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STUDIES ON
THE FLORAL MORPHOLOGY AND PHYLOGENY OF THE AMENTIFERAE

BY

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Introduction.

The group *Amentiferae*, which consists of a series of orders related to one another but seldom regarded as a special taxonomical unity, is of a great systematical interest. According to one school of scientists, among the foremost names of which ENGLER and RICHARD WETTSTEIN may be mentioned, the *Amentiferae* belong to the most primitive of all Angiosperms; it is thought that this group, or in any case the larger unity to which it belongs, forms the transition from the Pteridophyta or the Gymnosperms to the Angiosperms. Another school, founded by BENTHAM and HOOKER and especially adhered to in England, regards the *Amentiferae* as reduced descendants of higher organized types; their simple flower structure, according to this school, is not an original feature but a secondary character resulting from reduction. Accordingly, the group is placed high in the system. There are, thus, two quite different opinions on the systematical position of the *Amentiferae*, and, according as the one or the other is adopted, quite a different picture is received of the whole system and the origin of the Angiosperms. Our view of the *Amentiferae* is to a great extent decided by how we interpret certain morphological conditions in the flower structure, and it is therefore an important purpose of research to elucidate these. Another matter of importance is the clarification of the affinities and evolutionary lines within the group itself, among its different lower systematical units; it will thus be easier to bring it in relation to other groups. The present study is an attempt to elucidate the affinities of the *Amentiferae* on the basis of morphological investigations, especially of the flower.

Most of the earlier investigations made into the floral morphology of the *Amentiferae* are rather old, dating from the latter half of the 19th century or the beginning of the 20th century. In recent times, however, valuable contributions have been made to the knowledge of the flower morphology of the families in this group by American scientists (FISHER, 1928; ABBE, 1935 and 1938; ABBE and EARLE, 1940; MANNING, 1938, 1940), who have generally made combined anatomical and morphological analyses. These investigations have been of great value for the present study. Some families (e.g. *Fagaceae*), however, have not been the subject of any such thorough analysis — they will here be treated in greater detail —, and it may also be of value to give a comparative account of the whole group, laying stress upon the characters important for judging its systematical position.

In concluding this work I wish to express my great gratitude to all the persons and institutes — Botanical gardens and museums — which have given me aid in the procurement of material or in other ways. Especially I thank my Chief at the Systematical Department of the Botanical Institute of Lund, Professor HERIBERT NILSSON, for his interest and benevolence. My thanks are also due to the heads of the botanical museums in Geneva (Conservatoire et Jardin Botaniques), Paris (Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie), Kew (R. Botanic Gardens), Edinburgh (R. Botanic Garden), Copenhagen, Arnold Arboretum, and Washington (U. S. National Museum) for having provided me with opportunities of studying material difficult to procure.

The range of the group.

To the group *Amentiferae* belong in the first place four orders: *Juglandales, Fagales, Betulales,* and *Salicales.* The delimitation of these orders varies: thus the *Juglandales* are often divided into two orders, *Myricales* and *Juglandales,* and the *Betulales* have hitherto always been united with *Fagales.* Still, there is no doubt that the plants belonging to them are related to each other. They constitute a large natural group. To this group, however, some systematists have referred, with more or less hesitation, some other small orders.

One of these orders is *Julianiales,* with the family *Julianiaceae.* Already when HEMSLEY (1908) proposes the family, he advances as his opinion that it is related to *Cupuliferae* (*Fagaceae*), and places it between this family and *Juglandaceae;* to the latter family it is in his opinion not closely related. He also points out, however, the existing similarities with the family *Anacardiaceae,* in the anatomy as well as in the embryology. HALLIER (1908) unites *Julianiaceae* with *Anacardiaceae,* but at the same time he also refers the *Juglandaceae* to the family, *Terebinthaceae,* wherein he makes these and some others be merged; he is then of the opinion that there is a close relationship between *Julianiaceae* and *Juglandaceae,* and also regards the other amentiferous plants as reduced descendants of the family *Terebinthaceae.* Following HEMSLEY A. ENGLER (1909) and several other authors after him have made the family *Julianiaceae* a special order, *Julianales* or *Julianiales,* among the *Amentiferae.* WETTSTEIN (1935) goes so far that he refers the family to the same order as *Juglandaceae, Juglandales.* On the other hand, e.g. NAGEL (1914) in his thorough investigations of the *Juglandaceae* has come to the opinion that they are not at all related to *Julianiaceae.* As a matter of fact, much speaks for the correctness of this view and for the *Julianiaceae* not being at any rate closely related to the *Amentiferae,* to which group they therefore are not to be referred.

As early an observer as HEMSLEY stated that the family differed anatomically from *Juglandaceae* and resembled *Anacardiaceae*. The more recent investigations of KRAMER (1939) have confirmed this fact; this author finds a great agreement with *Anacardiaceae*, none with *Juglandaceae*. Emphasis is perhaps to be laid especially upon the occurrence of resin ducts in the stem, which are entirely lacking in the latter family but are present in the former.

The occurrence of a »cupule», an involucre that surrounds the fruits, has been considered to show the affinity of *Julianiaceae* with the *Amentiferae*, where cupule-structures also occur. The cupule is in *Julianiaceae* formed of coalescent bracts, which surround 3—4 female flowers, although only in one or two of these is fruit developed. A cupule, originating from leaf-structures, is also to be found in *Juglandaceae*. Here, however, each flower is surrounded by a cupule. Within *Fagaceae* it occurs that several flowers are surrounded by a single cupule, but this is here a stem- and not a leaf-structure, and, moreover, it is no doubt derived from a primary type with one cupule round each flower; such a development is not indicated by any known facts in *Julianiaceae*. Further, in the latter family there are some special peculiarities without correspondence in the *Amentiferae*: the narrow edges of the fruits are adnate to the inner wall of the cupule and the stalk of the cupule is often broad and winged.

The male flowers of the *Julianiaceae* have a simple perianth, of much the same appearance as in *Fagaceae*, but they show an important deviation from the flowers of the *Amentiferae*, a fact that seems never to have been emphasized. In *Julianiaceae* the stamens are distinctly alternating with the perianth leaves. In *Amentiferae*, on the contrary, they are typically superposed; sometimes by splitting they become more than the perianth leaves, and then partly also alternate with them, sometimes there is no clear relation between perianth lobes and stamens, but only alternating stamens are a feature that is foreign to the *Amentiferae*.

Thus, in the author's opinion, the similarities that exist between *Julianiaceae* and the *Amentiferae* are a result of secondary convergence, and there is no real affinity between these groups, at any rate no near affinity. *Julianiaceae* should instead most likely be placed in the proximity of *Anacardiaceae*.

A second order that often is attributed to the *Amentiferae* is *Batidales*, consisting of the family *Batidaceae*, with the monotypic genus *Batis*. In placing the order VAN TIEGHEM (1903) is generally referred to, who has carefully investigated the systematically important characters. The male flowers have no perianth, but are surrounded by a cup-like leaf, at first close, later on irregularly bursting, according to VAN TIEGHEM an adossate bracteole, which at the top has a crest-like appendage. Further alternating with the stamens there are four diagonal scales, long-stalked, spatulate, according to VAN TIEGHEM arising as emergences from an extra-staminal disc. In the female flowers, also without perianth, there is a four-chambered ovary, which however, as VAN TIEGHEM has pointed out, is composed of two transverse carpels and originally has two chambers, each of which is again divided into two by a false partition. The number and position of the carpels is thus the same as in many of the *Amentiferae*; false partitions not infrequently occur also there, and the scales of the male flowers might have a correspondence in the disc-structures that occur in *Salicaceae*. The divergences, however, are also great; adossate bracteoles of the peculiar structure that is to be found in *Batis* do not occur in the *Amentiferae*, and the scale-like structures have quite another shape and position than the glands of *Salix*. VAN TIEGHEM himself, in fact, did not refer *Batidaceae* to some group *Amentiferae*, but he placed the family in his order *Piperales*, between *Salicaceae* and *Liquidambaraceae*; thus, he connected it not only with *Salicaceae*, but also with several families that do not belong to *Amentiferae*. On account of its peculiar characters the family is difficult to place in the system, having, as many authors affirm, an isolated position. By reason of the great divergences from the *Amentiferae* that exist I think it is not justifiable to refer it to this group, but I leave the question open whether it has some distant relationship with it.

The family *Garryaceae*, which earlier was placed near *Cornaceae*, is sometimes also referred to the *Amentiferae* as a particular order, *Garryales*. More recent investigations (HALLOCK, 1930), however, have shown that morphologically the order in question attaches itself to *Umbelliflorae* (to which *Cornaceae* also belong), and embryologically in certain respects resembles the *Sympetalae*. In WETTSTEIN's handbook (1935) it is therefore placed last among the *Choripetalae*, after *Umbelliflorae*. The old statements that *Garrya* may be grafted on *Aucuba japonica* (MOLISCH 1918) also show that it is related to *Umbelliflorae*. With the *Amentiferae* the family certainly has nothing to do.

The order *Balanopsidales*, proposed in later time, which consists of one family, *Balanopsidaceae*, with one genus, is usually assigned to *Amentiferae*. Externally the fruits are very reminiscent of acorns. However, the cupule surrounding the base of the fruit is not a stem-structure as that of *Quercus*, but is composed of bracts, the fruit is not a nut, but a drupe, and the flowers have no true perianth. In these respects the order differs from *Fagaceae*, but within the order *Juglandales* corresponding characters are to be found. Other features resemble more those of *Fagaceae*, and, judging from the material in hand, the order seems to fit within the bounds of the *Amentiferae*. There are however still some gaps in our knowledge of the *Balanopsidales*.

The order *Leitneriales* with the family *Leitneriaceae* and the species *Leitneria floridana* is placed by, for instance, WETTSTEIN (1935) in the proximity of *Myricales*, which he regards as a special order, thus within the *Amentiferae*, though he denotes this arrangement as apparently provisional. In the vegetative construction there are without doubt some characters that are without correspondence in the *Amentiferae*, but in the structure of the flower, which is of greatest importance for the placing in the system, the order apparently attaches itself to the *Amentiferae*, especially to the order *Juglandales* (with *Myricales*). Concerning the pistil there is the divergence, it is true, that it is built up of one carpel, while the other *Amentiferae* have two or three carpels, but there is clear evidence of its development through reduction of a bicarpellary pistil of the same type as is to be found within *Juglandales* and other *Amentiferae*. In an embryological respect there are some deviations from *Juglandales* which mark some difference as against this order. These deviations, however, are not greater than it is possible to find similar characters within other orders of the *Amentiferae*. In the essential flower-morphological conditions there seems to be good agreement with the type of the *Amentiferae*, as will be further developed later on, when the question will also be taken into consideration as to whether the genus *Didymeles*, as is sometimes done, is to be placed in the proximity of *Leitneriaceae*.

The result of this review of the range of the group *Amentiferae* is, thus, that besides the orders *Juglandales*, *Fagales*, *Betulales*, and *Salicales*, the members of which are generally referred to the group, *Balanopsidales* and *Leitneriales* are also attributed to it, while *Julianiales*, *Batidales*, and *Garryales* are excluded from it.

Order 1. Juglandales.

Family 1. Myricaceae.

Among earlier investigations especially CHEVALIER's monograph (1901) is to be mentioned, in which morphological conditions are also described. However, no detailed study seems to have been made on the homologies in inflorescence and flower, although these here afford much of interest. In order to illustrate them it will be appropriate to begin with a survey of the organization of the floral parts within different genera and sections.

Within the section *Morella* of the genus *Myrica M. Nagi* [1] seems to be at a very primitive stage. The male flowers form compound catkins, which emanate from the leaf axils. The primary catkins are quite short (Fig. 1 *a*). At their base there is a bract of the inflorescence, gland-dotted, above it about four large bracts, with generally two stamens in the axil of each, thus male flowers of very simple organization (Fig. 1 *b*). At the top there is often a small, rudimentary bract with only one stamen. The female catkins, contrary to the male ones, are simple. Corresponding to the primary male catkins here are flowers (Fig. 1 *c*), which outermost have a bract that wholly resembles that of the male catkin. Further there are around the central pistil four large bracts, which have some small, rudimentary, in part clavate structures in their axils, strongly reminiscent of transitions between stamens and papillae; sometimes a second flower is developed at some point (Fig. 1 *d*). There is no doubt that the female flower of *Myrica Nagi* has originated through reduction of a small inflorescence, with female flowers in the centre.

Myrica nana, which is related to *M. Nagi*, is somewhat more advanced. The male flowers are generally simple, with only about four

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[1] In the nomenclature of the *Myricaceae* I follow the monograph of CHEVALIER (1901). If, as proposed (BRIQUET, 1935), the type species of *Myrica* should be *M. Gale*, the genus *Myrica* of CHEVALIER must have another name. It is, however, not necessary to take this species as type species of *Myrica*, as LINNAEUS (1753) has described three other species, which belong to *Myrica* s. str. (cf. HYLANDER, 1945).

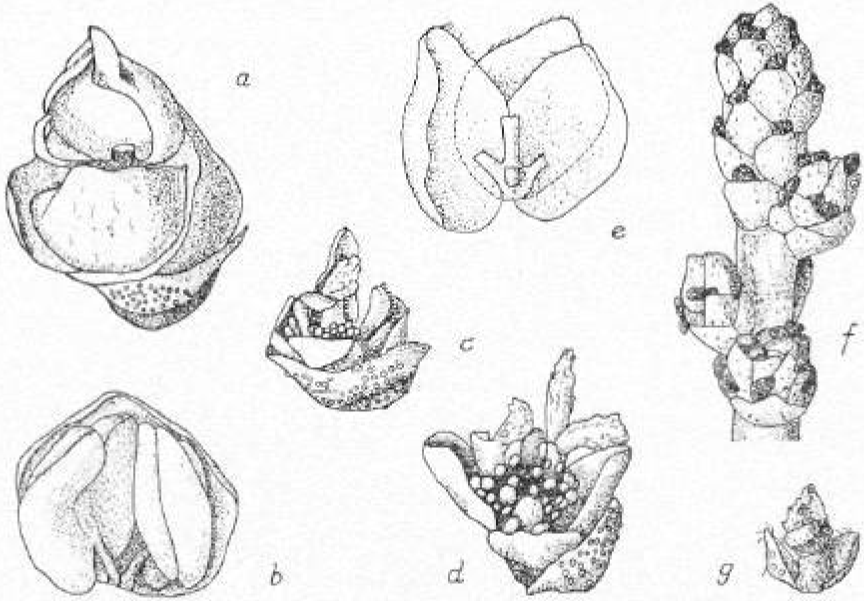

Fig. 1. *a Myrica Nagi*, male part catkin, the stamens removed; *b* the same, staminate flower; *c* the same, female flower in front view; *d* the same, female flower from the side with an extra pistil having a large and a small stigma; *e M. nana*, male flower, the stamens cut off; *f M. javanica*, female catkin, the upper part; *g* the same, female flower in front view, the bract removed. *a* about × 10, *f* about × 6, the others about × 15.

stamens, but the two bracteoles are in some flowers of such shape and size that they are strongly suggestive of bracts (Fig. 1 *e*). CHEVALIER (l.c.) is of the opinion that actually they are not bracteoles but bracts in a — through reduction — one-flowered inflorescence; in some cases he has observed two separate male flowers in this. As a matter of fact, on account of the similarity to the primary male catkin of *M. Nagi* it is near at hand to suppose that the flower has derived from such an inflorescence by reduction. The female flowers are arranged in a simple catkin, but they show by their encircling whorl of bracteoles and by the emergences of the fruit that they have the same origin as in *M. Nagi*.

Another species that is referred to the section *Morella* is *M. javanica*. This species differs rather much from the two species just mentioned. In *M. javanica* both male and female catkins are compound. The former are built up of part-catkins, lateral and terminal, which contrary to the conditions in *M. Nagi* are relatively long and many-flowered; in each flower there are four stamens, but no bracteoles. The part-inflorescences of the female catkins (Fig. 1 *f*), on the other hand, are small and few-flowered, most of them having about four to six flowers; at the top, however, there is generally a terminal part catkin, which is somewhat larger and may contain about 15 flowers. The individual flowers have each two transverse bracteoles. In the fruit stage the fruits may coalesce with each other to so-called *syncarpia* (CHEVALIER, l.c.). It might be thought that the small part-inflorescences were a correspondence to the part-catkins of for instance *M. Nagi*. There cannot however be such a homology; a close examination of a female flower (Fig. 1 *g*) shows that on the ovary there are some emergences, one or two of which are often larger and appear as reduced scale-structures; undoubtedly they correspond to similar structures in other *Myrica* species. Moreover, the developed female flowers are not placed at the top but in the lower part of the part-catkins, while their upper part is occupied by a bud of sterile bracts; these are more numerous in the lateral part-catkins than in the terminal; apparently the number of flowers is greatly reduced, especially in the former. The individual flowers of *M. javanica* are thus apparently homologous to the male part-catkins of *M. Nagi*, the part-catkins of the former to the compound catkins of the latter species. As regards the inflorescence *M. javanica* represents a far advanced type, where the flower, originally formed by an inflorescence, has obtained a simple structure through reduction, and where, moreover, a ramification occurs in the catkin, which is without correspondence in most other species. Conditions similar to these in *M. javanica* also prevail in the *M. esculenta* likewise referred to the sect. *Morella*.

Within the section *Faya* of the genus *Myrica* the species *M. Faya* shows several interesting peculiarities. The male catkins are also here compound. The part-catkins (Fig. 2 *A*) contain a number of male flowers, only consisting of a few, often three, stamens, which emanate from the axil of a bract, slightly above it. The stamens are irregularly arranged with extrorse anthers. In one case I have observed at the base of a compound catkin a part catkin which in its turn was compound; instead of the solitary flowers there were branchlets with several small stamens and two to four bracteoles, in part intermingled with the stamens. This, together with the position and orientation of the stamens, points to the male catkins having developed through reduction of doubly compound catkins, though it does not afford sufficient proof

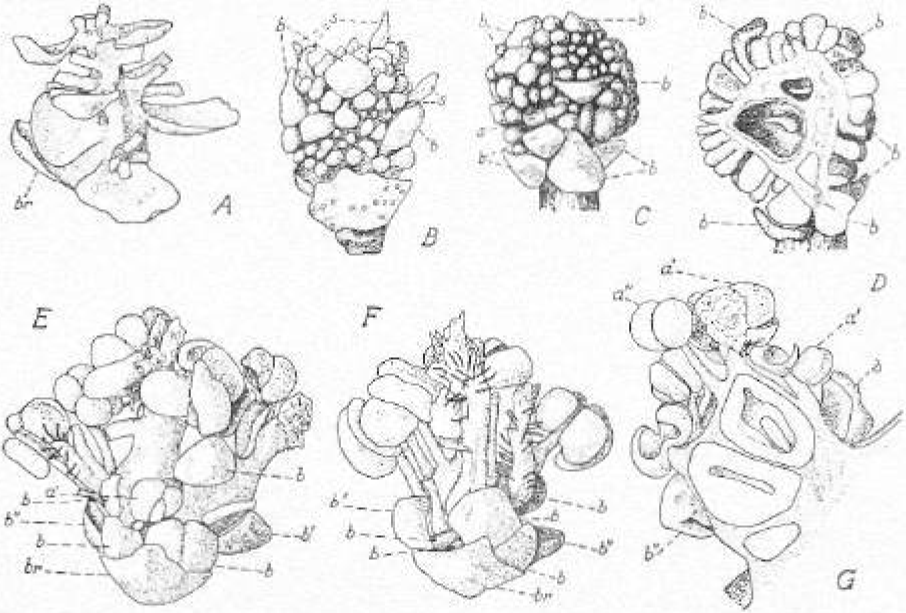

Fig. 2. *Myrica Faya.* *A* male catkin, the stamens cut off; *B* female part catkin in flowering; *C* female part catkin in young fruit stage; *D* the same in longitudinal section; *E* androgynous part catkin with three branches, the side branches, supported by the bracteoles *b'* and *b''*, with more or less undeveloped pistils; *F* androgynous part catkin with two side branches, supported by the bracteoles *b'* and *b''*, the one bearing stamens only, the other an undeveloped pistil and one stamen; *G* androgynous part catkin in longitudinal section. *br*=bracts, *b*=bracteoles or fleshy structures probably arisen from bracteoles, *s*=stigmas, *a*=anthers or stamens. About × 12.

of this. The female catkins are not composed of small part catkins but of flower agglomerations with each about three or four flowers, sometimes more, sometimes only one. A rather common condition is that there is a central female flower and two lateral ones, often in addition a fourth, at the abaxial side. At their surface they bear fleshy papillae, and the surrounding bracteoles are partly placed high up on ovary and fruit (Fig. 2 *B*—*D*). In each agglomeration the fruits coalesce with each other to a »*syncarpium*». A third kind of inflorescence, androgynous catkins, sometimes occurs, too. The catkins are here at least sometimes very like the female inflorescences, composed of small agglomerations (Fig. 2 *E*—*G*), the lateral ones of which, if vigorously developed, divide into some branches, often three, one in the centre and two lateral. Each of these may consist either of a female flower or of a central pistil and around it three to four stamens, spirally arranged at different height and connate with the pistil, and some bracteoles. Parallel with the occurrence of the stamens runs the disappearance of the papillae characteristic of the female flower. In the side branches the pistil is often somewhat reduced, for instance has only one stigma, and in more weakly developed agglomerations in the upper part of the catkin it often disappears entirely and there only remains a group of three or four stamens within a bract. Such a group corresponds no doubt to a flower of the male catkin. Thus, there is a complete transition between female and male flowers. The androgynous agglomerations are surrounded by a varying number of bracteoles; besides the bracts supporting the different (often three) branches there are some »bracteoles» of varying position; in the agglomeration reproduced in Fig. 2 *E* the total number of bracteoles or fleshy structures probably arisen of transformed bracteoles is eight. Sometimes it may be seen that one or two stamens are placed above the axil of a bracteole (a' in Fig. 2 *E*, and a' in Fig. 2 *G*; in this figure a'' and a''' are also placed above a bracteole, on the other side). These facts, as well as the empty bracteoles on the surface of the fruit and the above-mentioned conditions in the male catkins, speak strongly in favour of the fact that the branches of the bisexual agglomerations and the female and male flowers homologous to them have arisen from an original inflorescence with a central female flower and a number of simply built male flowers around it, so that the flowers are pseudanthia. In contradistinction to *M. Nagi* but in some similarity to *M. javanica* these pseudanthia are arranged in compound catkins; another likeness to the latter species is the coalescence of the female pseudanthia occurring in both species, in *M. javanica* in exceptional cases, in *M. Faya* as a rule.

