotoneaster* agrees with *Malus* and *Sorbus,* inasmuch as it has two integuments, a developed micropylar canal, and an obturator. The remaining genera deviate in one respect or another; thus only one integument occurs in *Aphanes, Potentilla* and *Rubus,* a micropylar canal is absent in many *Alchemilla* and *Potentilla* species and sometimes in *Aphanes,* and in most genera obturator is not developed.

As regards the early development *Cotoneaster* agrees with the majority of the mentioned genera in the fact that only a central primary MMC is formed, later possibly followed by secondary MMC:s; the sole genus that deviates is *Potentilla,* where there already from the first are several equal MMC:s. While the secondary MMC:s in *Alchemilla* and some *Sorbus* species arise early, they in *Cotoneaster* are considerably later than the primary one.

As in *Alchemilla* the primary MMC in *Cotoneaster* always degenerates without having divided, but the degeneration takes place earlier than in this genus, often so early that the meiosis has scarcely begun. In this respect *Cotoneaster* instead agrees with certain *Sorbus* species. However, in these species the secondary MMC:s that later may possibly be formed always degenerate, whereas those in *Cotoneaster* may in some cases develop further. Thus in this general mode of development *Cotoneaster* differs from all genera mentioned: an early degeneration of the primary MMC, but possibly a later development of secondary MMC:s, which always seem to have better opportunities than the primary one. In *Sorbus,* it is true, the secondary MMC:s may in rare cases (observed in two species; Liljefors, 1953), in *Rubus* more generally pass through meiosis, but in these cases also the primary MMC is capable of development, contrary to the conditions in *Cotoneaster.*

As regards the development of unreduced embryo sacs there is scarcely any difference between the genera described here with respect to their origin: they may derive their origin from the original archesporium — from lateral cells, from secondary archesporium cells, or from parietal cells —, or from other parts of the nucellus, generally the chalazal tissue. Within the different genera, however, there is a certain variation, both in *Cotoneaster* and in other genera, which has caused that in *Rubus,* for example, a distinction has been made between species with dominating diplospory (E.I. originating from the archesporium) and apospory (E.I. originating outside the archesporium). If this distinction is to be maintained, there is also in *Cotoneaster* a certain difference: for instance, in *C. bullata* the unreduced embryo sacs generally develop from the original archesporium, beside or even above the primary MMC, but in *C. acutifolia* var. *villosula* they for a great part develop beneath the primary MMC, in tissue outside the archesporial one. However, it does not seem quite appropriate to denote these two developments with different names, apospory (or somatic apospory) and diplospory (generative apospory) as the development in both cases takes place by way of a quite regular mitosis (and the cells also lie beside each other in the same nucellus). In agreement with Fagerlind (1944) and Liljefors (1953, p. 297), all these unreduced embryo sacs should rather be regarded as formed through somatical apospory, if they have not arisen through transformation of MMC:s, which has not been observed in *Cotoneaster.*

Within *Sorbus* Liljefors (l.c., p. 321) distinguishes between different groups which show differences i.a. in time of development and number of the aposporical EI:s. In *Cotoneaster* there is a correspondence at least to the latter difference: certain species, as *C. bullata* and *obscura,* have a comparatively low number of unreduced EI:s, which usually also are large and rich in cytoplasm, while other species, as the one designated as *C. obscura* var. *nova,* have a greater number, sometimes up to ten EI:s.

With respect to the origin of the unreduced embryo sacs especially Christen (1950) for *Rubus* has emphasized the difference between those that arise from whole secondary archesporial cells and those that are formed from their daughter cells. In *Rubus* there is a comparatively sharp contrast between species where the one or the other mode of development is dominating; these species however are connected by transitional species. In other genera, as *Alchemilla* and *Aphanes,* the only possibility seems to be that daughter cells of the secondary archesporial cells form EI:s; Murbeck (1901), as a matter of fact, regarded the regularly occurring divisions of the lateral rows as a kind of tetrad division. Within *Potentilla* as in *Rubus* it may happen that secondary archesporial cells directly develop into unreduced embryo sacs, but this is rare. The same is true about *Cotoneaster,* where perhaps it is a little more common: it sometimes occurs in *C. bullata* and *C. obscura.* Christen (l.c., p. 188—189) is of the opinion that this failing division of the secondary archesporial cells means a reduction phenomenon. As regards *Cotoneaster,* it may be possible that the species where this development is found are a little more advanced; in their apomixis they appear to have proceeded rather far towards total apomictic reproduction.