A species related to *Myrica Faya* is *M. californica.* This species has a male flower which at least in some cases is furnished with a large number of »bracteoles», and the stamens are united in stems (Fig. 3 *A*). It is hardly possible to find any distinct relation between certain stamens and certain bracteoles. Such a flower is somewhat reminiscent of the bisexual flower agglomeration of *M. Faya,* though here evolution has gone a step farther. The female flower (Fig. 3 *B—D*) is in a high degree inflorescence-like, too; there are often two or three pistils, corresponding to as many original female flowers, and in addition there are large rudimentary stamens outside, sometimes perfectly developed stamens, a remnant of surrounding male flowers. As in *M. Faya,* from each »flower» there may develop more than one fruit, two or three, which

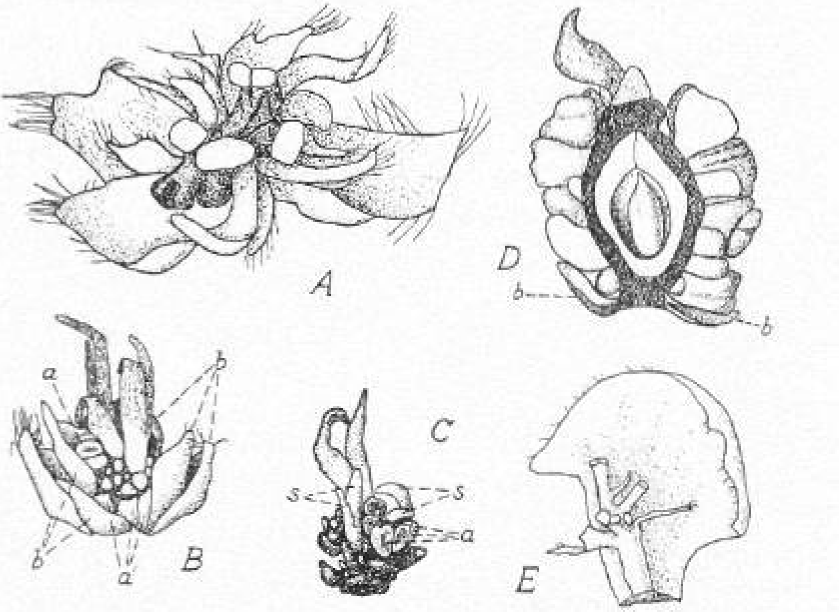

Fig. 3. *A Myrica californica,* male flower from an androgynous catkin with four larger bracteoles and several smaller ones above, and about twelve stamens, the branches of the staminal column cut off; *B* the same, flower from an androgynous catkin, in front view, with two pistils, one of them with three stigmas, one normal anther (*a*) and some small rudiments, probably of anthers (*a′*); *C* the same, female flower from an androgynous catkin with rudimentary pistils (*s*) and stamens (*a*), the larger bracteoles are removed; *D* the same, fruit im longitudinal section, *E M. inodora,* staminate flower with bract and three narrow bracteoles at the staminal column, the branches of the column cut off. *b*=bracteoles. *A, D* about × 20, the others about × 15.

coalesce to a »*syncarpium*», although in this species such only occurs in exceptional cases. Without doubt the flower has here arisen from an inflorescence; the similarities to the androgynous inflorescences of *M. Faya* suggest that the primary form was not a simple but a compound, ramose one.

The third species of the section *Faya, M. inodora,* is more strongly reduced than the others. The catkins are here apparently simple. However, in the male flowers the stamens form a small, ramose column with one or two small bracteoles among the stamens (Fig. 3 *E*), and in the female flower there may, according to CHEVALIER (l.c.), occasionally be two ovaries located in the axil of the same bract, thus conditions reminiscent of the other species. Evidently *M. inodora* is a later link in the evolutionary line issuing from these species; the reduction is considerably greater, but the flower has also here arisen from an original inflorescence.

The third and most comprehensive of the sections, *Cerophora*, shows also a certain evolutionary chain from more complicated to more simply built flowers, though the flower structure here is, on the whole, more derivative. Some more primitive species still show rather obviously the origin of the flower from an inflorescence.

In *Myrica salicifolia* there is thus in the male flower a large number of stamens branching off from a common column-like stem (Fig. 4 *A*). In the lower part there are a number of so-called bracteoles, in the reproduced flower, four. These bracteoles are not placed below the stamens, but one or two of them may also be intermingled with the stamens, emanate higher up than the lowest ramifications. No doubt this flower represents a further step in the evolution compared with the male flower of for instance *M. californica*; the reduction is somewhat greater, but it is still possible, especially by comparison with *M. californica* and *inodora*, to establish its origin in an inflorescence. The female flower of *M. salicifolia* (Fig. 4 *B*) is surrounded by about three to five bracteoles inside the bract. In the centre there is as a rule one pistil with two median stigmas, but as already stated by CHEVALIER (l.c., p. 225) it sometimes occurs that there are more than one ovary in the axil of the same bract. An instance of this is shown in Fig. 4 *C*; here, inside the bract there are three bracteoles and in the midst of these a large pistil with two median stigmas and by the side of this and separated from it a small one with two rather transverse stigmas, each of the pistils of course representing one female flower. In the front of the larger pistil there is a small appendage (*r*), for the greater part connate with the style, possibly representing a reduced third pistil (=female flower). Here, thus, there may exceptionally occur miniature inflorescences similar to those earlier described for *M. Nagi*, which do not otherwise, in bracteole number or in any other way, differ from the common, simple female flowers, the extra pistil (or pistils) showing signs of reduction. This must be considered as a proof that the female flower here, as in *M. Nagi*, has arisen through reduction of an inflorescence.

Another species of the section, *Myrica conifera*, is, in agreement with *M. californica* but in contradistinction to most other species, monoecious, often with androgynous catkins. The male flowers are

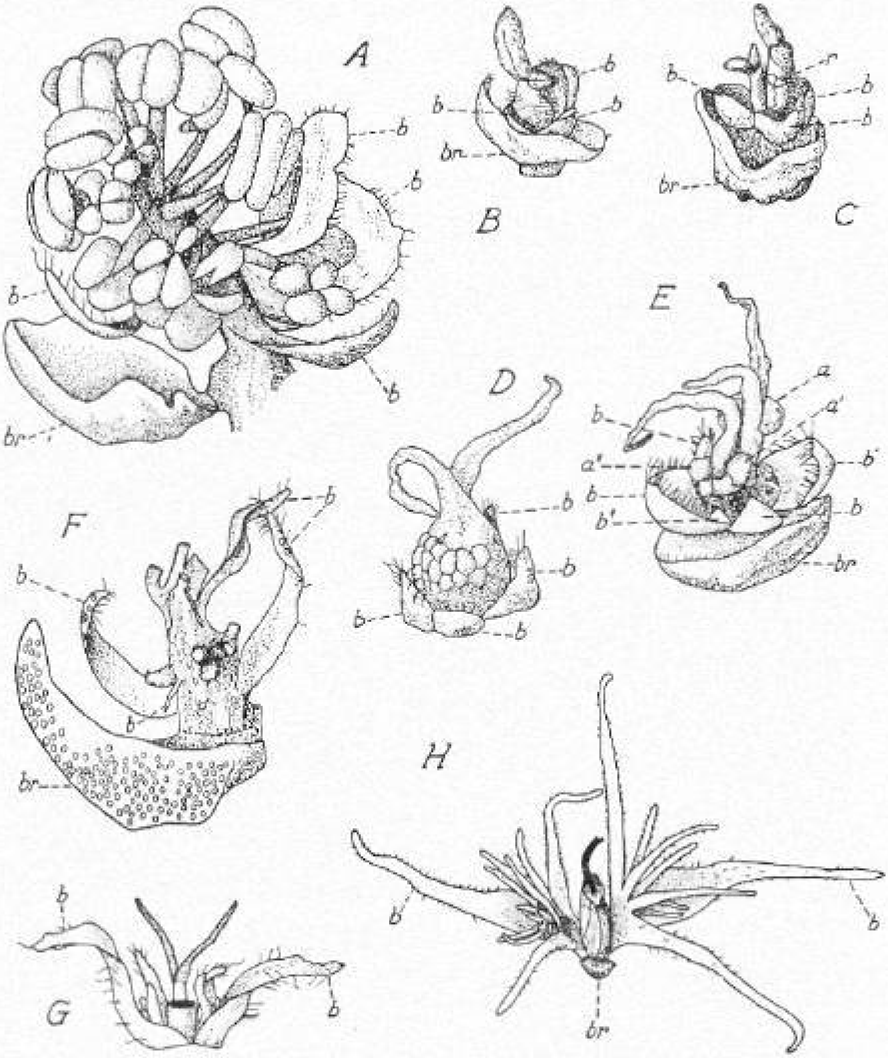

Fig. 4. *A Myrica salicifolia* var. *subalpina*, male flower; *B M. salicifolia*, female flower of usual type; *C* the same, female flower with two pistils; *D M. conifera*, female flower in front view, the bract removed; *E* the same, bisexual flower from an androgynous catkin; *F M. pubescens*, male flower with staminal column; *G Comptonia peregrina*, female flower from the axis, the bract removed; *H* the same, young fruit with leaf cupule, at the left it is seen that new scales develop amidst the older ones. *br* = bract, *b* = bracteole, *a* = anther or stamen, *r* = rudiment, probably of pistil, see further the text. *A* about × 10, *H* about × 6, the others about × 15.

of a simple structure, with four stamens and no or occasionally one or two small bracteoles below. The female flower (Fig. 4 *D*) has about four bracteoles. In the androgynous catkins however bisexual flowers also occur, which in this connection are of the greatest interest. Besides a normal pistil there are often one or two perfectly developed stamens in such a flower. Sometimes there are rudimentary stamens too and other peculiarities, as in the flower reproduced in Fig. 4 *E*. In this there are six bracteoles, the two transverse ones of which are the largest. Three developed stamens have occurred, the two of which are removed; one, the larger, was located in the axil of the large bracteole at the right (*b′*), the other, the smaller, above a small bracteole (*b″*). The third stamen (*a*) is placed on the posterior side of the flower, and is connate with the posterior style branch. Besides these there are two small, rudimentary stamens (*a′* and *a″*), adnate to the ovary, especially the one (*a″*) small and suggestive of a papilla. The flower deviates in addition by the occurrence of three carpels. Thus conditions here are met with that are reminiscent of *M. californica*, where in the same »flower» there may occur more than one pistil and several stamens, most of them rudimentary. The reduction is stronger in *M. conifera*, in most cases much stronger, but the origin of the flower must be the same as in *M. californica*, i.e. from an inflorescence.

Besides these two more closely described species there are also some others which afford clear evidence of the pseudanthic character of the flower. Thus, there may sometimes occur more than one female flower inside the same bract in *M. Pavonis* (CHEVALIER, 1901) as well as in *M. Curtissii*. In *M. pubescens* it may happen as in *M. salicifolia* that the stamens form a ramose column with so-called bracteoles intermingled with the stamens (Fig. 4 *F*). In the majority of species there are, however, no such evident signs of the development, but a testimony to the origin of the flower from an inflorescence is the whorl of bracteoles, in reality bracts, surrounding the ovary in a large number of species.

Somewhat different conditions from those within *Myrica* are met with in *Comptonia peregrina*. In the female flower of this species there are two bracteoles, and inside each of them a group of small scales, which together with the bracteoles grow out into a leaf cupule after flowering (while emergences are lacking on the ovary). In an early stage, at the very flowering, it may be observed (Fig. 4 *G*) that in the scale groups inside the bracteoles there are some scales next to the ovary which are larger than the others; this being especially true of the two outermost of them, nearest the bract and the axis respectively. The other scales are only seen as some small emergences on the side of these scales turned from the ovary. The development of the first scales thus proceeds more or less centrifugally. In a later stage (Fig. 4 *H*), when the leaf cupule has almost grown out around the young fruit, it may however be seen that new scales develop amidst the others. Thus at this stage the development is no longer centrifugal. CHEVALIER, l.c., states that the first development of the cupule structures in *Comptonia* is exactly the same as that of the emergences on the ovary of *Myrica,* which moreover may sometimes occur on the surrounding bracteoles too. It must on this account be considered that they are structures homologous to these, i.e. bracts and possibly flower primordia in an inflorescence, which surround the single developed flower and which have here acquired a special development for fruit dissemination by wind. A deviation is that these structures do no occur here on all sides but form two groups only in the axils of the primary bracteoles.

The flowers of *Gale palustris,* finally, might be thought to be of a primitive type, as the flower is of a relatively simple organization, without bracteoles in the male flower, and with two lateral bracteoles only in the female flower, adnate to the ovary. In the androgynous catkins which not infrequently occur (cf. DAVEY and GIBSON, 1917) there are however some bisexual flowers of a peculiar structure, which show that this is not the case. Flowers transitional between female and male flowers have been earlier described by HAGERUP (1934), who however seems only to have examined alterations of original female flowers, which never have more than two bracteoles. Similar cases have also been observed by the author, but of greater interest are some other deviations, probably arisen through transformation of original male flowers, which partly have a rather complicated organization. In the bisexual flowers there is sometimes as normally a bicarpellary pistil, which generally has however an unusual orientation: the carpels often stand obliquely to the median plane, sometimes quite transversely. A more common event, however, is that the pistil is built up of one carpel only, of varying position. The stamens are one to three in number, fused with the ovary. If there are only one stamen and one carpel, these may both have a median position (Fig. 5 *B*) or both have a transverse one (Fig. 5 *A*); if there are one stamen and a bicarpellary pistil, the carpels may stand transversely and the stamen either medianly or transversely by the side of the pistil. If two stamens occur, then often one stamen and one carpel stand transversely alongside each

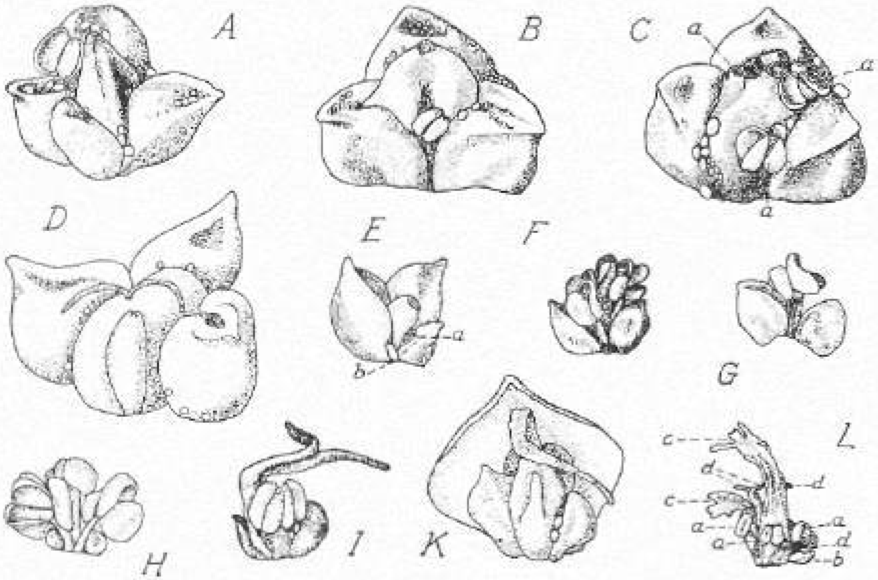

Fig. 5. *Gale palustris*, flowers, partly in fruit stage, of androgynous catkins. *A* flower with four bracteoles, a monocarpellary pistil and one stamen, transverse; *B* flower with three bracteoles, a monocarpellary pistil and one stamen, median; *C* flower with three bracteoles, an oblique bicarpellary pistil and three stamens (*a*); *D* flower with three bracteoles and a fleshy structure, transitional between stamen and bracteole, the pistil oblique, bicarpellary; *E* flower with four bracteoles, one of them small, rudimentary (*b*), a probably monocarpellary pistil and one lateral stamen (*a*), now fallen; *F* flower with two small lateral bracteoles, a monocarpellary pistil and two stamens, the one median before the pistil, the other lateral; *G* flower with two small lateral bracteoles, one developed stamen and two rudimentary carpels; *H* flower with two very small bracteoles and three stamens, two transverse and one median nearer the bract; *I* flower with two small bracteoles, a pistil with two carpels of oblique orientation and one stamen with a broad filament; *K* flower (the bract is drawn) with two unequal bracteoles, a pistil with one developed and one rudimentary carpel, and one stamen, median, abaxial; *L* flower with one small bracteole (*b*), four rudimentary stamens, three of which are visible (*a*), and the pistil dissolved into two large branches (*c*) and four narrow lobes (*d*). A—C, E—F, I, in front view, G—H, K from behind. About × 10.

other, and the second stamen medianly inside the bract (Fig. 5 *F*); they may also all stand medianly. (In one case [Fig. 5 *C*] a bicarpellary pistil with oblique orientation was observed, and three stamens in a whorl around.) The pistil may exceptionally be broken up into lobes of irregular shape, generally two larger and two to four smaller, narrower ones, some of which as well as the more or less rudimentary stamens may be placed outside the former (Fig. 5 *L*). Of special interest is, now, that in these bisexual flowers the number of bracteoles is often more than two. In the cases reproduced in Figs. 5 *B*, *C*, and *D*, there is, besides the two transverse ones, a third, median, abaxial (a common condition), and sometimes a fourth, adaxial bracteole occurs also, as illustrated in Figs. 5 *A* and *E*. When four bracteoles occur, one of them is sometimes cleft in the tip, possibly composed of two. If the pistil is well-developed, the bracteoles are large; if it is weakly developed or rudimentary, they are quite small. Structures transitional between stamens and bracteoles (Fig. 5 *D*) occur too. (On the other hand, transitions between stamens and carpels, which are common in androgynous catkins of *Salix*, were never observed.) It might then be thought that the bisexual flowers had originated from male flowers, where in connection with the appearing of a pistil some stamens were transformed into bracteoles. That this is not the case as regards the origin of the bracteoles is however evident from the fact that in an androgynous catkin a male flower was observed with four stamens as usual and in addition four small rounded bracteoles; no pistil-rudiment was here to be seen. The bracteoles must therefore at least for the most part be true bracteoles (or bracts), and that their number may be three or four in the same flower, as in many *Myrica*-species, must be taken as a proof that the flower has here also arisen through reduction of an inflorescence, a reduction in most cases so far advanced that the real nature of the flower is difficult to decide.

Thus, from this review it is clear that there occurs within *Myricaceae* a whole series of transitions from an inflorescence of very simply built flowers to flowers homologous to this, at first of more complicated organization, later on by greater and greater reduction of simple construction. As not only monoecious species with androgynous catkins but also *Gale palustris*, which as a rule is dioecious, may exceptionally possess bisexual flowers with one or more stamens outside the central pistil (or pistils), it must be supposed that the original inflorescence has also been bisexual, with one or more female flowers in the centre and male flowers around.

The origin and the general organization of the flower having now been treated, it remains to examine some details in the floral structure. As mentioned above, the ovary is often surrounded by a whorl of bracteoles. Often there are two more strongly developed transverse bracteoles and two smaller median ones. Sometimes there are

Fig. 6. *a Myrica microbracteata*, female flower in front view with six bracteoles, carpels transverse; *b* the same, female flower, six bracteoles, median carpels; *c M. cerifera*, female flower from in front with four bracteoles; *d M. punctata*, male flower with bract and two small bracteoles from the staminal column; *e* the same, male flower with four bracteoles; *f M. kilimandscharica* v. *microphylla* ENGL., male flower with bract and two bracteoles; *g M. cerifera*, male flower with bract and one bracteole, from the column; *h M. cordifolia*, male flower with bract and column of two stamens, no bracteoles; *i* the same, male flower with bract and one stamen. *c* about × 20, *f* about × 6, the others about × 15.

(*M. microbracteata* H. WEIM., Fig. 6 *a*—*b*) four transverse, two on either side of the ovary, the one inside the other, and two median, thus six in all. If the number is 4, which is rather usual, they may be regularly developed and resemble a simple perianth (Fig. 6 *c*). Sometimes, however, one of the median bracteoles is lacking and sometimes, as exemplified above, both may have disappeared through reduction.

In the male flower the bracteoles are not so well developed, but in certain cases there may also occur four bracteoles here, as is exemplified by Fig. 6 *e* for *M. punctata*; the general condition is nevertheless also in this species that the number is 2 only (Fig. 6 *d*).

Even as the bracteoles bear witness of the origin of the flower from an inflorescence, the organization of the stamens may also in many cases be explained by such a development. As stated above, the stamens of *Myrica californica, salicifolia,* and *pubescens* may form a ramose column with so-called bracteoles intermingled with the stamens. Other species have also large, bushily ramose stems with many stamens (e.g. *M. kilimandscharica,* Fig. 6 *f*), but the bracteoles emanate here below the branches only. That the filaments are in this way united into stems, »grown together», is common within the family. Even when the number of stamens is only 4, 3, or 2, the filaments are often united, at least at their base, sometimes high up (for inst. *M. punctata,* Fig. 6 *d, e*). With regard to the transitions to the richly ramified stamen aggregates that are found — among these is also *M. cerifera,* where one or two narrow bracteoles may occur at the lowermost ramifications (Fig. 6 *g*) — these cases must also be considered as originating through — a here strong — reduction from an original inflorescence and not be (as it has been done) compared with the divided stamens within *Betulaceae*; these differ also by the two branches having each only a half anther. If a comparable structure is sought within *Amentiferae,* it can instead be found within *Salicaceae*; some *Salix* species have the filaments united in a similar way. In *M. cordifolia* there are in some male flowers (Fig. 6 *h*) two stamens with united filaments, in others one stamen only occurs (Fig. 6 *i*). Here thus an example is met with of the greatest conceivable reduction of the original inflorescence.

While in other *Amentiferae* the stamens — owing to conditions of coalescence — often emanate seemingly from the surface of the bract, this is not generally the case within *Myricaceae.* The stamens or the common column of stamens spring here instead generally from the main axis at the attaching point of the bract; sometimes (*M. cordifolia* and others) they even emanate a bit above the bract. In some *Myrica* species there may however be seen a tendency of the stamens to turn out on the base of the bract, and in *Comptonia* it has gone so far that they have grown together with the narrow claw of the bract and emanate from the border district between this and the broader plate (Fig. 7 *a*); the male flower of *Comptonia* is by this very reminiscent of certain *Corylaceae.*

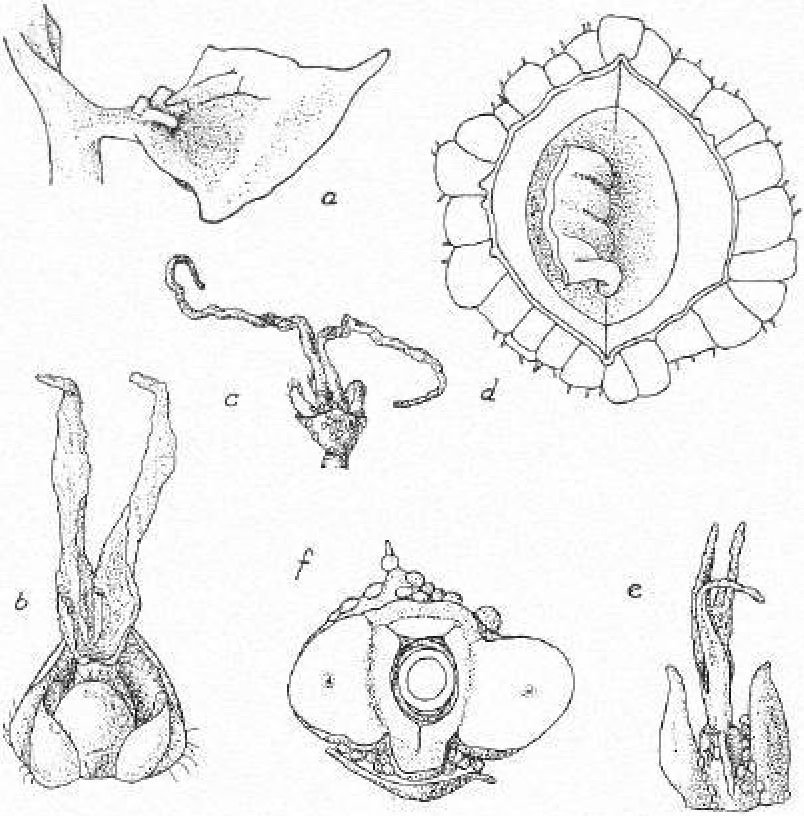

Fig. 7. *a Comptonia*, male flower, the stamens cut off, *b Myrica humilis*, female flower from the axis, with transverse carpels, *c M. cacuminis*, female flower with obliquely placed stigmas; one bract and 3 bracteoles, *d M. pennsylvanica*, fruit in cross section, with a median stripe in the wall, *e Gale palustris*, undeveloped fruit with one abaxial and two adaxial stigmas, from in front, *f* the same, trimerous fruit in cross section, besides the two transverse bracteoles, sectioned, there is a small, posterior, horn-like bracteole, issuing below the section surface; mid-stripes through the carpels. About × 15.

The two stigmas have generally a median position (though they may be turned by the pressure of surrounding leaves), and the ovary, which is often somewhat extracted in the direction of the stigmas, becomes by this more or less flattened from the sides, an orientation easily understood in those cases, when there are only two transverse bracteoles or these are considerably larger than the others. It has however been stated above, that when in *Gale palustris* the bracteoles are more than two, and possibly stamens also occur in the flower, the stigmas frequently get an oblique position, or even a transverse one. The same may be observed in those *Myrica* species which have more than two bracteoles. In *M. humilis* for instance, which has four about equal bracteoles, the stigmas are often transverse; in my material this orientation (Fig. 7 *b*) was more common than the median, and in other species also the position may vary; it is obviously not very firmly fixed.

Concerning the position of the carpels it was supposed already by EICHLER (1878) that they had the same orientation as the stigmas. The correctness of this view is proved, as shown by BENSON and WELSFORD (1909) for *Gale palustris*, by the course of the vascular bundles in the ovary. No line of union between the carpels is however possible to observe. On the other hand, both in *Gale* and *Comptonia* and — especially fairly — in several *Myrica* species (see for inst. Fig. 7 *d*) I have observed a stroke in the fruit wall which runs through the mid of the carpels, thus generally medianly, and marks the plane, where the fruit breaks at germinating. Sometimes there is, as in the illustrated case, a small ridge on the fruit over this stroke. This opening line corresponds to the often very strongly conspicuous one that is found in *Juglandaceae*; in this family there is however frequently a union line perpendicular to this too.

Sometimes there are within the family three carpels instead of two, and three stigmas. Instances of this are shown in Fig. 7 *e* and *f* for *Gale palustris* (from a normally female catkin, not an androgynous one), where there in one of the flowers is a small third bracteole too. A corresponding trimery occurs also in *Juglandaceae* and has there been considered to prove a descendance from types with ternary number in the gynoecium (BENSON and WELSFORD 1909). Perhaps this trimery should rather in both cases be considered as a witness of unstable conditions owing to a primitive organization.

The structure of the fruit and the different development of the bracteoles of the female flower in the fruit stage are described by CHEVALIER (1901), who foremost on these characters founds his division of the family into three genera. On this account I do not dwell upon these conditions but am content with stating that there are so great differences that with regard to them and to the other existing differences a division into different genera appears well justified. It will only be taken up a matter of more general interest to discussion, namely the origin of the fleshy or wax-secerning papillae which occur on the fruit in the genus *Myrica*. In some more primitive species there may, as mentioned above, be observed structures intermediate between stamens and papillae in the female flower, which emanate above leaf-like scales. In the androgynous catkins of *Myrica Faya* there sometimes occurs above a »bracteole» only a group of stamens without any papillae. In an apical flower agglomeration there was in one case observed above such a bracteole a normal stamen, above this two large fleshy lumps, and by the side of the stamen, probably belonging to the same group, a fleshy structure on a short stalk, apparently a transition between stamen and papilla. In the same flower agglomeration there was at about the same height a bracteole with one normal stamen and a large number of papillae, arranged in two groups and considerably smaller than the two large papillae at the other bracteole. No doubt these groups had arisen through splitting of two original primordia. In this and other similar cases the papillae thus seem to arise through transformation and splitting of stamen primordia in undeveloped flowers of the original inflorescence; in other cases, when no bracteoles are found on the surface of the fruit, these take probably also part in the formation of papillae; stamens and bracteoles are besides known easily to pass from one to the other, as shown for *Gale palustris*. It is of course also possible that within the family in some cases bracteoles only take part in the formation of the appendicular structures of the fruit; especially this could be thought to be the case in the leaf cupule of *Comptonia*.

In their shape the stigmas are sometimes long and narrow, almost thread-like (Fig. 7 *c*), sometimes they are more broad and flattened, reminiscent of certain *Juglandaceae* (for instance *M. javanica*, Fig. 1 *g*). In *M. pennsylvanica* the stigmas are thin and flattened and are below united with their edges to a tubular structure. In *M. humilis* they are also flattened and sometimes grown together below at the one side (Fig. 7 *b*) and turned to the one side in the same way as it may occur within *Juglandaceae* (e.g. in *Engelhardtia apoënsis*). The fruit wall of *Myrica* is also reminiscent of *Juglandaceae* through its thick, hard endocarp, which (for inst. in *M. parvifolia*) may be furrowed and sculptured on the outside in some similarity with the conditions for instance in *Juglans*.

Concerning the position of the ovule BENSON and WELSFORD (1909) think that it is appendicular to a carpel, HAGERUP (1934), on the other hand, is of the opinion that it in *Myricaceae* (*Gale palustris*) as in many other families is formed from the apex of the axis. The former authors plead as support for their conception that in *Gale* the vascular bundle supplying the ovule is formed by branching from the bundles of the anterior carpel; it receives no axillary bundle, and no branch from the posterior carpel either. These observations of the course of the bundles are no doubt quite correct and seem to be sufficient proof for the ovule being appendicular to the anterior carpel. Probably each carpel has originally been furnished with one, possibly two, ovules and the remaining of these has at the disappearing of the other (or the others) been displaced to the centre of the ovary, and got a seemingly apical position.

The original position might with this presumption be reminiscent of for instance the one occurring in *Balanopsidaceae* and the members of *Salicaceae* having two or four ovules; yet the ovule in *Myricaceae* at least in most cases is orthotropous, while it in the former two families becomes anatropous in the course of development.

Kershaw (1909, 1909 a) has called attention to some features in the embryology, which she regards as primitive, namely that the integument is furnished with a whorl of vascular bundles and that it is quite free from the nucellus, which rises with a small stalk above the departing point of the integument. Benson and Welsford (1909) do not consider these features as primitive, as they occur in quite different places in the system, and later authors (for instance Kühn 1928) have found further instances of bundles in the integument, not only within *Monochlamydeae* but also in groups widely separated from this, and by this reason they do not either regard this quality as a primitive character. Wettstein (1935), however, makes a comparison in this respect with the Gymnosperms and thinks that it may be a primitive feature, though it sometimes occurs in other groups too, and also Schnarf (1929, p. 58) inclines to the same opinion; he holds further examinations of the details for necessary in order to decide, whether the occurrence of bundles in the different cases is quite comparable or not.

Concerning the development of the embryo-sac the family does not show any such deviations as some other *Amentiferae*, nor occurs there chalazogamy, known from several other families, but the normal porogamy; yet only two species are examined, *Gale palustris* (Kershaw 1909, Hagerup 1934), and *Myrica Lobbii* (=*M. esculenta* var. *Lobbii*, Treub 1891), and the investigation of the latter form is of a rather old date.

If the three genera of *Myricaceae* shall be compared with regard to their floral organization — the most important matter from a phylogenetical point of view —, it must be said that this in *Gale* is at most derived. For one thing both male and female flower are here through reduction of a very simple structure, for the other there are rather far advanced transformations for fruit dissemination, in as much as the two bracteoles in the female flower increase after flowering and develop into floating organs, adnate to the fruit. At comparison between *Comptonia* and *Myrica* it may be more doubtful what genus is more primitive. Within *Myrica* there are no doubt species that are more primitive than *Comptonia*, but on the other hand there are among its rather numerous species some which are at least as derived as the only now living *Comptonia* species. On the whole, however, it must perhaps be said that this latter in its floral morphology is somewhat more advanced than *Myrica*. The bracteoles of the female flower have here got a special development for the fruit dispersion, in as much as they increase after flowering and form a leaf cupule round the fruit, which makes a dissemination by wind possible; in *Myrica* the bracteoles do not increase, and only in some, by far not all, species there are possibilities for endozoic dispersion. Further, in the male flowers of *Comptonia* the stamens in contradistinction to *Myrica* are markedly carried up on the bract, and as in *Gale* the catkins are developed on special branches, soon perishing. *Comptonia* must thus be regarded as a somewhat, but not much advanced type in comparison with *Myrica* and separating from this genus in an other direction than *Gale*.

The preliminarily described genus *Canacomyrica* (GUILLAUMIN, 1939) from New Caledonia, has, according to the description, like some primitive *Myrica* species, both male and bisexual flowers, the latter with fully developed stamens at the ovary wall, all surrounded by bracts and bracteoles, but differs from all other *Myricaceae* by bifid stigmas and a pendulous ovule from an erect funicle, with the micropyle downwards. If this genus really — as is probable — belongs to *Myricaceae*, it represents a deviating type and forms a transition from this family and the order *Juglandales* to the orders with anatropous ovules, and the bifid stigmas form an interesting parallel to the partition of stigmas and styles in *Juglandaceae*, *Balanopsidaceae*, and *Salicaceae*.

The relation of *Myricaceae* to other families of *Amentiferae* should most properly be discussed first after these have also been treated. At present it may only be stated that there occur several features that reappear in other families or are reminiscent of them. With *Juglandaceae* there are great similarities in flower structure, fruit, embryology etc., reminiscent of *Corylaceae* is for instance the male flower and leaf cupule of *Comptonia*, and there are certain points of contact also with *Salicaceae* (for inst. as to the androecium) and the other families.

Family 2. Juglandaceae.

Important earlier papers: ÖRSTED, 1856, 1870; BRAUN, 1872; C. DECANDOLLE, 1862, 1911; EICHLER, 1878; ENGLER, 1889; KARSTEN, 1902; NICOLOFF, 1904—1905; NAGEL, 1914; STANDLEY, 1927; KOIDZUMI, 1937; MANNING, 1938, 1940; HEIMSCH and WETMORE, 1939; KUANG, 1941.

To begin with the inflorescence, the conditions concerning this have recently received an exhaustive description and elucidation by MANNING (1938), and I have not much to add to this. As MANNING expounds in considerable detail, in the genera *Engelhardtia, Oreomunnea, Alfaroa* and *Platycarya* there is a more primitive type of inflorescences, in their typical form composed of a terminal female catkin and lateral male catkins under it. From this type the less complicated, often simple inflorescences of the other genera, *Pterocarya, Juglans,* and *Carya,* as expounded by the author mentioned, may be derived through reduction, and then *Pterocarya* forms the transition from the one type to the other. In the former type, the *Engelhardtia* type, *E. Wallichiana* LINDL.[1] has in MANNING's doubtless correct opinion a very original type of inflorescences, groups of inflorescences with lateral male catkins and a terminal female catkin, which are located partly on side branches, partly at the tip of the main branch (Fig. 8 *d*). *Alfaroa,* whose inflorescence was only partly known in 1938, is also of a primitive character. According to the description of STANDLEY (1927), the inflorescences of the fertile specimens are terminal and in their greater part female; at the base only there are two short branches with two to four male flowers on each or in other cases a few sessile male flowers (Fig. 8 *a*). A later collection (A. F. SKUTCH, No. 4685, Herb. Washington) shows a specimen with entirely male inflorescences, very likely from an entirely male tree (Fig. 8 *b*). The inflorescence groups are partly located in the branch tips, partly on lateral branchlets, which emanate — one or two — from the leaf axils and bear some leaves below; they are large and many-flowered, and the particular catkins are generally arranged in groups of two or three or more, which especially below are rather widely separated. The position of the catkin groups is thus the same as in *Engelhardtia Wallichiana.* That there is a transition towards dioecism, is, of course, a more advanced character, although in *Eng. Wallichiana* also there are often branches with only male or only female inflorescences (earlier regarded as a particular

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[1] In the nomenclature REHDER's Manual (1940) is followed for this and the following families, as far as the species are taken up there; only in other cases are the authors' names cited.

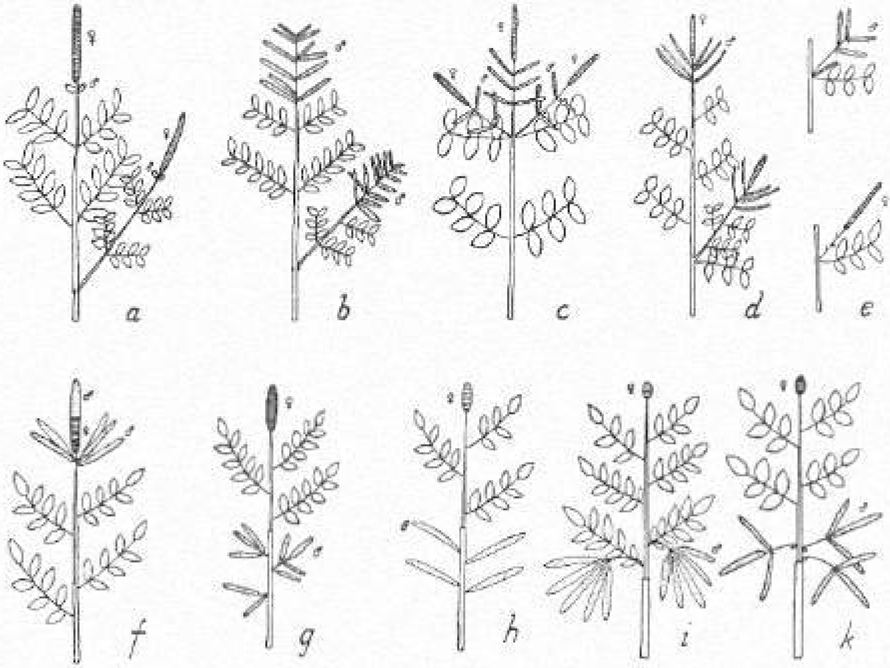

Fig. 8. The arrangement of the catkins in *Juglandaceae*, schematically. *a—b Alfaroa*, *c Oreomunnea*, *d Engelhardtia Wallichiana*, *e E. nudiflora*, *f Platycarya*, *g Pterocarya Paliurus*, *h Juglans* (similarly in certain *Pterocarya*-species), *i Carya integrifoliolata*, *k Carya*, the common condition.

species, see MANNING, 1938, p. 409), while in other species the reduction is greater. The inflorescence type of *Oreomunnea*, too, seems to be primitive. The catkin-bearing branches in the leaf axils are small, it is true, but the catkin groups — consisting of both female and male catkins — may also be located in the branch tips (judging from material in Herb. Geneva) and the male catkins are generally arranged two and two at different height (Fig. 8 c). MANNING (l.c.) is of the opinion that the original inflorescence within *Juglandaceae* was a terminal panicle, comparable with that which occurs within *Anacardiaceae* in the genus *Rhus*. In *Platycarya* it sometimes occurs that two or three catkin groups are inserted in immediate proximity to each other in a panicle-like cluster; the same may, according to MANNING (l.c.) occur in *Engelh. Wallichiana*; it may also be observed in *Oreomunnea* (Fig. 8 c). This, however, must most likely be regarded as a special case of the common inflorescence arrangement: one or more catkin-bearing side branches have come close to the inflorescence group of the main branch, an arrangement that might develop further to a compound panicle but can hardly have originated from such an inflorescence. I would rather — as will be further justified later on — compare *Juglandaceae* with *Myricaceae* and, as most primitive, consider the inflorescence groups where, as in *Oreomunnea* and *Alfaroa,* the male catkins emanate singly or in groups from an extended axis, which may correspond to a catkin-bearing branch of *Myrica* with one catkin (or two to three) in each leaf-axil. The supporting leaves are strongly reduced in *Juglandaceae,* but the position of the catkins, e.g. in *Oreomunnea* — generally opposite as the leaves —, agrees with the presumption that the inflorescence group corresponds to such a catkin-bearing branch of the *Myricaceae,* which sometimes may also have reduced leaves. The dense agglomeration of catkins that occurs in *Platycarya* (Fig. 8 *f*) must, on the other hand, be regarded as a more derived condition, just as several other characters of this genus are more advanced (e.g. the androgynous terminal catkin).

The development that takes place within the »*Juglans* type», to which the three genera *Pterocarya, Juglans,* and *Carya* belong, consists to a great extent in continued reductions and has been illustrated by MANNING (1938). Some differences from the common conditions in *Carya* are shown by the recently discovered species that by its describer, KUANG (1941), is regarded as a genus of its own, *Rhamphocarya,* but in my opinion should rather be referred to *Carya* as *C. integrifoliolata* (n.c., = *Rhamphocarya integrifoliolata* KUANG in Ic. Fl. Sin. I, 1, 1941, p. 1). According to KUANG the male catkins, which here are comparatively numerous, 5—8 together, are arranged at branchlets that do not spring from the axils of bud scales as in other *Carya* species, but from leaf-axils of the year's shoots (Fig. 8 *i*), bud scales being according to the description totally absent, while the female catkin is of the common *Carya*-type. In the arrangement of the male catkins, thus, this species forms a transition from *Pterocarya* to *Carya.*

An interesting condition within the *Juglans* group is that the male catkins sometimes spring from the base of the present year's branches (*Carya*), sometimes from last year's wood, out of the axils of last year's leaves. To understand how these conditions have arisen it is best to go back to the genus *Pterocarya,* which also in this respect is more primitive than *Juglans* and *Carya.* Here, in the autumn most species develop side branches which bear undeveloped male catkins in the leaf axils and female catkins in the top. The male catkins pass the winter without any shelter and the female catkins are not either enclosed in buds; they are only surrounded by loosely aggregate leaf primordia. Next year the bud point is developed to a new shoot, which may bear a female catkin at its tip, while the male catkins are arranged on the lower parts of the branch, formed the precedent year but not sharply distinguished from this year's shoot. From this type the development then follows two different courses. In *Juglans* conditions are almost the same, the only difference being that the side branches developed in the autumn have their tips surrounded by true bud scales, though only few in number. Hence the difference is here greater between this year's shoots with their female catkins and last year's wood, with its male catkins. In *Carya*, finally, the whole branches are in most species enclosed in buds, a sole exception being *C. integrifoliolata*, which is transitional to *Pterocarya*. The primordia of the basal male catkins, then, are also surrounded by the bud scales; thus, the male catkins are inserted on the same year's shoot as the female catkins. In one species of the genus *Pterocarya* (*Pt. rhoifolia*), which seems to be the most hardy in the genus (cf. REHDER, 1940, p. 116—117), there is moreover an inchoate bud formation of the same kind (though the bud scales are early deciduous), and it is not difficult to bring the whole development in line with the biology of the species; it is associated with a transition from tropical to temperate climate with greater demands for shelter in the rest period.