The degeneration of the MMC may according to Liljefors (l.c., p. 299 etc.) in *Sorbus* follow two types: the one, that occurs in many *Sorbus* species, is characterized by an earlier degeneration of the nucleus than of the cytoplasm, the other — occurring in one *Sorbus* species and in *Alchemilla* — shows an earlier degeneration of the cytoplasm. *Cotoneaster* seems in this respect to be of the latter type and agrees rather well with *Alchemilla.*

As regards the behavior of the polar nuclei in the mature embryo sac, it is stated for several of the mentioned genera that they do not fuse (*Potentilla, Sorbus, Rubus,* certain *Aphanes* species, possibly *Malus hupehensis*); in *Alchemilla,* however, they are united into a secondary nucleus. In *Cotoneaster* in one case (*C. nitens*) a clear fusion was observed, while in several other cases the two polar nuclei also in late stages were lying close to each other without having fused. In these cases the fusion, if it takes place at all, must be delayed; possibly there is a weakened tendency to fusion, as this seems often to be the case in apomictic genera. However, also in amphimictic species it may happen that the fusion of the polar nuclei takes place at different times and is sometimes considerably delayed (*Malus communis,* Wanscher 1939, p. 42).

Searching for an explanation of the mode of development that is characteristic for *Cotoneaster,* viz. that the primary MMC always degenerates, while the later formed MMC:s occasionally may divide and compete with the unreduced EI:s, and even if they do not divide still have a greater vigor and longer duration than the primary one, the general background to the apomictic development must be taken into consideration. According to a general theory (Fagerlind, 1944; Nygren, 1949, p. 294—295, 1950, p. 56; Liljefors, 1953, p. 297, 309) inhibition of the meiosis in the apomicts is caused by too small or too great concentration of the active hormone. If the theory is correct (Nygren, 1950) that too great a concentration prohibits the meiosis and causes apospory, the explanation to the conditions in *Cotoneaster* could be that in the young nucellus, consisting of some few cells, the concentration is stronger than in the older and larger, which consists of numerous cells and often also contains more than one MMC. Of course, it is also possible that the hormone production is different in older and younger stages. For comparison it may be mentioned that in a type of *Calamagrostis purpurea* (Nygren 1949, p. 295) the first panicles had meiosis, the later mitosis, obviously depending upon changes in the hormone production at different ages. Changes of a corresponding kind — but in an opposite order — might be thought to cause the different behavior of the MMC in younger and older stages of *Cotoneaster*.

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BOTANISKA NOTISER 1962 · VOL. 115 · FASC. 2 · LUND

Smärre uppsatser och meddelanden

Om Ceterach officinarum och dess ekologi

Det märkliga fyndet av *Ceterach* på Gotlands östkust (Nyhlén 1949) medförde ett nytt tillskott till de sydliga arterna i Skandinavien. *Ceterach* har sin största frekvens och abundans i Mediterranområdet, men arten går så långt nordvästut som till Skottland och Irland. Från Medelhavsområdet är det känt att *Ceterach* förekommer nästan uteslutande i klippspringor och på gamla murar i torrt, soligt läge (jfr Rouschal 1938 p. 305). Emellertid går arten även mycket högt i bergen vilket redan framhållits av Nyhlén (1949), som vid sin redogörelse för fyndet berörde det intressanta i att arten förekommer i tämligen skilda klimattyper. Huvuddelen av utbredningsområdet har en varm vinter. Det är påfallande, att ormbunken går längst mot norr i maritima områden, såsom exv. Irland. Praeger (1934: 352) räknar *Ceterach* till »moisture-loving plants», och anger, att arten på Irland växer »deep down in the joints of the limestone» (tillsammans med *Adianthum capillus-veneris*), vilket utgör den naturliga ståndorten; men arten har enligt Praeger spritts därifrån över hela Irland tack vare att man byggt stenmurar med murbruk.