In all genera, perhaps with exception of *Platycarya*, it often happens that the catkin-bearing branches or the inflorescences corresponding to these emanate from serial buds in the leaf axils. This has no direct correspondence in *Myricaceae*; it may there certainly occur two or three catkin-buds in the same leaf axil, but they are then arranged beside and not above each other. In the genus *Lithocarpus* of *Fagaceae*, however, there are similar serial inflorescences.

The involucre or so-called (leaf-)cupule that surrounds the ovary and fruit of the *Juglandaceae* may with respect to its development be divided into four different types.

The first type occurs in the genera *Engelhardtia, Oreomunnea,* and *Alfaroa* and is characterized by the connection of the leaves of the involucre to a thin wing, the greater part of which is free from the fruit. This wing may either be 3-lobed (*Eng. Wallichiana, Alfaroa*) with a larger median lobe and two side lobes, or, opposite the median lobe, there may in addition be an adaxial minor lobe (Fig. 9 *a*—*b*), sometimes divided into two or even in more (*Eng. spicata* BL., *Eng.*

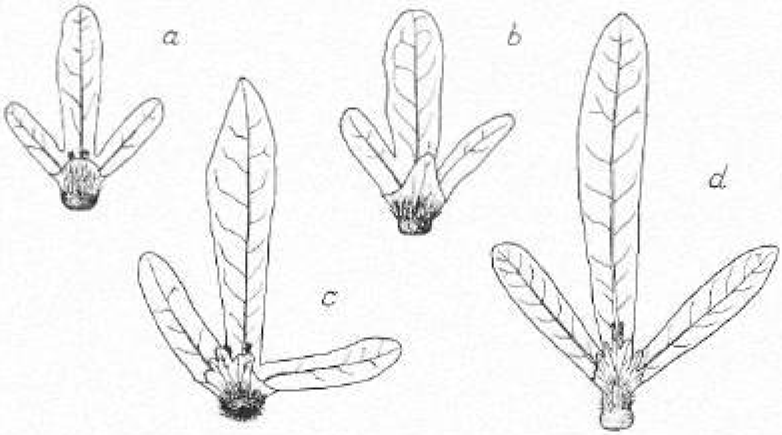

Fig. 9. Fruits of *Engelhardtia* species with involucre. *a E. spicata* var. *Colebrookeana*, fruit of common type. *b* the same, fruit with protracted mesoprophyllum, *c E. spicata*, fruit with lobate mesoprophyllum, *d E. apoënsis*, fruit with 10-lobate mesoprophyllum. Nat. size.

apoënsis ELM., here up to 11, Fig. 9 *c—d*). There are different opinions about the identity of the different leaves of the involucre. NAGEL (1914) considers in agreement with some older authors that the larger leaf is the bract of the flower, the two lateral ones bracteoles. The fourth lobe that often occurs he signifies as »mesoprophyllum» and regards as a supernumerary bracteole, whose existence is explained by the flower having developed from a small inflorescence, similar to the two-flowered dichasia of *Fagaceae*; as a matter of fact there sometimes occur two flowers in the same involucre. MANNING (1940), on the other hand, in attachment to an earlier interpretation of DECANDOLLE, thinks that the bract is 3-lobed and that the bracteoles are either wanting (*Alfaroa*) or, two in number, together form the »mesoprophyllum» and the proximate parts of the side lobes; in this he has support in the fact that in the male flower there is a 3-lobed bract, which sometimes grows out in the same way as that of the female flower and for this reason must be homologous to this. No doubt there is actually such a homology, as is proved by the great agreement that may sometimes be found (see Fig. 10 *A*), but it is not sure that the three-lobed leaf of the male flower is made up only of the bract. Examination of some male flowers reveals a rather great variation in this leaf. In some flowers, as the one reproduced in Fig. 10 *B*, the mid- and side-lobes are connected high up, and the whole may give the impression of a

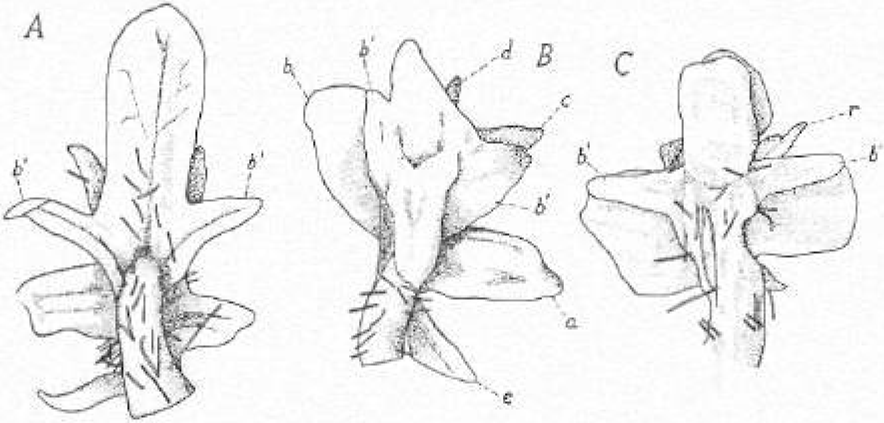

Fig. 10. *A* *Engelhardtia spicata* var. *Colebrookeana*, male flower with bract and bracteoles enlarged, from below (5 perianth-leaves), *B* the same, male flower from the same specimen with bract and bracteoles rather strongly connate (5 perianth-leaves; *a* and *b* are also perianth-leaves, are not further out than the others, on the contrary *a* is further in than *c* and *d*), *C* the same, male flower from the same specimen, bract and bracteoles more separate (3 perianth-leaves, *r* rudimentary pistil, partly stamen-like). In all figures *b'*—bracteole. About × 12.

3-lobed leaf. In other flowers of the same species, on the other hand, the side lobes are almost quite separated from the median lobe and outstanding at right angles (Fig. 10 *C*). In this case the side lobes must represent independent leaves, bracteoles, and then this must also be the case with the involucre-like leaves occurring in the male flowers of the same species, and in the involucre of the female flower. In the opinion of the author, thus, there must be two lateral bracteoles in the involucre of the *Engelhardtia* type, often in addition a third adaxial one, or, if this is lobed, perhaps still more. The parallel with *Juglans* and *Carya* also speaks in favour of this interpretation; in these genera there are an undivided bract, two lateral bracteoles, and — as in the *Engelhardtia* type — often in addition one or two (or still more) adaxial lobes. NAGEL's interpretation of the supernumerary lobes as bracteoles in an inflorescence, reduced to a flower, is no doubt correct, but their origin is most probably not connected with a reduction of previous dichasia within the family *Juglandaceae*. In number and position they do not agree with the bracteoles of the dichasia, and their occurrence in several widely separated genera indicates that the condition should be traced back to an older type. The bracteoles most likely correspond to the supernumerary »bracteoles», occurring in the family *Myricaceae*, whose origin through reduction of an inflorescence, as earlier shown, is easy to follow. When the »mesoprophyllum» is lobate, it is probably composed of several bracteoles, this being indicated by the distinct nerves in different lobes (Fig. 9 *d*).

In the genus *Oreomunnea* the involucre is of about the same structure as in *Engelhardtia*, the only difference being that here the wing of the fruit is larger and coarser and with a somewhat deviating nervature. A minor fourth lobe is also present; sometimes it is slightly emarginate, three or four bracteoles thus taking part in the formation.

To the *Engelhardtia* type *Alfaroa* undoubtedly also belongs, though the fruit on account of its somewhat fleshy exocarp has sometimes been compared with *Juglans* (STANDLEY, 1927; KOIDZUMI, 1937). At the base of the fruit there is a diminutive, sometimes 3-lobed wing to be found, free from the fruit, thus of the same type as in *Engelhardtia*, only much smaller. Sometimes, however, it may be small in *Engelhardtia*, too; a specimen of *Eng. Wallichiana* (*chrysolepis*) »var. *bracteis parvis*» that I have seen (STEWARD and CHEO, Plants of Kwangsi No. 805, 1933, Herb. Stockholm) had on its fruits, apparently ripe, bracts only about half the length of the fruit.

A second type of involucre is shown by the genus *Platycarya*. Here the bract increases in size after flowering-time and becomes a rigid and acute scale, though it does not fall off with the fruit, but this loosens itself from it with a characteristic, concave fracture. According to an old interpretation, the leaves that make up the wings are bracteoles and a perianth is lacking in the flower. NAGEL (1914), however, following ALEXANDER BRAUN, makes himself an advocate of the view that they are composed of perianth leaves, while the bracteoles are suppressed, since in an early stage they seem to be morphologically equivalent to the two (more or less rudimentary) median perianth leaves that may often be observed. According to MANNING (1940) to a certain extent both conceptions are right, inasmuch as he thinks that the wings are formed through fusion of a perianth leaf and a bracteole; often the point is 2-dentate and there are considered to be anatomical indications of its double nature.

One way to seek clarity as to the function of the bracteoles is to search for some aberrations with bracteole-like leaves. In the female flowers I have not been able to find any such, but in the male flowers it has in several cases been observed that the bract at the one side has been furnished with a side lobe of about the same appearance as a

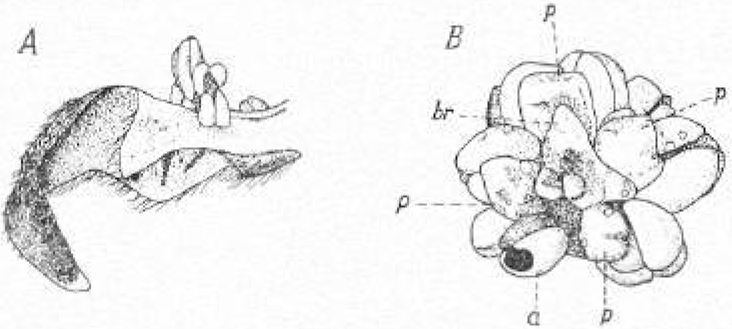

Fig. 11. *A Platycarya strobilacea*, male flower with a side lobe on the bract, *B Oreomunnea*, male flower, *br* bract with two adnate bracteoles, the one quite small, *p* perianth-leaves (in addition there are two not visible), *a* a half anther in the margin of a perianth-leaf. *A* about × 12, *B* about × 15.

side lobe formed by a bracteole in the *Engelhardtia* group (Fig. 11 *A*). More often there is no true lobe, but only a slight sinuation is observed. Such may also occur in the female flower, and as the bracts of the male and the female flowers are no doubt homologous and, in the androgynous catkins, without any further change show transition from the one to the other, it seems as though the bracteoles of both male and female flowers are strongly reduced and fuse with the bract. (A certain reduction of the side lobes also occurs elsewhere in the family, e.g. in the male flowers of *Oreomunnea*, Fig. 11 *B*).

Also in the intermediate flowers that occur between female and male flowers in the androgynous catkins there are some features indicating that fruit-wings and perianth-leaves are equivalent, though the conditions here are not easy to interpret.

The morphology of these flowers seems never to have been analysed in greater detail. Figs. 12 *A*—*G* show a number of flowers from the transitional zone between the female and the male part of the catkin. The first change (Fig. 12 *B* and *C*) consists in the disappearing of the wings and the appearing in their stead of small, irregular bumps. In a later stage of development (Fig. 12 *D*) a stamen, more or less abnormal, has been formed at each side — in the reproduced case the one (*a*) has very broad filament and connective, the other (*a'*) a small, rudimentary anther —, and further a scale has split off in the front (*b*) and a large, irregular bump has developed at the back. The styles also exhibit a tendency to division into four or five branches. Fig. 12 *E* shows a flower in which at one side a normal stamen has developed while at the other there is a small, sessile structure (*b*), about one-half of which is scale-like, the other half more stamen-like, with a loculus. In the front there are three fleshy scales, the right and the left ones of which show rudimentary thecae at the inner side and thus form transitions to

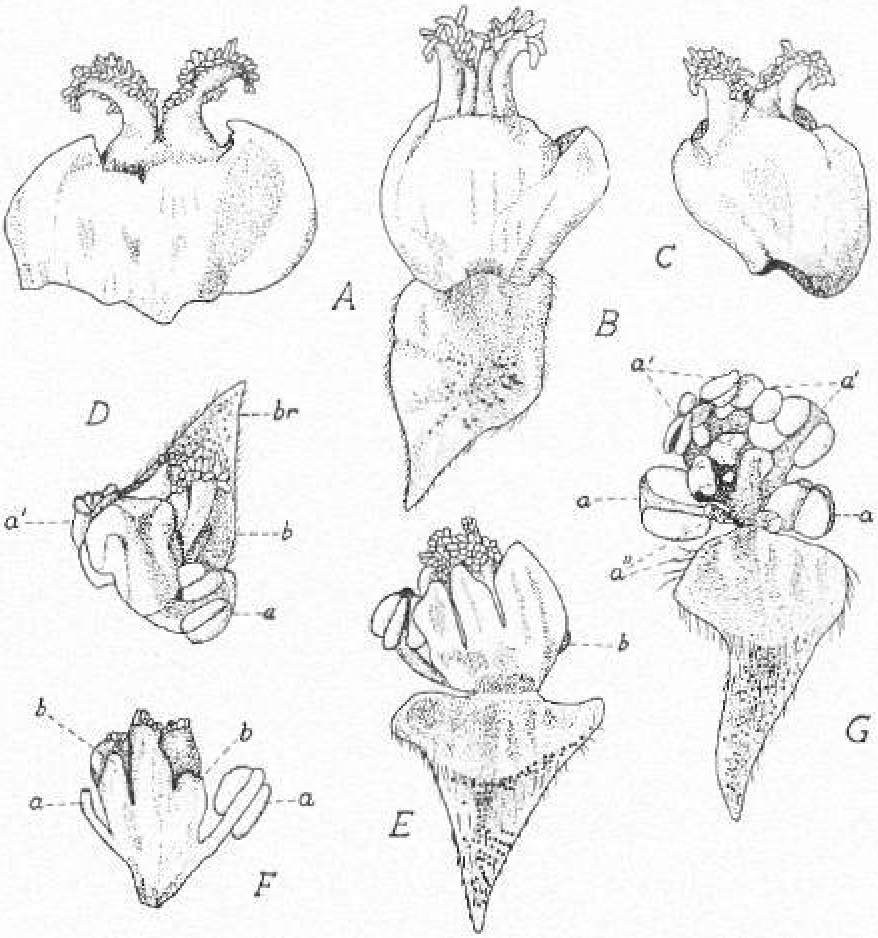

Fig. 12. *Platycarya strobilacea.* Flowers from an androgynous catkin. *A* normal female flower, *B—G* transitional flowers. *D* is seen obliquely from behind, the others from in front. *br* bract, *a* stamens, in *D* abnormally developed, *b* in *D* small scale (projecting at the right of the pistil), *b* in *E* and *F* transitions between scales and stamens. Further explanation in the text. × 15.

stamens. At the adaxial side of the pistil there is also here a large bump; there are three style branches, one of which — that at the right on the figure — shows transition to stamen lower down. A similar transitional flower is shown in Fig. 12 *F*. In this case a stamen has split off at each side and two structures (*b*) that are intermediate between scales and stamens have been detached in the front; in addition the pistil has divided into several branches. Finally, the flower that is illustrated in Fig. 12 *G* approaches further to a male flower. In the centre it has a pistil-rudiment with three large branches, which show an incipient development into stamens. Posteriorly there are four stamens (*a'*), branches of the same part. Anteriorly there are two stamens (*a"*, the anthers are removed), and at each side, inserted lower, one stamen (*a*).

It thus appears as if at the transition from female to male flowers scale-like structures were split off in transversal as well as in a median direction, which, wholly or divided, developed into stamens, as well as the style branches. All these scale-like structures appear to be homologous with each other; very likely they all correspond to perianth-leaves, and it is probably not correct to regard the lateral ones as bracteoles, contrary to the others. The fact that the lateral structures are split off earlier and are inserted lower than the others must be taken as a proof that they really correspond to the leaves developed to fruit-wings, though no direct transition is to be found. In the transitional flowers there seem to be no signs of the occurrence of additional leaf structures interior to these lateral ones.

A third type of involucre is the *Pterocarya* type. It is only found in *Pterocarya*. As in *Platycarya*, the fruit has two wings, which here, however, are formed by two bracteoles, whereas the bract does not enlarge, but disappears after flowering-time. The coarse, more or less fleshy wings are partly adnate to the fruit and generally unite with each other at the one side, sometimes at both sides (*Pt. Paliurus*), so that a wing is formed that surrounds the whole fruit. In these respects the type forms a transition to the *Juglans* type. That only the bracteoles, but not the bract, grow out to an involucre, is without correspondence in other *Juglandaceae*, but there is a parallel within *Myricaceae*, in the genus *Gale*.

The *Juglans* type occurs in the two genera *Juglans* and *Carya*. Here the leaves of the involucre are greatly transformed. The subsequently fleshy bracts and bracteoles join along their whole length with each other and with the fruit; only the outermost tips are free. In *Juglans* the different leaves of the involucre coalesce entirely, but NICOLOFF (1904), by investigations of the development, has shown that one bract and two bracteoles take part in its formation in *J. regia*. In for instance *J. mandshurica*, sometimes also in *J. Sieboldiana*, it is generally possible at the florification to distinguish rather clearly the lobe that is formed by the bract, which is generally longer and narrower than the other lobes and surrounded by deeper incisions, and one big lobe at each side (which may be toothed at the tip); in addition there sometimes occurs a fourth lobe opposite to the bract. In these and other species, consequently, the involucre appears to be made up of one bract and two or three bracteoles (perhaps in *J. regia*, too, there may sometimes occur three bracteoles, though this has not been so in the cases investigated by NICOLOFF). In *Juglans nigra* MANNING (1940) has shown the occurrence of a whorl of diminutive scales inside the outer involucre; no doubt these represent supernumerary bracteoles, more or less reduced. As to *Carya*, it has strangely enough been a common conception that among the — here clearly separated — involucral leaves there are besides the bract only two bracteoles; the fourth leaf, opposite to the bract, that generally occurs (and in the same way the 5th that has sometimes been observed) is generally regarded as the reduced perianth of the flower, this in spite of the parallel that exists with other genera having more than two bracteoles. That they are not perianth leaves is nevertheless shown by the fact that a perianth may sometimes occur above the involucre; in several species I have observed one to three small perianth leaves just below the stigmas, obviously deviating from the involucral leaves. These must accordingly be regarded as bract and bracteoles. In *Carya cordiformis* the number of bracteoles often rises to 4, sometimes even to 5. This is also the case in *C. integrifoliolata*, where, according to KUANG (1941), the valves often have projecting midribs, or sometimes two ribs at the same valve; the ribs are however sometimes lacking.

As in other *Amentiferae* the male flower is grown together with the supporting bract and more or less extended in the longitudinal direction of the bract. The two bracteoles are generally easy to distinguish, connected with the bract (cf. above for *Engelhardtia spicata*, also Fig. 10 *C*). In *Platycarya*, however, they are as a rule (cf. above) reduced, and likewise they are lacking in *Pterocarya paliurus*, where the bract also is very small. According to NAGEL (1914), they are not, either, to be found in the remaining *Pterocarya* species and in the section *Cinerea-Regia* of *Juglans*; the obliquely forward-directed leaves that here have been earlier regarded as bracteoles, are assigned by him to the perianth. In *Pterocarya fraxinifolia* and *stenoptera*, however, in some particular flowers there may exceptionally occur an obliquely forward-directed leaf, which lies above the edge of one of the supposed bracteoles (Fig. 13 *A*), a proof that these really are bracteoles of the same nature, as in other genera, and in for instance *Juglans Sieboldiana*, which belongs to the section mentioned, two leaves are probably also to be interpreted as bracteoles; they differ from the perianth-leaves proper in being, like the bract, irregularly outward-curved in the front. Probably the bracteoles occur also here, though they have more or less

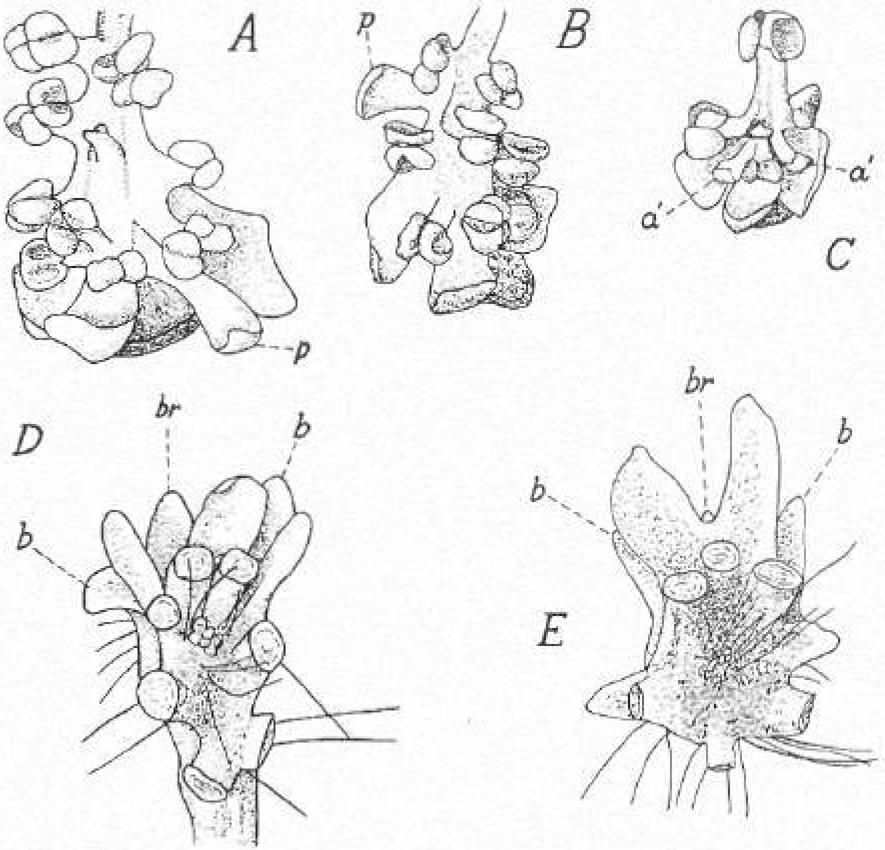

Fig. 13. *A—B Pterocarya stenoptera*, male flowers with additional perianth-leaf (*p*) besides the anterior median, *C* the same, flower with two structures (*a'*) that appear to be transitions between stamens and perianth-leaves; *D—E Engelhardtia spicata* var. *Colebrookeana*, male flowers with 3 and 4 perianth-leaves and the stamens in part superposed to them. *br* bract, *b* bracteole. *A—C* about × 13, *D—E* × 25.

been transformed to conformity with other leaves; they may so to say take part in the perianth formation. The conditions in *Carya* will be further treated below.