Mot bakgrunden av den allmänna utbredningen är ståndorten på Gotland av stort intresse. Östsidan av Gotland karakteriseras av fuktigare klimat än huvuddelen av ön; Grogarnsberget har (även frånsett *Ceterach*-förekomsten) en ymnigare pteridofytvegetation än klintkusten i nordväst. I den omgivande trakten växer flera ormbunksarter i solöppet läge, vilka inom andra delar av ön kräver mer skyddade och skuggiga lägen, exv. *Gymnocarpium robertianum* och *Cystopteris fragilis* (Pettersson 1958 p. 70). På sin nordligaste gotländska lokal växer *Gymnocarpium robertianum* i karstspringor.

Det ser alltså ut, som om *Ceterach* i de nordligaste delarna av sitt utbredningsområde skulle inta ståndorter, som utmärks av låg ljusintensitet, relativt hög luftfuktighet samt hög vintertemperatur.

Om man granskar *Ceterach*-förekomsten på Grogarnsberget närmare, visar det sig, att arten håller sig till torrare mikroståndorter än *Asplenium trichomanes* på de ställen, där dessa arter växer tillsamman (jfr fig. 1). Emellertid är det uppenbart, att arten på Gotland inte kan växa lika öppet och solexponerat som i Medelhavsområdet. Arten har vid sin nordgräns, såsom kunde väntas, en snävare ekologisk nisch. Den som xerofyt allmänt karakteriserade arten har på sin nordligaste lokal krav på att ljusintensiteten inte är för hög men heller inte för låg. Härmed torde sammanhänga kraven på hög luftfuktighet, kanske främst under våren, som är genomsnittligt torr på ön.

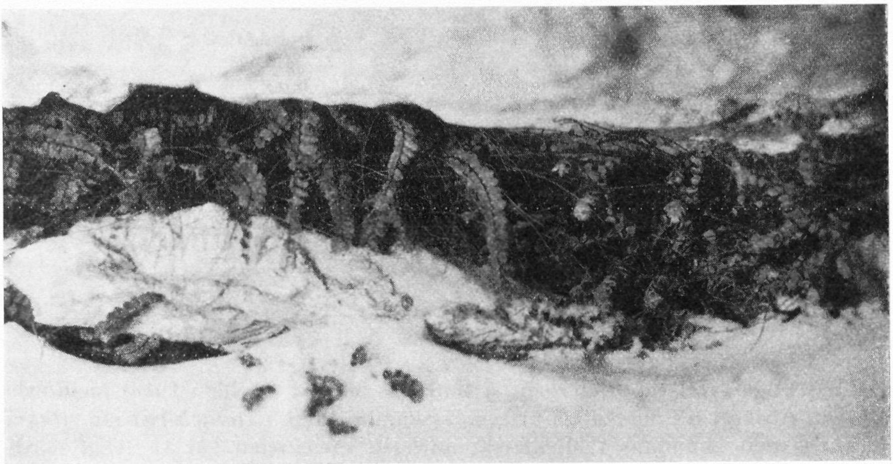

Fig. 1. En skreva med *Ceterach* på Grogarnsberget vintertid (samma skreva, där beståndets förändringar kontinuerligt följts från 1949). *Asplenium trichomanes* växer längst in i skrevan och visar ännu torkskador från sommaren 1959. *Ceterach*-bladen är något hoprullade (lufttemp. ca —5°). Åren 1949—58 ökade *Ceterach*-förekomsten i grottan men har nu åter minskat, sedan de i texten beskrivna obehöriga åtgärderna satte in. — Foto 30 jan. 1962.

De iakttagelser jag gjort i Medelhavsområdet tyder på att arten på högre nivåer uppträder i en mer mesofil miljö än i olivregionen. T.ex. växer den i Sydspanien (Sierra de Maria) i klippnischer vettande mot norr på en höjd av ca 1600 m och i Kroatien i *Acer pseudoplatanus* - *Fagus silvatica*-skog på en höjd av ca 1000 m. Högst tycks ormbunken växa i Nordafrika nämligen till 2.700 m (Maire et al. 1952 p. 46), men härifrån finns inga närmare ståndortsuppgifter.