The perianth of the male flower within the family is as rule irregularly developed, with a varying number of leaves of various size. NAGEL (1914) states that radial flower-construction occurs in some species of three quite different genera, *Engelhardtia* (*Wallichiana*), *Pterocarya* (*Paliurus*), and *Juglans* (sect. *Nigra*). The morphology of the flower, however, does not seem to be at all the same in these three different cases; they are at various stages of development, and it might be possible to follow a line of development between the genera also in the structure of the male flower. The conditions will probably be more closely illustrated by another author in the near future, and I will here merely give them a short review.

In *Engelhardtia* there is a great variation in the structure of the male flower, as in several other respects. *E. Wallichiana*, which is referred to a special section, has a well-developed perianth of four (to six) leaves (Fig. 22). These are however inserted at different heights and each of them includes cup-like a small group of one to three, usually three stamens, thus giving the flower an appearance resembling the pseudanthia of the *Myricaceae*; certainly it represents a very primitive type. The other *Engelhardtia* species have a more irregular and reduced perianth. In *E. spicata* there are sometimes three to four perianth-leaves in the male flower (Fig. 13 *D, E*), while in other flowers of the same specimen there is no perianth. *E. nudiflora* Hook. f. has one or two narrow perianth-leaves. *E. rigida* Bl. is according to Nagel (1914) entirely devoid of perianth. Also in *Alfaroa* and *Oreomunnea* the male flowers are of a similar, irregular structure — generally however somewhat better developed —; in *Alfaroa* there are about five perianth-leaves, in *Oreomunnea* about three to six broad leaves (Fig. 11 *B*). *Platycarya* is quite without perianth in the male flower; the reduction is here still stronger than in the female flower.

Pterocarya Paliurus has a comparatively regular perianth in the male flowers, four leaves of approximately the same size. They are not however quite equal in size, and their position varies to some degree; the type should on this account not be regarded as specially far advanced, though perhaps it is somewhat more derived than in the other species. These have like the one *Juglans*-section (*Cinerea-Regia*) an irregular perianth with more or fewer leaves. The radial perianth in *Juglans*, section *Nigra*, has a really regular construction and no doubt represents a far advanced type.

In the genus *Carya* there are as a rule only three leaves in the staminate flower, the bract and two transverse leaves generally regarded as bracteoles. In addition there is exceptionally a fourth leaf opposite the bract, mentioned by DeCandolle (1862) for *C. Pecan*, by the present writer observed in several cases in *C. ovata* and *tomentosa* (see Fig. 14 *g*), in one case there were even two leaves side by side in this position in the latter species. The fourth leaf was assumed by DeCandolle to be a perianth-leaf in the same way as the fourth leaf of the

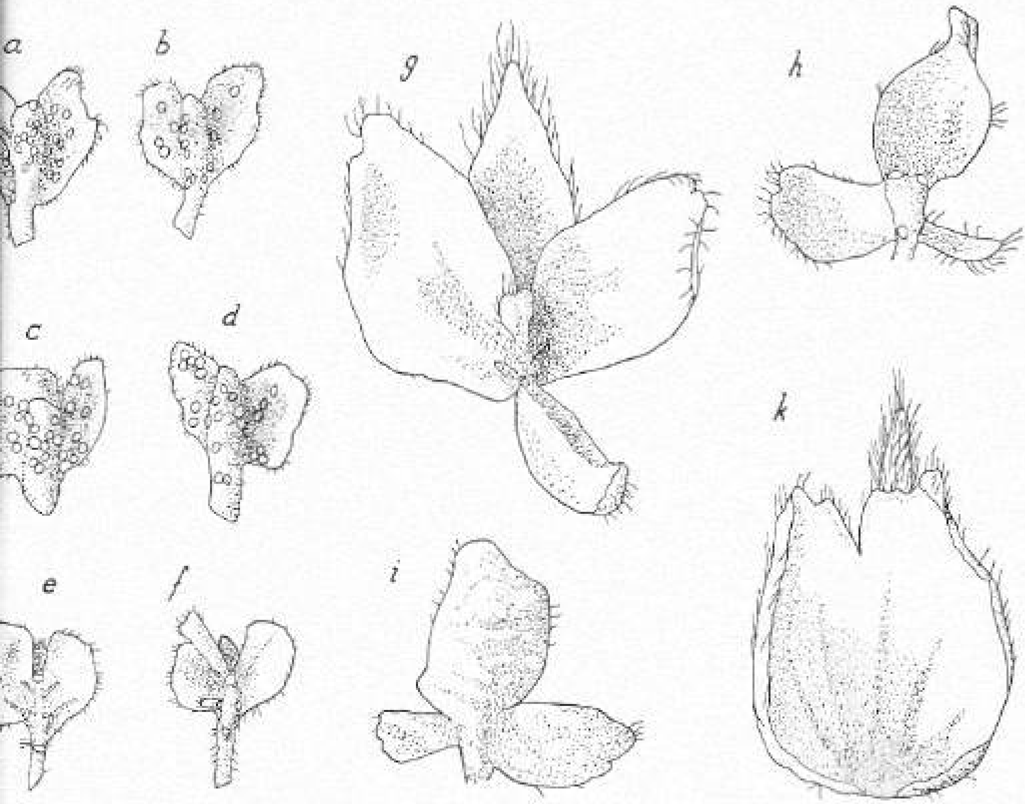

Fig. 14. *a—d Carya tonkinensis*, male flowers from below, the transverse leaves of irregular shape and size, *e—f* the same, male flowers from above, in *f* the one lateral leaf is bipartite, stamens 4, in *f* one stamen partly scale-like; *g Carya tomentosa*, male flower with an additional leaf opposite the bract and one sterile stamen (the others removed), *h—i C. cordiformis*, the lateral leaves partly reduced, *k C. tomentosa*, the lateral leaves fused into one structure. About × 15.

involucre. In my opinion this involucre-leaf is certainly a bracteole like the transverse involucral leaves, but as to the fourth (and fifth) leaf of the male flower the conditions are somewhat different, because the two transverse leaves occurring here are apparently not bracteoles but perianth-leaves. In *Carya tonkinensis* Lec., which appears to be an original species, these leaves are (Fig. 14 *a—f*) considerably larger than the bract, unequal in size to one another, and irregular in shape, sometimes two-parted above (Fig. 14 *f*); they appear in consequence to be a reduced perianth, at least partially arisen through fusion of the original leaves. In *C. tomentosa* (Fig. 14 *g, k*) they may also be larger than the bract, in *C. cordiformis* (Fig. 14 *h, i*), they may be small, reduced, in both they are often crenate-lobate in their edge; occasionally they fuse into a unitary structure above the bract (Fig. 14 *k*): these facts argue in favour of their perianth nature. Thus, I am of the opinion that in *Carya* there exists a perianth in the male flower, generally consisting of two leaves, sometimes of another one (or two), this perianth however being reduced-transformed, while the bracteoles, as in *Pterocarya Paliurus,* have quite disappeared. In their position the perianth-leaves are reminiscent of the arrangement in the pistillate flower, which will be described later on.

Sometimes intermediate structures between stamens and perianth-leaves may be observed in the male flower. Thus, according to ÖRSTED (1870), the lateral perianth-leaves of *Pterocarya fraxinifolia* are often transformed into stamens, something that I have not myself observed; on the other hand, I have found intermediate forms between perianth-leaves and stamens in a few flowers of *Pterocarya stenoptera* and *Juglans mandshurica* and in several cases in *Oreomunnea.* The question then arises whether the perianth-leaves are homologous with stamens, inasmuch as they are possibly made up of transformed stamens. In *Pterocarya stenoptera,* where any perianth-leaf beyond the anterior median but rarely occurs (Fig. 13 *A—B*) and where the number of stamens is relatively small, there seems however to be no decrease in the number of the stamens at the appearance of an extra perianth-leaf; they appear independent of each other — save possibly in exceptional special cases (Fig. 13 *C*). And in *Engelhardtia spicata* (var. *Colebrookeana* HOOK.), which seems to represent rather primitive conditions, the extra perianth-leaves may come in just outside stamens, which are thus superposed to them (Fig. 13 *D—E*). This speaks in favour of the view that the perianth-leaves are at least to a great extent of bract-nature. It seems as if a flower such as the one reproduced of *E. spicata* rather strongly resembles those *Myrica*-flowers where the »perianth» is composed of a number of »bracteoles», in reality bracts of florets in a pseudanthium. At all events most of the perianth-leaves in the male flowers of *Juglandaceae* appear to be homologous with these bracteoles.

The perianth of the female flower is more regularly developed than that of the male flower and is not entirely lacking in any genus, though in the genera *Platycarya* and *Carya* it gives proof of a rather advanced reduction or transformation. As a rule it consists of four scale-like, epigynous leaves, two median and two transverse, all about equal in size. However, several minor deviations occur from the common type, and it may be possible also here to find a certain line of development from more original to more derived forms. In the genus *Alfaroa* the perianth-leaves have an irregular position — they are not exactly median and transverse — and a varying size. They are rather coarse and stiff, sometimes broader towards the apex, and resemble staminodia. This is still more the case in *Oreomunnea*, where they are quite narrow, almost clavate in shape; besides, they emanate here at flowering-time (cf. DeCandolle, 1914) not from the top of the ovary but from about the middle, being carried up on the top first later on. The two median lobes are somewhat lower inserted than the two transverse. Within *Engelhardtia* the two transverse perianth-leaves are often smaller than the others; sometimes one of them is quite absent. One species, *E. apoënsis*, which has a regular 4-membered perianth inside the involucral whorl, has, like *Oreomunnea*, the two median lobes obviously lower inserted than the transverse ones (Fig. 15 *A*).

As to the perianth of *Platycarya* my opinion, as shown above, agrees with that of Nagel (1914), that there are two transverse leaves, transformed into fruit-wings, and in addition one or two median ones. The two pairs are, as in *Oreomunnea* and *Engelhardtia apoënsis*, inserted at different heights, but with the median pair higher. As, contrary to these two species, the carpels are here transverse, the leaf-pairs — as in the two other cases — alternate with the carpels. The median lobes, if present, are firmly adnate to ovary and fruit, and are only discernible at the fruit as small scars, consequently strongly reduced. On the whole, the perianth of the female flower of *Platycarya* must be said to be of a strongly reduced-metamorphosed type.

In *Pterocarya* and *Juglans* the perianth is generally regularly 4-membered, but in exceptional cases — not so uncommon in the former genus — an irregular development of the perianth may be observed, often consisting in one or two of the lobes (which then may be more than four) being quite small and inserted higher than the others (*a* in Fig. 15 *C*, 4 and 5 in Fig. 15 *B*, observe further the small lobe at the base of leaf 3). Judging from these deviations, it appears as if the perianth leaves had originally been spirally arranged but through secondary displacements and suppression of one leaf or fusion of two had come to form a 4-membered whorl.

In the genus *Carya* a perianth corresponding to that of the other genera has never been observed in the female flower; for this reason

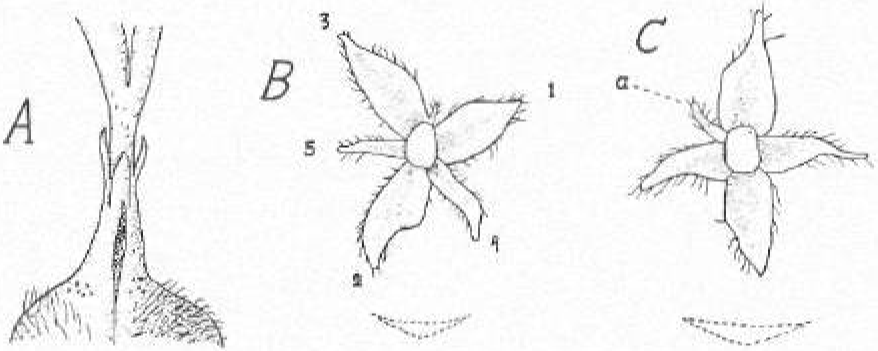

Fig. 15. *A Engelhardtia apoënsis*, the upper part of a fruit with median opening fissure, 3 of the 4 perianth-leaves visible (another median leaf is present, low inserted as the visible one), 2 transverse style branches, *B—C Juglans Sieboldiana*, the perianth from above in two female flowers with unequal perianth-leaves, in *B* in a rather obvious spiral. The bract is indicated. *A* about × 6, *B—C* × 8.

it has generally been supposed that the third bracteole (and the fourth that may occasionally be present) represented the reduced perianth. MANNING (1940) is of the opinion that this has fused with the stigmas to a »stigmatic disc». As mentioned above, however, a true perianth may often be observed above the involucre. It is easy to observe on living flowers. Fresh flowers of *Carya tomentosa* and *ovata* from cultivated trees in Lund were thus found for the most part to have a perianth; a third species, *C. cordiformis*, which was also examined, had such in exceptional cases, though generally it was here absent. When a perianth is present, it generally consists of two leaves, more or less short, rounded, inserted close beneath the stigmas, one at either side of the bract, in the space between this and the adjacent bracteole (Figs. 16 and 17). Sometimes, more rarely, only the one of these leaves is developed. Occasionally a third leaf also occurs — fully developed only observed in *C. tomentosa* (Fig. 16 *D*). This is opposed to the bract and, as a rule, is only developed if the third bracteole, opposite the bract, is lacking, so that the edges of the two lateral bracteoles meet on the ovary. The three perianth-leaves then become regularly alternating with the three involucral leaves as in a perianth with two whorls. In one case it was observed that a third perianth leaf was developed, though the opposite bracteole was present; the perianth-leaf was then quite small, rudimentary (Fig. 16 *G*). On the whole, it must be admitted that even if there may be a perianth in *Carya*, it gives the impression

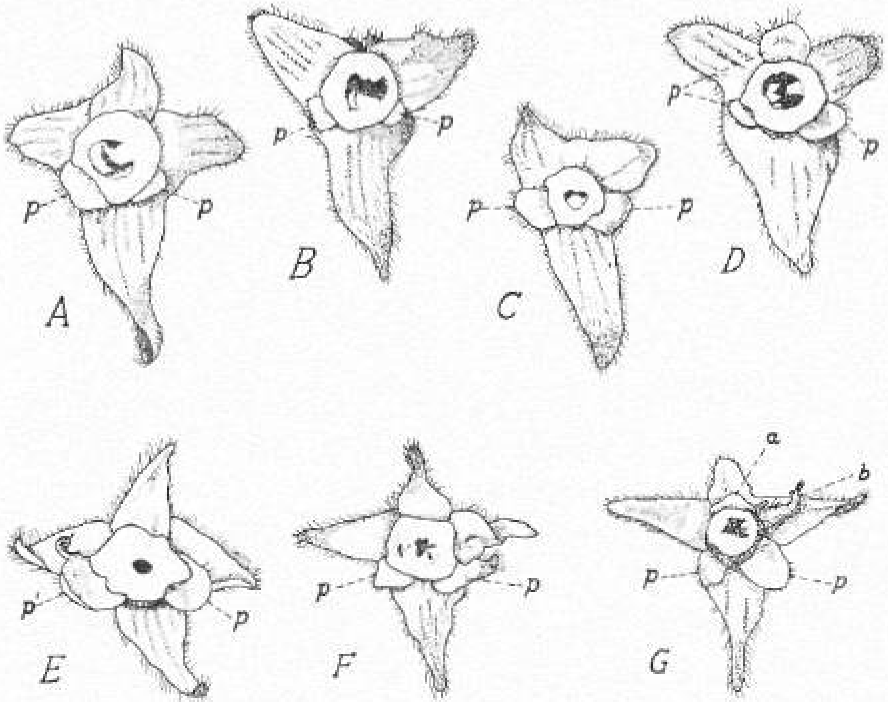

Fig. 16. *A—D Carya tomentosa*, female flowers with 2 or 3 perianth-leaves (*p*) and in addition 2 or (*A*) 3 bracteoles; *E—G Carya ovata*, female flowers with 3 bracteoles and 2 perianth-leaves (*p*); in *E* the one perianth-leaf (*p'*) has a stamen-like structure in its margin, in *G* there is an incipience to a third perianth-leaf (*a*) and a stamen-like structure (*b*). Stigmas removed in all flowers. × 5.

of being reduced; one or two of the leaves often are quite small, and often it totally disappears. The unusual position probably depends on a displacement for the sake of room of the two leaves to the two gaps in the involucre, where there is better place, and suppression — normally — of the other leaves. The perianth of *Carya integrifoliolata* is probably reduced in a similar way as that of other *Carya* species; no perianth is mentioned in the description of KUANG (1941). I have however not had any opportunity to investigate flowering specimens.

Concerning the origin of the perianth in the female flower some information may be given by certain conditions in the genus *Engelhardtia*. As mentioned above, a fourth lobe often occurs here in the involucre, which is sometimes divided into more. In *E. rigida* (Fig. 18 *A*, *B*, *D*) this fourth lobe (or the middle-most of its components) is

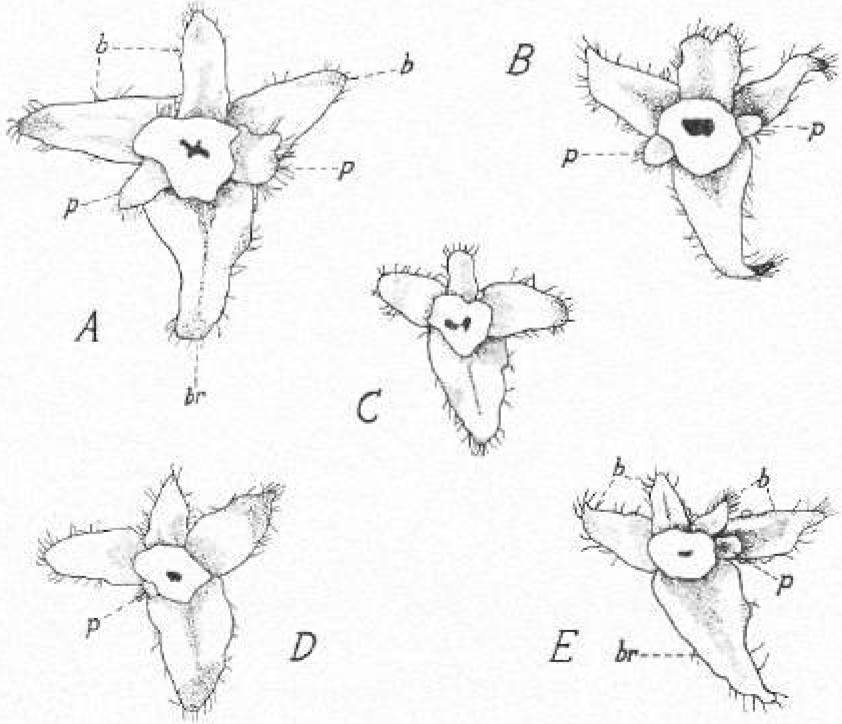

Fig. 17. *Carya cordiformis.* Female flowers from above, the stigmas removed. *A—B* with two perianth-leaves, *C* without perianth-leaves, *D—E* with one perianth-leaf. *br* bract, *b* bracteole, *p* perianth-leaf. About × 7.

narrow and oblong in shape, well separated from the others and firmly adnate to the fruit. There is no perianth-leaf inside of it, but it serves as perianth-leaf; in addition there are one perianth-leaf just opposite, considerably smaller, and one or two lateral ones (generally still less developed: sometimes the one of them is entirely lacking). In another species, *E. zambalensis* Elm. (Fig. 18 *C*), the corresponding lobe is smaller and differs from the three true perianth-leaves only by being somewhat larger and obtuser. A third species, *E. nudiflora* Hook. f., has at flowering-time sometimes — in some flowers — two median perianth-leaves, which are about equal in size (Fig. 18 *E*), sometimes — in other flowers — the posterior one, turned towards the axis, is evidently larger, which indicates that it has originated from an involucre-lobe, a bracteole. The lateral perianth-leaves are also here small, sometimes the one is totally lacking. Thus it is obvious that to

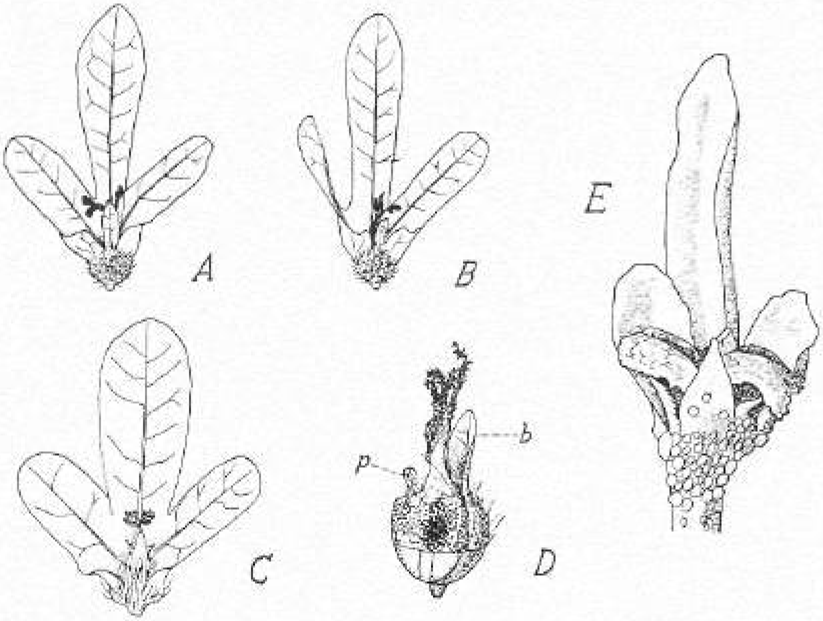

Fig. 18. *A—B Engelhardtia rigida*, fruits with involucre, in which a small median segment serves as perianth-leaf; *C Eng. zambalensis*, do.; *D Eng. rigida*, fruit from the side, the involucre removed except the small median segment (*b*), one perianth-leaf, median, visible (*p*), another, transverse, not visible; *E Eng. nudiflora*, female flower with 4 perianth-leaves, the posterior one, opposite the bract, probably arisen from a bracteole. *A—C* × 2, *D* × 5, *E* × 15.

a certain extent the perianth of the female flower may be formed by leaves of bract-nature. On the other hand, there are facts arguing in favour of the view that stamens also take part in the formation. In *E. rigida* the anterior median perianth-leaf may be twisted and buckled on the surface in a way that is suggestive of transitions between stamens and perianth-leaves, in *Oreomunnea* all four perianth-leaves are narrow and more or less clavate, strongly resembling staminodia, in *Alfaroa*, too, they may be more or less staminode-like. In *Platycarya* the perianth-leaves appear, as above stated, to be transformed into stamens at the transition from female to male flower. In one case the author has observed in *Juglans mandshurica* that one of the four perianth-leaves was converted into a structure that might be regarded as intermediate between stamen and carpel, and in *Carya ovata* there occur structures that might be held for transitions between stamens and

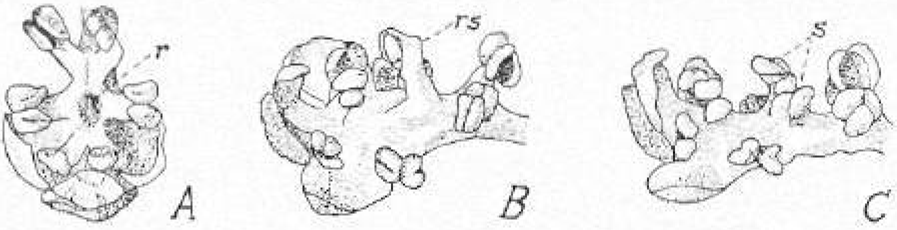

Fig. 19. *Pterocarya stenoptera*, male flowers. *A* flower with rudimentary pistil (*r*) in the centre; *B* the rudimentary pistil shows transition to stamen (*rs*); *C* two stamens (*s*) have been formed at the place of the pistil-rudiment. About × 12.

perianth-leaves (Fig. 16 *E* and *G*). Probably the perianth of the female as well as of the male flower is formed both of bracts and stamens, but while in the male flower the bracts play the greater part and the stamens seem to participate only in more exceptional cases, in the female flower the stamens appear to be of greater importance and the bracts to play a subordinate part; they are in the first place engaged in the formation of the involucre.

The stamens are generally of very varying number even in the same catkin. They seem to be arranged in transversal rows, 3, 4 or even 5 in the flower, and it is a matter of question whether their arrangement may be referred to a common plan. Elucidative of the question are the conditions in the genus *Pterocarya*. In *Pt. stenoptera* the number of stamens is not so great and not so various; it is generally eight, three in the two anterior and two in the posterior of the three transversal rows in which the stamens appear to be arranged. The middle-most stamen of the middle row is sometimes replaced, however, by a pistil-rudiment (Fig. 19 *A*), and on its place transitions may often be observed between pistil-rudiment and stamen (Fig. 19 *B*). No doubt the stamen that occurs here has arisen by transformation of the rudimentary pistil to a stamen, which often differs in some degree from the others through its long filament, etc.; sometimes there are two such somewhat deviating stamens side by side, evidently both arisen from an original pistil (Fig. 19 *C*). In *Pterocarya fraxinifolia* the number of stamens is somewhat greater; generally they make four transversal rows, the posterior one often only with two stamens. A rudimentary pistil sometimes occurs and it then generally has its place in the second row as in *Pt. stenoptera*, or close to this row. The two anterior rows correspond on this account to the two anterior ones of *Pt. stenoptera*,

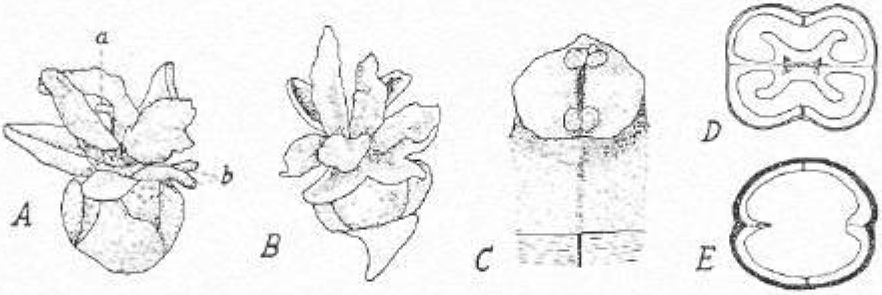

Fig. 20. *A—B Pterocarya stenoptera*, female flowers with supernumerary stigma lobes. *A* with 3 larger stigma segments and a small appendage (*a*), *B* with 5 stigma segments. In *A* the one perianth-leaf has been split into two lobes (*b*), in *B* there are 5 perianth-leaves. *C Engelhardtia Wallichiana*, the upper part of a fruit with two median, bipartite, sessile stigmas, the line of coalescence of the carpels visible at the surface and (below) at section through the fruit wall. *D E. apoënsis*, cross section of fruit. *E E. spicata*, do., the transverse coalescence lines and the median opening fissures are visible. *A—B* about × 10, *C* × 15, *D—E* × 5.

the two posterior are apparently formed by splitting and displacement in the third row. Further splittings and displacements, especially in the posterior part of the flower, may be conceived as giving rise to the larger number of stamens that is found for instance in *Juglans regia* (where they may appear to make four or five transversal rows, the posterior of which however is often irregular). The original type, according to the author's opinion, is the one that is met with in the flowers of *Pterocarya stenoptera*, where the stamens in reality form a simple, somewhat irregular circle round a rudimentary pistil. The same type occurs in *Engelhardtia* (e.g. *E. spicata* v. *Colebrookeana*, see Fig. 13 *D—E* above) and may also occur in *Alfaroa* (according to STANDLEY, 1927) and *Oreomunnea*. In *Carya* the stamens are few and of a fixed number, often four, no doubt a secondary condition; in the apparently primitive *C. integrifoliolata* the number may rise to 15 (KUANG, 1941).

The stamens are often quite without filaments (e.g. *Juglans Sieboldiana*), sometimes there are quite short filaments (*Pterocarya fraxinifolia*). The connective often has a well-developed appendage, for instance in *Juglans regia* and other species; the occurrence thereof may, however, be different in the same genus, as in *Engelhardtia*, where some species possess (e.g. *E. spicata* and *nudiflora*) and others lack such an appendage (NAGEL, 1914). These characters may scarcely be used for the systematics of the family itself, but are of

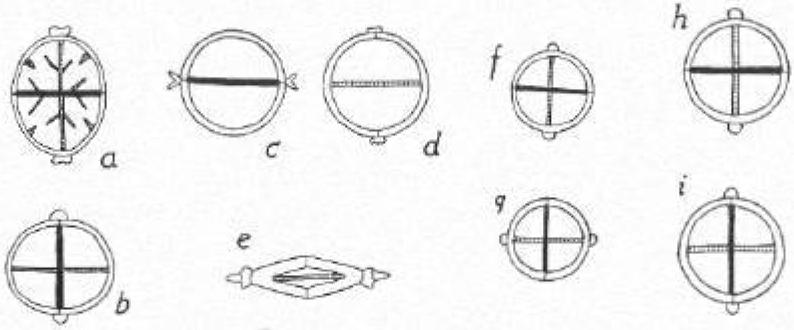

Fig. 21. Diagrams of the fruit structure of *Juglandaceae*. *a Oreomunnea*, *b Alfaroa*, *c Engelhardtia spicata*, *d E. Wallichiana*, *e Platycarya*, *f—g Pterocarya*, *h Juglans*, *i Carya*. The coalescence lines of the carpels are marked. True partition walls black, false streaked.

interest for comparison with other families where similar conditions exist (sessile stamens in *Balanopsidaceae*, appendaged connective in certain *Fagaceae*, *Balanopsidaceae*, and *Salicaceae*).

The carpels are generally two as in *Myricaceae*, but not rarely there are three carpels, which is exemplified by Manning (1940), who also mentions flowers of *Juglans* with one or four carpels. A very varying species is *Pterocarya stenoptera*; here in certain catkins often four or even five carpels occur (Fig. 20 *A—B*). Thus, as in *Myricaceae*, the number of carpels is also rather unstable in *Juglandaceae*.

If the carpels are of the normal number, two, they may either have a median or a transverse position, and the stigmas may in both cases be either carinal or commissural, differences which generally follow the generic limits (Fig. 21). The genus *Oreomunnea* has both carpels and stigmas median, like the *Myricaceae*. In *Engelhardtia* the conditions are different in the two sections of the genus: in sect. *Trichotocarpeae* at least several, probably all, species have median carpels (Fig. 20 *D*, *E*) and transverse stigmas; in sect. *Psilocarpeae*, to which only *E. Wallichiana* (*chrysolepis*) belongs, the carpels are transverse — there is a distinct median line of demarcation —, but the stigmas median (Fig. 20 C). In both cases, thus, the stigmas are commissural; conformably with Manning (1940) it may be said that the bipartite stigmas of *E. Wallichiana* are transitional between the carinal and commissural type. In *Alfaroa* the stigmas are median; according to Manning the carpels have the same position; judging from my own material — fruits only —, however, they are transverse; as far as I can understand, the transverse walls have a dividing fissure, the median, on the other hand, have a narrow, dark line, which must be the limit between the carpels. The stigmas, thus, might here as in *Engelhardtia* be commissural. In *Platycarya,* on the other hand, the stigmas are carinal as in *Oreomunnea*, but they as well as the carpels are here transverse, not median (Fig. 21 *e*). In *Pterocarya* (Fig. 21 *f*—*g*) the carpels have, as earlier mentioned, a very varying position, even in the same species. *Pt. fraxinifolia* generally has median carpels, but sometimes they are obliquely or quite transversely directed. In *Pt. stenoptera* they have a varying position, too: in a tree that I have investigated they were generally transverse. The stigmas, however, always have the same position as the carpels; they are always carinal. This they are in *Juglans,* too, where the carpels are more regularly median (Fig. 21 *h*); the conditions have acquired more stabilisation. In *Carya,* on the other hand, the carpels are transverse and the stigmas median (Fig. 21 *i*), commissural, a more advanced condition than in *Juglans* and *Pterocarya. Carya* (*Rhamphocarya*) *integrifoliolata* seems to have the same carpel position, as well as stigma type, as other *Carya* species (judging from KUANG's Figures and a specimen with fruit in Herb. Kew).

The shape of the stigmas has been described in detail by MANNING (1938 a, 1940), who is of the opinion that the subglobose stigmas of *Oreomunnea* and *Alfaroa* are the most primitive and that the evolutionary development from this type has followed three different lines, (i) one over *Engelhardtia Wallichiana* with its sessile stigmas to the elongate, on the edges papillate stigmas that are the common type in *Engelhardtia,* (ii) one to the type occurring in *Platycarya, Pterocarya* and *Juglans* with stigmatic areas on the inner side, and (iii) one to the dense, bushy stigma-agglomerations of *Carya.* This development seems very probable; only concerning *Alfaroa* am I inclined to call into question whether the — according to my opinion — commissural stigmas are not somewhat more advanced than those of *Oreomunnea*, perhaps even than than those of *Engelh. Wallichiana.*

After this review of the organization of the flower the important question of its origin will be considered.

It may be said that the type of the flower in *Juglandaceae* is the following: furthermost a whorl of bracts, in the female flower at least in the greater part developed as involucre, in the male as a perianth, within this a circle of stamens that in the male flower may partly, in the female totally, be transformed into perianth leaves, and in the centre a pistil of as a rule two carpels, in the male flower rudimentary. With regard to the often occurring pistil rudiments of the male flower — which have been recorded for all genera of the family — and the occasional stamens of the female flower (according to MANNING, 1940, recorded for *Platycarya, Pterocarya,* and *Juglans*) it has been supposed that the flower has arisen from an originally bisexual flower (NAGEL, 1914; MANNING, 1940). The present author cannot share this opinion. In the floral structure of *Juglandaceae* there are so many details reminiscent of the pseudanthia of the *Myricaceae* that I am compelled to conclude that the flower here has arisen by a further development of these. The primeval point of departure, thus, might be an inflorescence with outer male flowers and one or more female flowers in the centre. Concerning firstly the female flower, the remarkable, supernumerary bracteoles indicate the pseudanthic nature of the flower and bring it into fairly close agreement with that of *Myricaceae.* In this family, besides the two transverse bracteoles there often occur, as mentioned above, one or two median »bracteoles», actually bracts in the original inflorescence; sometimes the number is greater, in all 5—6 or more. The number may thus be quite as great as the leaf number in the involucre of *Juglandaceae,* and when in this there are one bract and three bracteoles, it has its correspondence also in *Myricaceae,* viz. in those cases when only the posterior median bracteole is developed besides the transverse ones (e.g. *M. cacuminis,* Fig. 7 c). In most species of *Myricaceae* bract and bracteoles are not further developed after flowering-time — as in *Alfaroa* —, but in certain cases there is a development that is quite parallel with that of some *Juglandaceae.* In the genus *Gale* the two bracteoles enlarge after flowering, coalesce with the fruit and form coarse wings in a way similar to that in *Pterocarya,* and in the genus *Comptonia* the bracteoles form thin wings in a manner that is reminiscent — though not in details yet in principle — of *Engelhardtia.* Within *Myricaceae* stamens sometimes occur in the female flower, connate with the ovary, often clavate staminodia, emanating high up on the ovary; the former has a direct correspondence in some *Juglandaceae,* the latter is suggestive of the staminode-like perianth-leaves that are found in certain genera and probably are a further development of such structures. With regard to the male flower of *Juglandaceae,* then, it has in the more original form that occurs for instance in some *Engelhardtia* species and *Oreomunnea* a circle of bract-like perianth-leaves of irregular position with stamens superposed to them. Such a flower must be said to be very pseudanthium-like and in some cases it calls strongly to mind the

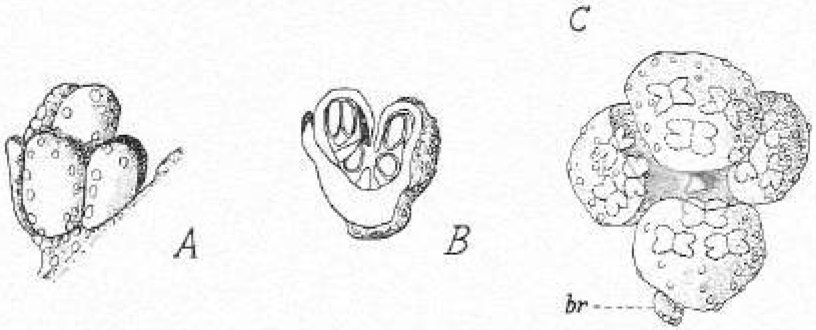

Fig. 22. *Engelhardtia Wallichiana.* *A* male flower in bud, *B* longitudinal section of undeveloped male flower, *C* male flower from above; the anthers, for the greater part hidden by the perianth-leaves, are indicated. *br* bract. *A—B* about × 15, *C* × 10.

conditions in *Myricaceae.* Especially this is true of the male flower of *Engelh. Wallichiana,* where the cup-like leaves, inserted at different heights, each surround a small group of stamens (Fig. 22), an arrangement that is very reminiscent of the small primary spikes of *Myrica Nagi.*

Thus, there is much arguing in favour of the view that the flower of *Juglandaceae* represents a further stage of the development that may be observed within *Myricaceae*; the reduction here has only become stronger, the original inflorescence-nature more obscure.

The fruit is generally described as a drupe, in *Carya* and *Juglans* as a false drupe, as the incolucre here takes part in the formation of the fleshy covering. The limit between fruit-wall and involucre is difficult to determine, and Manning (1940) is of the opinion that the fruit in all genera is a nut, in *Juglans* and *Carya* enclosed in an involucral husk. In *Pterocarya,* however, where the bracteoles are only partly connate with the fruit, it is clearly discernible that the fruit is fleshly on the surface also above the point of separation of the bracteoles, and in *Alfaroa, Oreomunnea,* and *Engelhardtia* the fruit has a thin parenchymatous tissue at the surface; on this account it may rather be said to be a drupe with a thin flesh in these genera as well as in *Juglans* and *Carya.* (*Platycarya* has a dry and hard nut.)

In the fruit-structure there are some peculiarities very characteristic of the family. Lacunae occur in the hard endocarp of the fruit in *Juglans* and *Carya.* They also occur, as DeCandolle (1862) states, in *Pterocarya* — the contrary account of Örsted (1870) probably depends on the fact that they do not always occur. There are further a varying number of incomplete partitions, true as well as false, and early established fissures by which the fruit is divided at germination along the midrib of the carpels. Some species of *Engelhardtia, Pterocarya* and *Juglans* have only true partitions in the fruit (below), otherwise there are false partitions, especially richly developed in *Oreomunnea,* where they as well as the true ones ramify into lamellae; a ramification of this kind is also found, though to a much less degree, within *Engelhardtia* (*E. apoënsis*, Fig. 20 *D*). It is a matter of question how the false partitions have arisen; they are entirely lacking in *Myricaceae.* According to the author's opinion, they need not be derived from another type. In for instance the genus *Engelhardtia* there may be seen, on the outer side of the fruit-wall, a regular number, often 8, somewhat impressed veins. In one species, *E. rigida,* which has true partitions only, low down on the inner side of the fruit-wall some ridges or bands may be discerned, corresponding to these veins. If it is supposed that these ridges or some of them were to become higher, incomplete partitions would arise; in their location the partitions correspond to these ridges and veins.

The ovules have the same number and position as is common in *Myricaceae.* For *Juglans* as well as for *Gale* BENSON and WELSFORD (1909) have shown that the ovule is appendicular to a carpel and further that a second placenta is sometimes developed, rudimentary; thus originally there were at least two ovules in the ovary. The cotyledons are strongly plicate and divided into lobes. ÖRSTED (1870) points out the difference that exists between, on one hand, *Juglans, Carya,* and *Oreomunnea,* where the seed-coat accompanies all whirls of the seed, and, on the other hand, *Pterocarya* and *Engelhardtia,* where it forms an even covering over them all. This is possibly — as assumed by ÖRSTED — connected with the fact that the cotyledons in *Pterocarya* — according to ROXBURGH (1874) also in *Engelhardtia* — are epigeal, whereas at any rate in *Juglans* and *Carya* they are enclosed in the fruit at germination, serving only as depots for reserve nourishment.

In their embryology the *Juglandaceae* show some peculiar features reminiscent of the Gymnosperms. According to KARSTEN (1902), at anthesis the carpels are often not quite connate with each other but an opening is left between them. NAWASCHIN and FINN (1912) state that the cytoplasm of the pollen tube is preserved very long in *Juglans,* contrary to the common condition in the Angiosperms but in some similarity to that in the Gymnosperms. In the anthers there may sometimes be found six loculi (recorded for *Juglans,* NICOLOFF 1905).