Under torkeperioder rullar *Ceterach* ihop bladen, så att den brunfjälliga undersidan vänds utåt. Maire et al. (l.c.) kännetecknar arten som en »plante xérophile se desséchant l'été et reviviscente». I Medelhavsområdet har jag på talrika lokaler observerat, hur alla *Ceterach*-rosetter under sommartorkan intagit en sådan ställning. Även temperaturer under fryspunkten har ungefär samma verkan, ehuru icke så utpräglad (jfr fig. 2).

Ceterach officinarum erbjuder ett av de många exempel på bladrörelser som rapporterats hos ormbunkar. Wittrock (1891) synes ha varit den förste, som gjort undersökningar av de inhemska ormbunkarnas av upptorkning betingade bladrörelser under kyla och värme. Även hos sådana arter som *Polypodium vulgare* och *Asplenium trichomanes* förekommer såsom Wittrock visat betydande bladdeformationer, vilka går tillbaka, då fuktigheten ökas. De är dock icke så betydande som hos *Ceterach*.

Walter och Bauer (1937 p. 393) anser, att hoprullandet av bladen hos de poikilohydra ormbunkarna från ekologisk synpunkt är ett betydelselöst fenomen, emedan Walter i Arizona-öknen funnit såväl sådana xerofytiska arter,

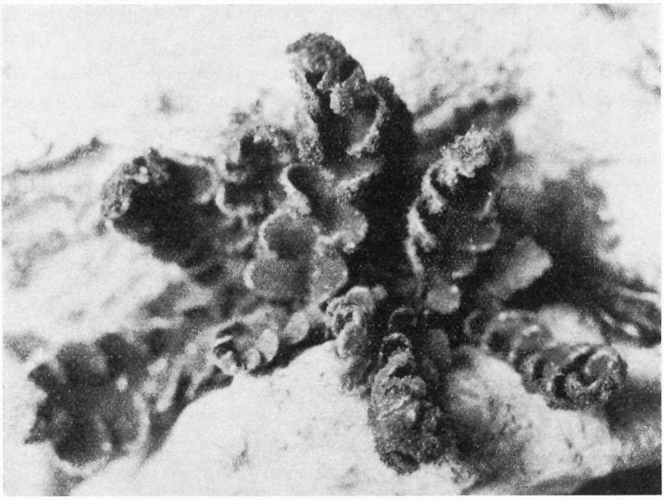

Fig. 2. Ett litet *Ceterach*-ex., som närmare visar de vintertid något inrullade bladen (lufttemp. ca. —5°). — Foto 30 jan. 1962.

som icke rulla ihop sig, och sådana som har dylika rörelser. Till den förstnämnda kategorin räknade Walter den mot torka mest resistenta ormbunken, *Notholaena sinuata* var. *integerrima*.

En grundligare framställning av problemet hos *Ceterach officinarum* ges av Rouschal (1938), som funnit, att en anatomisk organisation i form av kollenkymartade förtjockningslister på palissadcellernas längdväggar hindrar celldeformationer hos denna art. Även finns ett rymligt intercellularsystem, som möjliggör förskjutningar av cellerna utan att dessa deformeras. Därjämte torde cellsaftens innehåll av katekingarvämnen möjliggöra, att cellinnehållet blir fastare vid vattenförluster och motverkar osmotisk volymminskning. Rouschal liksom Gessner (1956 p. 238) karakteriserar *Ceterach* som en xerofytisk ormbunke, som dock skulle sakna en särskild organisation mot transpirationsförluster. Den skulle också kunna förlora 98 % av vattnet utan att skador uppstår. Vid torka deformeras översidans epidermisceller starkare än undersidans; dessa celler har icke någon kollenkymatisk förstärkning. Detta medverkar till bladets hoprullning.

Under den torra sommaren 1959, liksom under andra torkeperioder, rullade *Ceterach* på Grogarnsberget ihop bladen. Detta råkade några naturintresserade personer observera, och man trodde, att växten höll på att dö ut. Detta är skildrat i en tidningsartikel (Tidningen Gotlänningen nr 149 B), »Expert skall nu försöka rädda dvärghjorttungan». Svenska Naturskyddsföreningen ställde enligt artikeln omedelbart medel till förfogande för att en expert skulle få besöka växtplatsen, och i en senare artikel, »Dvärghjorttungan räddades av vatten» (A-d 1959), skildrar Svenska naturskyddsföreningens länsombud på Gotland dramatiskt, hur ormbunken (»dvärghjorttungan») räddades genom vattning och instoppning av våt mossa. Den 13 okt. 1959 hade jag tillfälle att undersöka *Ceterach*-beståndet på Grogarnsberget och måste då plocka en hel påse full med torra mossor, som Naturskyddsföreningens representanter hade stoppat in i den skreva, som har den rikaste förekomsten av *Ceterach*. Växten hade i denna springa fortfarande till hälften inrullade blad till skillnad från de exemplar, som icke kunde nås av vare sig vattning eller mossinpackning.

Just denna påverkade skreva har varit föremål för kontinuerliga observationer av *Ceterach* 1949—58. I min gradualavhandling (Pettersson 1958 p. 74—76) sökte jag visa, att relativt hastiga förändringar skett inom det ganska obetydliga beståndet på Grogarnsberget. Sedan upptäckten har det i stort sett minskat, men samtidigt kunde genom fortlöpande fotografisk registrering av den förut nämnda skrevan en så påtaglig ökning konstateras, att det skulle kunna tyda på att *Ceterach* åtminstone där kunde anses ha invandrat under senare år.

BENGT PETTERSSON

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Dryopteris abbreviata (DC.) Newm. från Lofoten

Härom året påträffade ingenjör Torleif Björnberg en egendomlig form av *Dryopteris filix-mas* (coll.) vid ett besök på Moskenesöya i Lofoten. Han hade lovat att skaffa mig några intressanta växter från denna ö och på så sätt erhöll jag ormbunken. Då jag för någon tid sedan gick igenom samlingen på nytt visade det sig att den tillhörde arten *Dryopteris abbreviata* (DC.) Newm., vilken art verkar vara ny för Skandinavien eftersom den ej finns upptagen i de nyare Skandinaviska florora. Den är den diploida motsvarigheten till den tetraploida *Dryopteris filix-mas* (s.str.), från vilken den skiljer sig i ett antal morfologiska karaktärer. Av den anledningen är det väl motiverat att hålla isär de två typerna som skilda arter.

Exemplaret från Moskenesöya överensstämde med beskrivningen i följande viktiga karaktärer. Bladen äro relativt små och faller inom längdintervallet

30—50 cm. Sekundärsegmenten äro lätt konkava med trubbiga tänder. Nedersta sekundärsegmentet på övre sidan är märkbart längre än sina grannar på några av primärsegmenten. Det finns vidare sällan fler än tre sporangiesamlingar på något av sekundärsegmenten. Med andra ord finns det ej anledning att betvivla riktigheten av bestämningen.

Arten är tidigare känd från Grönland, på vilken ö den tycks ensam företräda artkomplexet *Dryopteris filix-mas - Dryopteris abbreviata*. På Island har paret Löve påvisat arten vid Búdahraun. Även på denna ö verkar *Dryopteris abbreviata* företräda artkomplexet, då den isländska populationen är förhållandevis enhetlig. Från Storbritanien är den känd från ett flertal lokaler, speciellt i rasmarker, men den förekommer mycket lokalt.

Fyndet på Moskenesöya — Moskenes herad — ansluter sig till dessa lokaler runt norra Atlanten. Tyvärr har jag ej uttömmande data om lokalen, som är belägen i rasbranterna efter fjorden in mot Hermannstind. Däremot förekommer den icke i botten på den stora Vestfjorden. I rasmarkerna innanför Rombaksbotten har jag påträffat vanlig *Dryopteris filix-mas*.

Arten borde kunna eftersökas efter den norska kusten liksom på Färöarna. Ändamålet med denna notis är att väcka intresse för denna art.

C. I. SAHLIN

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Botaniska Notiser 1962 · Vol. 115 · Fasc. 2 · Lund

Notiser

Professuren i växtbiologi i Uppsala. De sakkunniga för den efter prof. G. E. Du Rietz ledigförklarade professuren i växtbiologi vid Uppsala universitet, proff. G. E. Du Rietz, Uppsala, och H. Luther, Helsingfors, samt statsgeologen J. Iversen, Köpenhamn, ha i första förslagsrummet till professuren uppfört laborator H. Sjörs, Stockholm. Proff. Du Rietz och Luther uppförde i andra rummet doc. M. Fries, Uppsala, i tredje doc. O. Hedberg, Uppsala, medan statsgeolog Iversen placerade doc. O. Hedberg i andra, doc. M. Fries i tredje rummet.