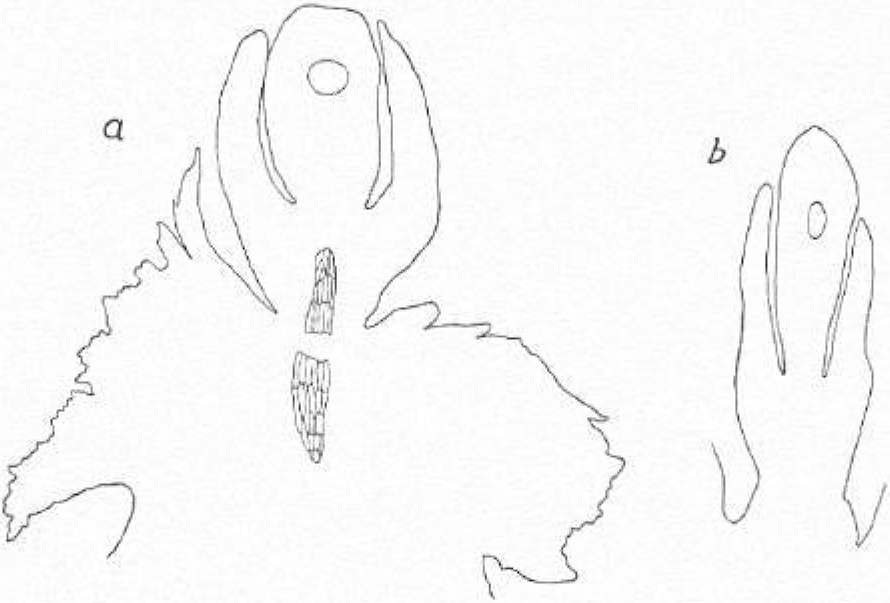

Fig. 23. *Platycarya strobilacea.* Longitudinal section of ovary, *a* transverse, *b* median.

Often there are also two embryo-sacs developed in the nucellus (Karsten, l.c.). In some *Engelhardtia* species, examined by the present writer, *E. spicata* and *E. parvifolia* DC., the integument is protracted upwards into a narrow tube, which perhaps should be compared with the integument-prolongations of some Gymnosperms (*Gnetales*). As in some other *Amentiferae* chalazogamy occurs, at least in the three genera — *Juglans, Carya,* and *Pterocarya* — that have been examined in this respect. Of special interest are the peculiar appendages that emanate from the placenta and extend up around the ovule to a greater or less height, sometimes as high as the nucellus. For *Juglans regia* they are described by Nicoloff (1905) as »corps ailés» and by Benson and Welsford (1909) as »packing tissue». By some authors (Karsten, 1902) they are considered as corresponding to an outer integument (which is disputed by Nicoloff), by others (Benson and Welsford, l.c.) they are supposed to be homologous with the hair-brush on the seeds of *Salicaceae.* In *Platycarya* (Fig. 23), where they are only developed in a transversal direction, they are bushlike lobated and may well be thought to be transformed by further development into trichomes; in other cases they are undivided and are more suggestive of rudiments of an outer integument, which, as is known, occurs in many *Amentiferae*. It is perhaps not quite impossible that these appendages may develop into both these structures.

From the point of view of the floral morphology the relationships of the family will now be considered. The family may be divided into some few natural groups. One group is formed by the three genera *Oreomunnea, Engelhardtia,* and *Alfaroa*. That the two first-mentioned are closely related is immediately quite clear; in fact they have often been brought together to one genus, this by most later authors (NAGEL, 1914; DECANDOLLE, 1914; STANDLEY, 1927 a — yet with some reservation —; MANNING, 1938 and 1940). As is evident from the preceding, however, the author's opinion is that *Oreomunnea* is a genus of its own, there being several important characters distinguishing it from *Engelhardtia,* as already in part pointed out by ÖRSTED (1856, 1870). An especially important difference is that the stigmas of *Oreomunnea* are carinal, median as the carpels, while those of *Engelhardtia* are commissural, whether the carpels are median or transverse. A second important difference is that the testa in *Oreomunnea* attaches itself to all irregularities of the cotyledons, while in *Engelhardtia* it forms an even covering. *Oreomunnea* in this respect approaches the type that is found in *Juglans* and *Carya,* the character possibly being connected with the fact that the germination is hypogeal as in these; the germination of *Oreomunnea* is, however, not described. Other distinguishing characters, though not of the same importance, are the primitive inflorescence-type of *Oreomunnea* (which however does not deviate much from that of *Engelh. Wallichiana*), the occurrence of numerous walls and lamellae in the fruit, the deviating nervature of the fruit-wing, the characteristic horseshoe-shaped stigmas, the staminode-like perianth-leaves of the female flower, at first inserted at the middle of the ovary, etc. To this some vegetative characters may be added: in *Oreomunnea* the leaves are as a rule opposite, as in *Alfaroa,* while *Engelhardtia,* as all other genera, has spirally arranged leaves. None the less, there can be no doubt that *Oreomunnea* and *Engelhardtia* are closely related.

By its discoverer, STANDLEY (1927), as well as by KOIDZUMI (1937) the genus *Alfaroa* was brought together with *Juglans,* and not with *Engelhardtia,* on account of the fleshy exocarp of the fruit. This, however, cannot be a correct arrangement. In the *Juglans* group the fruit is a false drupe, the outer layer of which is made up of the fleshy involucre, in *Alfaroa* it is a true drupe and the diminutive involucre is free from the fruit, of *Engelhardtia* type (cf. MANNING, 1940). This brings *Alfaroa*, instead, close to *Oreomunnea* and *Engelhardtia*; these three genera form together a natural group, which shows a similar organization not only in the involucre, but also as to inflorescence and in other respects, as well as in vegetative characters; for instance, the leaves in these three genera are paripinnate, in all others imparipinnate. *Alfaroa* has a fleshy exocarp, it is true, but it is thin, almost dry (STANDLEY, 1927) and does not differ much from the thin parenchymatous tissue that covers the fruit in *Oreomunnea* and *Engelhardtia*. Of the three genera, *Alfaroa* no doubt shows several primitive features, with regard to inflorescence as well as to fruit involucre; in the involucre it approaches *Myricaceae* and does not differ very much from some *Myrica* species with drupe and disappearing bract and bracteoles. A somewhat more advanced character, however, is that the stigmas, so far as the author can find, are commissural. *Oreomunnea* presents very primitive characters, too; the stigmas are for instance carinal and occupy the same position as in *Myricaceae*, inflorescence and perianth have an original structure, but with regard to the development of the involucre, the greater number of stamens, the ramose partition walls of the fruit, etc. it is more advanced. The genus *Engelhardtia* shows a great variation between different species; some of them, especially *E. Wallichiana*, are very primitive as to inflorescence, stigmas and fruit structure, others must be considered as, on the whole, a somewhat more advanced type with regard to inflorescence and stigmas. The commissural stigmas are of course a rather advanced generic character; the structure of the testa on the other hand resembles that of the *Myricaceae*. Biologically the evolution passed through by fruit and involucre is easy to understand. *Alfaroa* lacks special means of fruit dispersion; in *Oreomunnea* bract and bracteoles are organized as a wind-spreading organ, which by reason of the size of the fruit must be of considerable dimensions; in *Engelhardtia* the nut-like fruit as well as the wing diminishes, dispersion being thereby facilitated. It appears as if the three genera represented an old evolutionary chain of which the two monotypical[1] Central American genera were isolated remnants, while *Engelhardtia* had arisen through a later development of

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[1] The recently described *Engelhardtia mexicana* (STANDLEY, 1927 a), which is present in one collection only, does not appear, so far as the author can judge from the description and a photographical reproduction, to be separated to the species from *Oreomunnea pterocarpa*. The fruit-wing is smaller, it is true, than is common in this species, but there is a great variation in this respect.

some now extinct links which in some respects had been intermediate between the two other genera. To the old evolutionary chain probably belong the fossil finds that are described as *Palaeocarya* but that are referred by NAGEL (1914) to *Engelhardtia*; in the nervature of the wing they resemble rather much *Oreomunnea*. Whether they merit being regarded as a genus of their own, cannot be decided without knowing the details of the fruit-structure.

A second natural group in the family is composed of the three genera *Juglans*, *Carya*, and *Pterocarya*. Of these the two first-mentioned genera are no doubt closely related to each other, agreeing as they do in the few-flowered spike, the development of the involucre, as well as in other respects; as pointed out above, *Carya* must be regarded as a reduced type in various respects. *Pterocarya* differs not so little from the other genera, among other characters by the long, pendulous female catkin and the partially free involucre, only constituted by two bracteoles. Still, it no doubt attaches itself to them, especially to *Juglans*, showing several similarities to this genus, for instance in the location of the catkins, the arrangement of the stamens, the shape of the stigmas, and in vegetative characters, too, e.g. both genera have a chambered pith. *Pterocarya* must be considered to represent a more original type than *Juglans* and *Carya*. Arguing in favour of this view are the great variation in the characters of the floral parts, further the type of inflorescence, the arrangement of stamens, the even seed-coat, the epigeal germination, etc. The involucre is laid down as free leaves and it must therefore be regarded as more original, when its leaves as in *Pterocarya* are only partly connected with each other and the fruit. Biologically viewed it may be peculiar if an evolution has taken place to an entirely adnate involucre from one that is partly developed as wings and that seems to serve fruit-dispersion better. The importance of the wings for wind-dispersion, however, is at least in several *Pterocarya* species very doubtful (cf. NAGEL, 1914, p. 522); perhaps it is biologically more to advantage if the leaves entirely surround ovary and fruit as a protective covering. It seems as though *Juglans* and *Carya* could be traced back to the *Pterocarya* type; NAGEL (1914) supposes that a common ancestral genus first developed, as a representative of which he regards *Carya costata*, a fossil form with both *Juglans*- and *Carya*-characters. According to MÄDLER (1939), this form belongs to *Juglans*. There are however other forms which seem to have an intermediate position (NAGEL, 1914, p. 498). The recently discovered *Carya integrifoliolata* also approaches in some degree such an original type. It resembles *Juglans* in the high stamen number — which, however, in other *Carya* species as well may rise to at least 10 (REHDER, 1940) —, and in the arrangement of the male inflorescences it is even reminiscent of *Pterocarya*. Owing to the agreements in the essential flower characters, e.g. in the structure of the gynoecium, it should however, in my opinion, be included in *Carya*.

The genus *Platycarya* shows so great deviations in various respects from other genera that it must form a separate group. NAGEL (1914) is of the opinion that it represents the most primitive type in the family, from which the others have developed. MANNING, on the other hand, considers that with regard to floral characters it is among the most advanced genera, though the type of inflorescence is primitive (1940, 1938). No doubt flower and fruit are of a very simple structure that may be reminiscent of certain *Myricaceae*, but, as pointed out above, this is in part undoubtedly due to reduction. The absence of bracteoles in both female and male flower, occasionally rudimentary bracteoles in the latter, and the rudimentary development of the median perianth leaves in the female flower must be regarded as a result of reduction; the transformation of the transverse perianth leaves into fruit-wings must also be a secondary phenomenon. The arrangement of male and female flowers in the catkins does not either agree with that common in the androgynous catkins of *Myricaceae*. On the other hand, the genus seems in some respects to occupy a relatively original position, for instance as to the arrangement of the catkins and the varying size of the perianth leaves in the female flower. It should most likely be regarded as a reduced descendant of a relatively original type. In view of the aforesaid characters this type is to be sought within the *Engelhardtia* group; perhaps the genus constitutes the end of a side line that has emanated from the above-mentioned supposed series connecting *Oreomunnea* with *Alfaroa*. That the remaining genera should have developed from the *Platycarya* type, however, seems inconceivable.

It remains to discuss the question of what relationship the *Engelhardtia* group has to the *Juglans* group. Of course, it is conceivable that both groups form different parallel evolutionary lines. In the involucre *Pterocarya* is to some degree reminiscent of the genus *Gale* in *Myricaceae*, *Alfaroa* of some *Myrica* species. There are however so great common divergences from *Myricaceae*, for instance concerning involucre, fruit (especially the incomplete partitions), and also in the compound nature of the leaves, that it is impossible to imagine such a diphyletic descent; the family *Juglandaceae* must go back to a common origin. An this origin must lie nearer the *Engelhardtia* group. The more important morphological characters of *Pterocarya* may be derived from the type of the *Engelhardtia* group, but not *vice versa.* The involucre of *Pterocarya* may have arisen from the *Alfaroa* type by one of the initially free leaves, the bract, having stopped in its growth as here, both the others enlarging and partly joining with the ovary. As mentioned above, the inflorescence of *Pterocarya* and the whole *Juglans* group may be derived from the types of the *Engelhardtia* group through a development that appears biologically well-grounded, and the male flower of the *Juglans* group may be traced over *Pterocarya* back to a type occurring in the *Engelhardtia* group that is very reminiscent of the pseudanthia of *Myricaceae.*

As already several times pointed out, the family *Juglandaceae* attaches itself morphologically in different respects to *Myricaceae*, being more closely related to this family than to any other. Especially it may be mentioned that both the male and the female flower of *Juglandaceae* represent further developed stages, not much changed, of the pseudanthia of *Myricaceae.* In consideration of this and of the other great coincidences present it must be supposed that the *Juglandaceae* have developed from the *Myricaceae* type. It is scarcely possible to point out some particular type within *Myricaceae* as the proper origin; some of the characters of *Juglandaceae* may, though in a somewhat different form, be found in *Comptonia*, others in *Gale*, others in certain *Myrica* species. At the origin of a new group it seems often to be so, that characters already present at different places are united to a new combination characterizing the new group. Through such a recombination and further development the *Juglandaceae* may be thought to have originated from the *Myricaceae* type.

The question then arises whether the family *Juglandaceae* counts its lineage from any other group besides *Myricaceae.* In some respects it agrees more with other *Amentiferae* than with *Myricaceae.* The involucre of *Engelhardtia* is rather reminiscent of the corresponding structure in *Carpinus Betulus*; the female flower and fruit of *Platycarya* are suggestive of *Alnus.* Such similarities, however, do not necessarily mean any direct relationship between *Juglandaceae* and *Corylaceae* or *Betulaceae*, so that the former were descended from these or *vice versa*; they are no doubt parallel phenomena, natural within related groups with common origin and similar hereditary dispositions. The same seems to be true of the similarities in fruit-structure found between *Juglandaceae* and some *Lithocarpus* species, where lacunae in the fruit-wall occur as well as false partitions (cf. ÖRSTED 1867); so far as these structures really are homologous with those of *Juglandaceae,* they are certainly results of a parallel development. Of greater importance is the likeness in an embryological respect that exists to *Betulaceae* and *Corylaceae,* that chalazogamy occurs, while, as far as known, it is lacking in *Myricaceae.* The fact has to be borne in mind, however, that *Myricaceae* is an old group, whose now living representatives seem to bear traces of reduction in various respects. Perhaps chalazogamy has also occurred here in an earlier stage, perhaps it is still occurring in some primitive species, which have not been examined in this respect. In any case the chalazogamy of *Juglandaceae* cannot be taken as proof that the family is also derived from *Betulales*; if any direct phylogenetical line should actually exist, it must go in the contrary direction. I regard *Juglandaceae* as merely a further development of the *Myricaceae* type, by which, it must be emphasized, I do not mean that the now living *Juglandaceae* descend from the now living *Myricaceae,* but only that the type of the *Juglandaceae* has arisen from the *Myricaceae* type, whose representatives, according to the testimony of the fossils, appeared earlier than the *Juglandaceae* and showed a greater polymorphism in earlier times. Under such circumstances it cannot be proper to refer *Juglandaceae* to a particular order, as often is done, but the family should, in the author's opinion, form a common order together with *Myricaceae.*

Order 2. Balanopsidales.

Family Balanopsidaceae.

More important literature: Baillon, 1871—73, 1871—1873 a, and 1877; Engler, 1897; Schlechter, 1906; Guillaumin, 1932; A. C. Smith, 1942.

The male flowers, which are known only for some species, are gathered in small, narrow catkins, which are spirally arranged on the youngest internodes, only supported by diminutive scales. In the catkins some empty bracts usually occur below; otherwise there is inside each bract a small group of stamens, generally about five to six or fewer, or even only one stamen, no bracteoles or perianth leaves. The bracts are frequently curved upwards with the outer part darker (e.g. *Balanops microstachya* Baill., Fig. 24 *D*, *F*) and the stamens are more or less fused with the bract, seemingly emanating from it (especially obvious in *B. Theophrasta* Baill.), conditions reminiscent of other *Amentiferae*. A small rudimentary pistil sometimes occurs in the male flower (Fig. 24 *D*). In the apex of the catkin I have in *Balanops Balansae* Baill. (Fig. 24 *B*) as well as in *B. Vieillardi* Baill. (Fig. 24 *A*) and (Fig. 24 *G*) in *B. vitiensis* n.c. (*Trilocularia vitiensis* A. C. Smith, Sargentia, 1942, p. 11) observed a whorl of bracts with stamens in their axils, surrounding a central rudimentary pistil, often two- or three-parted, thus a small group of male flowers round a terminal, rudimentary female flower. The number of bracts in such a group is about five to six (in one case four) and the stamens are about as many; yet generally there is not regularly one stamen inside each bract, but some bracts are empty, while there are two stamens together inside others. The scales are inserted at somewhat different heights and are of varying size; sometimes there are three larger and three smaller alternating with each other. In the three species mentioned there are in addition at the base of the catkins similar groups of bracts and stamens, though somewhat smaller. Fig. 24 *C* shows such a group of *B. Balansae*, which emanates from the axil of a small, coarse, black-edged bract and con-

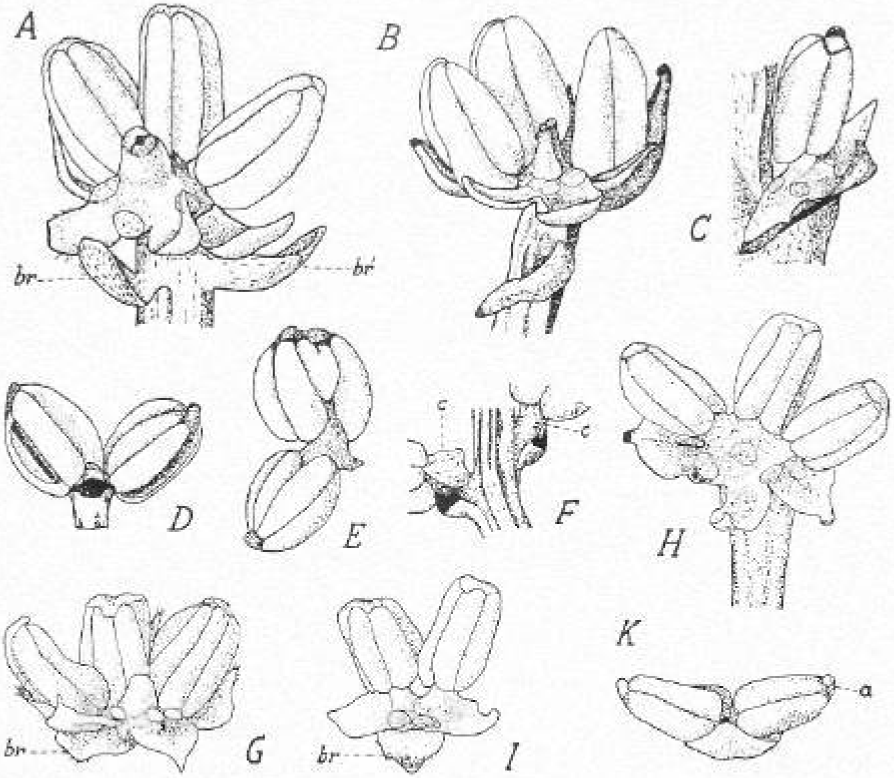

Fig. 24. Male flowers of *Balanops* species. *A* apex of male catkin of *B. Vieillardi* with 6 bracts and 6 stamens (three of these removed) around a bipartite pistil-rudiment (*br* empty bract, *br'* bract in whose axil there has been at least one stamen); *B B. Balansae*, apex of male catkin, 5 stamens (2 removed) and 6 bracts around a tripartite pistil-rudiment; *C* the same, a small side-branch at the base of a catkin with 3 scales and 4 stamens; *D* flower of *B. microstachya* with two stamens and a rudimentary pistil; *E* the same species, two stamens with a common column; *F* the same, part of catkin with two flowers, *c* staminal column; *G* apex of male catkin of *B. vitiensis* with 6 stamens and 5 scales around a flattened rudiment, in addition an empty scale (*br*); *H* the same species, side-branch at the base of a catkin with a whorl of bracts and stamens; *I* the same, small side-branch at the middle of a catkin with 2 scales and 4 stamens, *br* the bract of the branch; *K* the same, flower with two stamens, *a* connective-appendage, beak-shaped. About × 10.

sists of three scale-like bracts and four stamens. Fig. 24 *H* shows another instance, from *B. vitiensis*, a group that is of about the same development as the apical ones mentioned, Fig. 24 *I* shows a higher located group with four stamens and two lateral scales. Two or possibly three such side branchlets may occur at the base of the catkins and besides those there may be one or two higher up in the catkin, smaller than the basal ones. Thus we find that it occurs here as within *Myricaceae* that small flowers of simple structure (cf. Fig. 24 *F, K*) unite together into small flower-like inflorescences, pseudanthia, which in some cases are strongly reminiscent of the flowers of e.g. *Fagaceae*.

In *Balanops Theophrasta* the author has observed on a male specimen small undeveloped scale groups, in and above the leaf whorls of the catkin-bearing shoots, which appear to be undeveloped female flowers. Otherwise, however, the female flowers of *Balanopsidaceae* occur on particular specimens. They are arranged in the same way as the male catkins, being scattered over the youngest internodes and emanating from the axils of very small scales. Their arrangement argues consequently in favour of their being homologous to the male catkins; the cupule-like scales — sometimes comparatively numerous (*B. Pancheri* BAILL.), sometimes less numerous (*B. australiana* MUELL.) — that surround the female flower also indicate that this, as ENGLER (1897) states, represents a catkin reduced to a terminal flower. The surrounding scales may thus be regarded as empty bracts. The present writer has not seen any flower primordia in the axils of the cupule scales proper, but above the small scales that occur below the true cupule in *Balanops sparsiflora* n.c. (*Trilocularia sparsiflora* SCHLECHTER, Engl. Bot. Jahrb., 39: 1, 1906, p. 95), at the fruit stalk, there are sometimes some small, fleshy, low rudimentary primordia of some kind of shoot structures. The cupule scales, lignified at fruit maturation, broad and rounded, may show some likeness to the cone scales of some Conifers. Contrary to the cupule scales of the *Fagaceae*, they are larger in the neighbourhood of the flower; close to this, however, a scale may sometimes be found that is considerably smaller than the others. A true perianth is absent as in the male flower.