Professuren i fysiologisk botanik i Göteborg. Samtliga kvarstående sökande till den nyinrättade professuren i fysiologisk botanik vid Göteborgs universitet, doc. P. Halldal, Lund, doc. Birgitta Norkrans, Göteborg, doc. H. Rufelt, Uppsala, och laborator H. Virgin, Uppsala, ha av de sakkunniga förklarats kompetenta till professuren. Två av de sakkunniga, proff. H. Burström, Lund, och T. Hemberg, Stockholm, placera laborator Virgin i första rummet, doc. Halldal i andra och doc. Norkrans i tredje, medan prof. Fries uppför laborator Virgin i första, doc. Norkrans i andra och doc. Halldal i tredje rummet.

Professuren i systematisk botanik i Göteborg. Till den från den 1 juli 1963 nyinrättade professuren i systematisk botanik vid Göteborgs universitet hade vid ansökningstidens utgång den 26 mars 1962 anmält sig följande sökande: Doc. G. Degelius, Göteborg, doc. G. Harling, Stockholm, doc. O. Hedberg, Uppsala, prof. Á. Löve, Montreal, doc. B. Lövkvist, Lund, t.f. laborator Hedda Nordenskiöld, Uppsala, t.f. prof. A. Nygren, Uppsala, doc. H. Runemark, Lund, doc. M. Ryberg, Stockholm, lektor S. Suneson, Göteborg. Till sakkunniga ha utsetts proff. J. A. Nannfeldt, Uppsala, T. Sørensen, Köpenhamn, H. Weimarck, Lund, samt om en fjärde sakkunnig får utses, prof. F. Fagerlind, Stockholm.

Professuren i växtförädling vid lantbrukshögskolan. De sakkunniga för professuren i växtförädling vid lantbrukshögskolan i Uppsala, proff. K. Fröier, Stockholm, H. Wexelsen, Vollebekk, och E. Åkerberg, Svalöv, ha samtliga bland de sökande uppfört doc. A. Hagberg, Svalöv, i första rummet, agr. dr J. Mac Key, Svalöv, i andra, och doc. N. Nybom, Balsgård, i tredje rummet.

Docentförordnanden. Till docent i växtbiologi vid Uppsala universitet har förordnats fil. dr N. O. Rune. Docenten i botanik vid Stockholms universitet E. G. Rennerfelt har förordnats till docent i mikrobiologi därstädes.

Hedersdoktorat. Till fil. hedersdoktor vid Uppsala universitet promoverades den 30 maj doc. Auseklis Vegis, Uppsala.

Doktorsdisputationer. Följande doktorsavhandlingar ha ventilerats vid Lunds universitet: D. 10 maj: Åke Persson, Mire and spring vegetation in an area north of Lake Torneträsk, Torne Lappmark, Sweden; d. 14 maj: Vagn Tullin, Effects of injections of growth compounds on seedlings; d. 16 maj: Torsten Ingestad, Macro element nutrition of pine, spruce, and birch seedlings in nutrient solutions; d. 22 maj: Nils Malmer, Studies on mire vegetation in the Archaean area of southwestern Götaland (South Sweden). Vid Uppsala universitet ha följande avhandlingar försvarats: D. 14 maj: Bengt von Hofsten, Some aspects of the growth and enzyme formation of Escherichia coli; d. 21 maj: Gunnar Wistrand, Studier i Pite Lappmarks kärlväxtflora med särskild hänsyn till skogslandet och de isolerade fjällen; d. 24 maj: Reinhold Ivarsson, Lövvegetationen i Mollösunds socken. Vid lantbrukshögskolan, Uppsala, ha framlagts: D. 21 maj: Birger Granström, Studier över ogräs i vårsådda grödor; d. 23 maj: Helmut Kolk, Viability and dormancy of dry stored weed seeds. Studies in several species occurring frequently in Swedish grassland seed lots. Vid Stockholms universitet försvarades d. 14 maj avhandlingen: Gunnar Jansson, Studies on water-sensitivity in barley seeds, och vid Göteborgs universitet försvarade K. Gundersen den 30 maj sin avhandling: A study on microbial antagonism. The action of Streptomyces griseus and one of its antibiotics, cycloheximide, on Fomes annosus.

Forskningsanslag. Fysiografiska sällskapet i Lund har utdelat bl.a. ett anslag å 700 kr. till doc. O. Almborn för att vid Botaniska museet i Helsingfors studera typmaterial av lavar, speciellt från Sydafrika, och 2.500 kr. till fil. lic. B. Berglund för studier av senkvartär vegetationshistoria i sydöstra Sverige, i synnerhet Blekinges sydöstra del.

Från stiftelsen Lars Hiertas minne har i april 1962 utdelats 2.500 kr. till amanuens L.-K. Königsson, Uppsala, för slutförande av pollenanalys av material från Möckelsmossen på Öland samt 3.000 kr. till docenterna K. Torssell och G. Widmark, Stockholm, för apparatur för isolering och renframställning av substanser ur växtextrakt.

Vid Lunds universitet har i april 1962 ur Bokelundska fonden utdelats bl.a. 1.965 kr. till fil. dr Åke Persson för botaniskt undersökningsarbete på Island. — Ur fonden för Blekingsk hembygdsforskning har ett anslag å 700 kr. tilldelats Lunds Botaniska Förening, sektionen Blekinges Flora, för inventering av kärlväxtfloran i Blekinge.

Vetenskapsakademien har den 25 april 1962 utdelat ett Lindahlskt stipendium om 8.000 kr. till fil. mag. S. Pekkari, Uppsala, för vattenväxtundersökningar. Ur Enanderska fonden utdelades 1.800 kr. till fil. dr E. Almquist, Uppsala, för hieraciologiska fältundersökningar, 1.200 kr. till prof. F. Fagerlind, Stockholm, för undersökningar inom släktet *Rosa*, 1.200 kr. till doc. O. Hedberg, Uppsala, för cytologiska studier och odlingsförsök, 1.300 kr. till fil. mag. B. Jonsell, Uppsala, för cytologiska studier inom släktet *Rorippa* och 2.500 kr. till fil. mag. E. Kjellqvist, Lund, för odlingsförsök och undersökningar rörande *Festuca rubra*-komplexet.

Ur fonden för skoglig forskning har i maj 1962 utdelats bl.a. följande anslag: Till Föreningen Skogsträdsförädling, Uppsala, 23.790 kr. för en undersökning av odlingsvärdet hos olika arter, provenienser och arthybrider av lärk; fil. lic. G. Hadders, Uppsala, 7.000 kr. för fortsatta studier av ungdomsutvecklingen hos *Pinus silvestris*; f. överjägmästaren A. Holmgren, Stockholm, 2.000 kr. för undersökningar för belysande av frågan om orsakerna till den skadegörelse av klimatisk natur, som i en del fall drabbat kulturplantorna på höjdlägeshyggena i Väster- och Norrbottens län; prof. O. Langlet, Stockholm, 24.000 kr. för utförande av inventerande proveniensförsök med gran; laborator E. B. Oksbjerg, Stockholm, 3.500 kr. för beskrivning av skogens utveckling i Norra Rörums socken; amanuens A. Samuelsson, Stockholm, 6.180 kr. för fullföljande av undersökning av vegetationens förändring i samband med granskogens invandring på tidigare slåtter- och hagmark inom Garpenbergs revir; skogs- och lantbruksakademien 14.500 kr. för fortsatt forskning över hormonpreparatens fysiologiska verkningar; jägmästare G. Ullén, Bromma, 5.000 kr. för bearbetning av under år 1961 insamlade tillväxtuppgifter från år 1954 stormskadade bestånd inom Sala och Bjurfors revir och Hedesunda socken.

Anslag till genetiska institutionen i Lund. Som ersättning för det anslag, som genetiska institutionen i Lund under en följd av år uppburit från Rockefeller Foundation, men som innevarande år kommer att upphöra, har en anonym givare till Lunds universitet överlämnat en gåva om ca 195.000 kr. att användas för det vid institutionen bedrivna forskningsarbetet.