The stamens generally have very short filaments, the anthers are almost sessile (exceptionally longer filaments occur in *B. Theophrasta*), and the short filaments may be united with each other (Fig. 24 *E, F*). The anthers are generally furnished with perspicuous connective appendages at the apex (Fig. 24 *D—E, G—K*), and in virtue of this show a great similarity to some species within *Juglandaceae*, where the stamens also may have very short filaments. They not infrequently contain only two or three loculi.

The carpels are two or three in number. Those species that have a dimerous pistil, according to Engler (1897), have median carpels. The

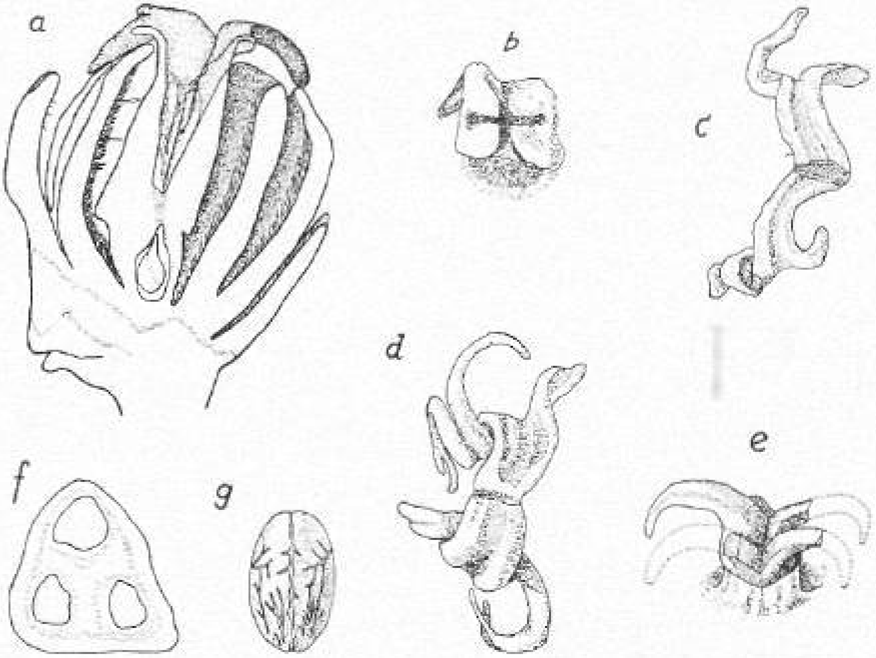

Fig. 25. *a* female flower of *Balanops sparsiflora* in longitudinal section with surrounding bracts; *b* stigmas of *B. Balansae*; *c* do. of *B. montana*; *d* do. of *B. australiana*; *e* stigmas of dimerous pistil of *B. vitiensis*; *f* ovary of *B. sparsiflora* in cross section; *g* stone of *B. pachyphylla*, from the convex side. *a*—*e* × 10, *f* about × 20, *g* × 1.

styles are vigorously developed and there may appear a marked enlargement of the pistil at the upper part of the ovary (*Balanops sparsiflora*, Fig. 25 *a*).

The two or three stigma lobes are deeply divided, and the two segments sometimes stand straight out from each other and approach the segments of the adjacent carpel (Fig. 25 *e*); this condition seems to be transitional between carinal and commissural stigmas. Sometimes the stigma segments are quite short, tapering outwards (Fig. 25 *b*, *e*), sometimes they are long and vigorous (Fig. 25 *a*, c, *d*) and may then be in turn bifurcated, once or (Fig. 25 *d*) even twice. Bifurcated stigma lobes occur, as mentioned above, in *Juglandaceae* too. According to Baillon (1871—73) there are incomplete partition walls in the ovary of some *Balanops* species, as in *Fagales*; the only species, however, that I have had an opportunity of examining in this respect, *B. sparsi-*

flora, had at anthesis the ovary completely divided by thick walls into quite separate cells (Fig. 25 *f*).

Concerning the embryology there are some statements by BAILLON (1871—73 and 1877). Each chamber of the ovary contains two ovules, one smaller and one larger, one of which only is generally developed. They are basal and apotropous, thus differing both from *Juglandales* and *Fagales*. In the few-seeded *Salicaceae* there is, however, the same position and, as mentioned above, it does not differ very much in an early stage from that of *Juglandales*, to which the new genus *Canacomyrica* (cf. above) may also form a transition. At the funicle there is an obturator-like enlargement towards the apex of the ovule; possibly this corresponds to the protuberance occurring at the base of the ovule within *Juglandaceae*, though it has here, where more than one ovule occurs, been unilaterally developed. The ovule has one integument only (WETTSTEIN, 1935).

The fruit is a drupe with thin flesh and generally two, sometimes three, stones. If two stones are developed, they are plane on the one side and convex on the other, if there are three, they are triangular with a rounded outside. In a dry condition they are often coated with a network of fibres (Fig. 25 *g*), in the same way as may occur within *Juglandaceae* too. Some species show a small, deep, sometimes almost quadrangular excavation at the base of the stone, possibly being of importance for the germination. The only structure possibly reminiscent of this in other families might be the narrow cavity that occurs in the basal part of the fruit of *Platycarya*.

The seeds possess, according to BAILLON (1871—73 and 1877), besides the large embryo which almost fills them up, a quite thin layer of endosperm around (cf. *Myricaceae* and *Salicaceae*).

The family has been divided into two genera, *Balanops*, characterized by a dimerous pistil, and *Trilocularia*, with three carpels in the pistil. Through the new species that was described in 1942 by A. C. SMITH and was referred by him to *Trilocularia* as *T. vitiensis* it is obvious, however, that the two genera cannot be kept distinct. The new species has on the same specimen some fruits with a trimerous gynoecium and some dimerous ones (see Fig. 25 *e*), and the staminate flowers, which were previously unknown for the species referred to *Trilocularia*, are of quite the same type as in species referred to *Balanops* (cf. Fig. 24 *G*—*K*, also A. C. SMITH, 1942, Fig. 2). There is no difference in the development of the stigmas either between the species referred to *Balanops* and those referred to *Trilocularia*; in both groups there is a change between long, vigorous, sometimes (doubly) bifurcated stigma segments as in *B. australiana* and *B. sparsiflora* and on the other side the short tapering segments occurring for instance in *B. Balansae* and the new species *B. vitiensis*.

In the matter of the systematic position of the family a reservation must be made with regard to the incompleteness of the material, several species being incompletely known; some embryological details have not been investigated. From the known facts it seems nevertheless evident that the family is a group that shows many attachments to other *Amentiferae* (and especially to the order *Juglandales*). Particularly this is true about the male catkins with their simply built flowers, bracts of amentiferous type, and fusion between stamens and bracts. That the bracts of the female flowers increase in size and lignify is also a feature having its correspondence in other *Amentiferae*.

Exteriorly the leaf cupule is very reminiscent of the cupule of *Quercus*; however, the elevated axial structure is absent that in the *Fagaceae* bears up the scales of the cupule and this is therefore more comparable with the one occurring in *Juglandales*. At an early stage of the development of the *Quercus* cupule, before the axial swelling has yet begun, there is nevertheless some structural similarity to this too. At several other points there are, as touched upon above, similarities to *Juglandales* — *Myricaceae* or *Juglandaceae* —, and on this account *Balanopsidales* probably stand nearest this order.

Of special interest is the development from inflorescence to flower that may be traced back within the family and that in the male catkin is at so early a stage as to be comparable with the — in this respect — most primitive members of *Myricaceae*. In the female flower, on the other hand, the development is more advanced; beyond the remaining apical flower there can hardly be found any further flower rudiment, as is the case in several of the *Myricaceae*. It is also of interest to see that in the male catkin, besides the apex, also two (or three) basal side branches are advanced, in a similar way as may be observed in *Myrica Faya*; perhaps *Comptonia* should also be compared in this connection. A continuation of this development might lead to a formation of 3-flowered dichasia, the common type within *Fagales* and *Betulales*.

While the general flower structure compared with *Myricaceae* is at a rather primitive stage, this is also true of the ovary, which is more or less divided into two or three chambers with two ovules in each. From such a type or a similar one the ovary of *Juglandales* may be thought to derive. A more advanced feature in comparison with at least most *Juglandales* is undoubtedly that the ovules in their later development take an almost perfectly anatropous position. Thus, original and less original characters are mingled together in the order. On this account the *Balanopsidales* can hardly be thought to constitute the original type, from which *Juglandales* have developed. It may however be possible that the order is a descendant of this type somewhat modified through secondary changes.

Order 3. Leitneriales.

Family Leitneriaceae.

Important earlier literature: BAILLON, 1877; v. TIEGHEM and LECOMTE, 1886; TRELEASE, 1895; PFEIFFER, 1912; ABBE and EARLE, 1940.

The only species belonging to the family, *Leitneria floridana,* was recently examined by ABBE and EARLE (1940) with respect to its floral morphology and anatomy. As regards the male catkin these authors arrive at the conclusion that owing to the course of the vascular bundles the particular flowers have arisen by coalescence of three flowers with four stamens each, in the same way as, according to ABBE (1935), occurs within *Corylaceae*. That the flowers are formed by union of rather simply built flowers also seems very probable in view of the statements of the authors about the vascular system and of the grouping of the stamens that may more or less obviously be observed in the flower. That just three tetrandric flowers form the point of departure is perhaps more uncertain, however; other possibilities are also conceivable. In one case analysed by ABBE and EARLE, regarded as original, a flower with twelwe stamens in the lower part of a catkin, the three larger vascular bundles divide into respectively 4, 3 and 5 branches, supplying one stamen each; it must thus be supposed either that one flower receives a bundle from another (the authors incline to this view), or that one flower is pentandric, one triandric. In other cases, with reduced number of stamens, the irregularities are greater. It must also be noted that the staminal number may not only rise to 12, the highest number found by ABBE and EARLE, but according to VAN TIEGHEM and LECOMTE (1886) may amount to 15, and that the grouping is very irregular; sometimes there seem to occur more than three groups with two or three stamens in each (Fig. 26 *A*). Perhaps the androecia should therefore rather be compared with the irregularly branched stamen groups of *Myricaceae* with varying number in each group, though there is generally a subdivision into three groups. The chief feature, however, is the compound nature of the flowers. A small perianth may according to BAILLON (1877) occasionally occur in the staminate flower; it has not been observed by the present author.

Concerning the pistillate flower a special interest is connected with the small perianth-like scales that surround the ovary. Two of these are more or less sharply separated from the others and should without doubt be regarded as bracteoles, as is done by ABBE and EARLE (1940). The remaining scales are of varying number, size and position. Not infrequently there are four approximately diagonal scales, but their position may also be different and the number larger (or sometimes even smaller). In the flower illustrated in Fig. 26 *B* there are, besides the bracteoles, two larger scales (*c*—*d*) towards the axis, one of them two-cleft, and two somewhat smaller (*e*—*f*) towards the bract. In another flower (Fig. 26 *C*) three larger scales were observed, two of them placed at the one side, the third at the other; in addition there were two small scales towards the bract, one (*c*) being placed further in than all the others, and a small, emarginate one towards the axis. A third flower (Fig. 26 *D*) had two larger lateral scales, a small about median scale towards the axis, and towards the bract a rather small one (*a*), the last-mentioned being inserted further out than all the others, and inside two very small scales, (*c* and *d*), one of them (*d*) seemingly being placed further in than all the others. Thus, it is not possible to refer the position of the perianth-leaves to any determinate plan, or to refer them to two definite cycles, as ABBE and EARLE (l.c.) think is suggested by their arrangement; there are inner and outer scales, it is true, but several different gradations, not merely two. They should most likely be regarded as a spiral of irregularly arranged perianth-leaves, where — owing to space-conditions — the lateral have been favoured, whether they are now one or two at either side. In their arrangement they resemble to some extent the bracteoles that in many cases surround the ovary in *Myricaceae*. It does not seem incorrect to regard them as perianth-leaves; similar perianth-leaves, somewhat fleshy and frequently with glands in the margin, occur for instance in *Betulaceae* (the bracteoles of the *Myricaceae* are also sometimes of similar development, but they are occasionally regarded as perianth-leaves too).

Occasionally it occurs, as already stated by BAILLON (1877), that some stamens are developed in the female flower, so that a bisexual flower arises. An instance of this is shown in Fig. 26 *E*. In the flower there reproduced (the pistil is removed) there are four inner perianth-

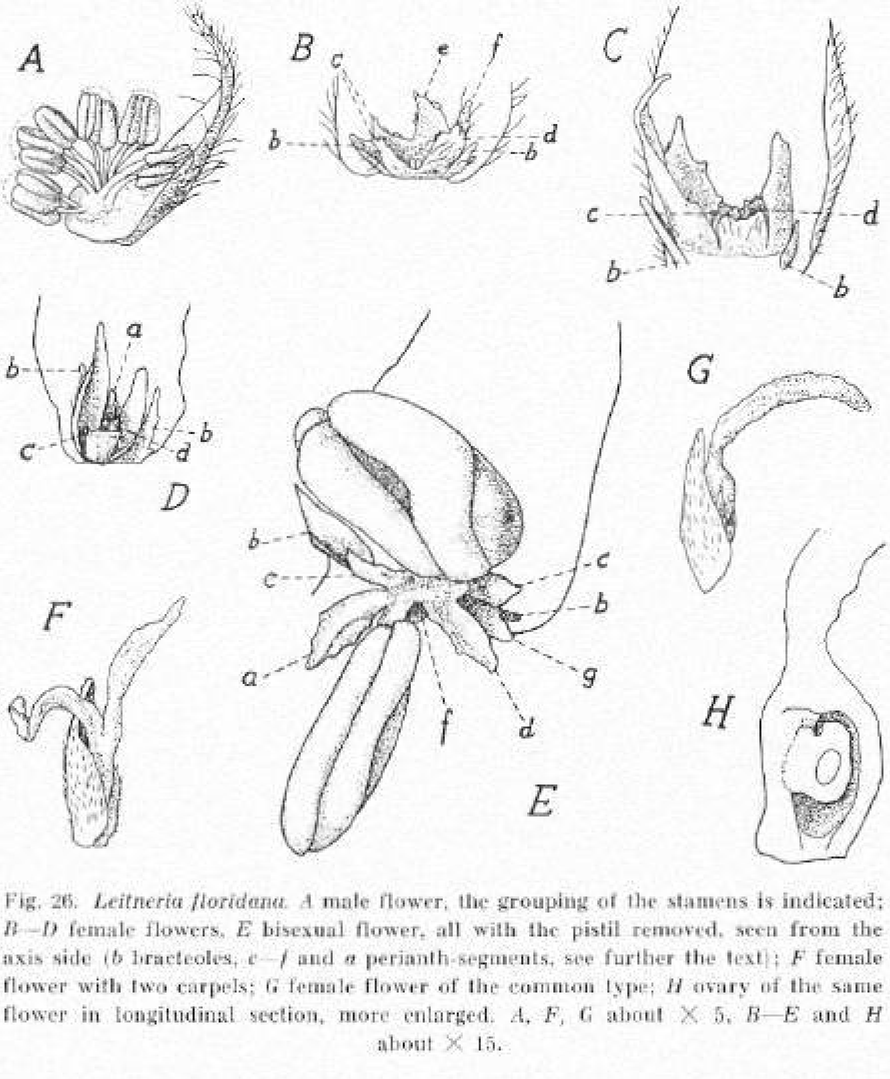

Fig. 26. *Leitneria floridana.* *A* male flower, the grouping of the stamens is indicated; *B—D* female flowers, *E* bisexual flower, all with the pistil removed, seen from the axis side (*b* bracteoles, *c—f* and *a* perianth-segments, see further the text); *F* female flower with two carpels; *G* female flower of the common type; *H* ovary of the same flower in longitudinal section, more enlarged. *A, F, G* about × 5, *B—E* and *H* about × 15.

leaves (*a, c, d, e*) and two outer (*f* and *g*). One of the stamens (with a short filament) stands further in than the outer perianth-leaves, but quite on a level with the inner; the other (without filament) is also placed in the margin of the flower. They represent no doubt transformed perianth-lobes. Quite similar conditions are met with in *Juglandaceae*, and within *Myricaceae* the corresponding transition between bracteoles and stamens is found.

Concerning the structure of the pistil it has been supposed on account of the peculiar position of the carpel — the ventral suture and the flattened stigmatic surface turned to the bract — that it has developed from a bicarpellary pistil, where the one carpel has disappeared through reduction; ABBE and EARLE (l.c.) state that there are also some details in the vascular system that may be interpreted as relics of such a development; these authors hold it probable that the bicarpellary pistil has been apocarpous. A proof that the pistil was originally bicarpellary is present in a case observed by the present author, where in one flower there was actually a pistil with two carpels (Fig. 26 *F*). These were here median, with a common ovary and with two style-branches, as is often to be found in other *Amentiferae*. The general type must have arisen by the anterior, abaxial carpel having been suppressed.

The single ovule has a position (pendulous, epitropous on the ventral side of the carpel, rather high up) which approximates that occurring in *Fagales*. According to ABBE and EARLE (l.c.), there is anatomical evidence that earlier there was (at least) two ovules on the placenta, thus a correspondence to the conditions in the *Fagaceae* and probably the original condition within *Betulaceae* and *Corylaceae*. In the occurrence of two well-developed integuments (PFEIFFER, 1912) the embryology agrees also with *Fagales* (and certain *Salicales*). The embryology offers otherwise, according to the investigation of PFEIFFER (l.c.), no especially remarkable features. PFEIFFER thinks there are some resemblances to the Gymnosperms in the deep immersion of the embryo-sac in the nucellus and in some other details, in the same way as other *Amentiferae* are known to show some agreements with them; no pronounced similarities to the Gymnosperms seem however to be educible from the account.

Concerning the taxonomic position of *Leitneriales* opinions have been to a high degree divergent. ABBE and EARLE (1940) give an account of different theories and think there is no reason for referring the order to *Amentiferae*, as is often done because of the catkin-like inflorescence; they regard this group on the whole as heterogeneous and unnatural. It is then however to be observed that these authors assign *Garryaceae* also to *Amentiferae*, a family that has quite another systematic position, and further that they regard the pistil of *Leitneria* as probably arisen from an originally apocarpous one, and the perianth of the female flower as bicyclic. It must be admitted that in the anatomy of the vegetation organs (the secretory passages of the stem and leaves, the structure of the bark, see TRELEASE, 1895) there are considerable deviations from the common conditions of the *Amentiferae*, both with regard to the floral organization, which must be of decisive importance in these relationships, the order can apparently very well be fitted into the group. We have in *Leitneria* simply built flowers, lacking perianth or having an inconspicuous perianth of irregularly arranged, scale-like leaves of varying number, which are reminiscent of bracts and not of reduced perianthial circles. In the male flower there is clear evidence that the flower has arisen through reduction of an inflorescence, and the scale group of the female flower must be considered to indicate the same origin, if compared for instance with *Myricaceae*. The axis of the flower is moreover fused with the bract and often unilaterally extended (see Fig. 26 *E*), as is usual within *Amentiferae*, and the gynoecium agrees in its original structure with the conditions in the group. In the most essential floral morphological conditions, thus, the order apparently attaches itself to the *Amentiferae*, and should therefore be referred to this group.

On a comparison of *Leitneriales* with other *Amentiferae* orders it must be said that the greatest agreements are found with *Juglandales*, especially the family *Myricaceae*. It has already been pointed out that there are considerable similarities to *Myricaceae* in respect of the perianth of the female flower, the arrangement of the stamens, and — as well as to *Juglandaceae* — in the development of the bisexual flowers; the original arrangement of the carpels and the nature of the fruit (drupe with thin flesh) are reminiscent of conditions in both families of *Juglandales*. Especially in the embryological conditions there are however considerable divergences from *Juglandales*; the ovule has another position, and is furnished with two integuments. In these respects the order comes closer to *Fagales* or *Betulales* and must be regarded as considerably more advanced than *Juglandales*. To *Salicales* as well it has certain similarities; the lobed disc that in many cases surrounds the inner parts of the flower in this order may show likeness to the basally connate perianth of the *Leitneriaceae*. It seems to be most correct to regard *Leitneriales* as a line issuing from the type of *Myricaceae*, where, however, — especially in the gynoecium — there have taken place considerable modifications, which in some cases are reminiscent of other groups of *Amentiferae*.

To the proximity of *Leitneriales* the genus *Didymeles* from Madagascar is sometimes also referred, either as a family of its own alongside *Leitneriaceae*, *Didymelaceae*, (LEANDRI, 1937) or even as a second genus parallel with *Leitneria* (BAILLON, 1877, with some hesitation).

There are also without doubt some resemblances to *Leitneriaceae*. The female flowers consist — as is proved by LEANDRI's (1937) discovery of a second species, *D. Perrieri* —, only of a monocarpellary pistil with an obliquely truncate stigma surrounded by one to four scales, and having an epitropous ovule of similar position as in *Leitneria*. The male flowers differ, it is true, from *Leitneriales* — so far as they are known (*D. madagascariensis* WILLD.); they contain only two stamens with connate filaments, but a similar structure may, as mentioned above, be met with in *Myricaceae*. There are however considerable differences too in the floral morphology. The inflorescence of *Didymeles* is not a catkin. In the pistillate flower there is nothing that indicates the development from bicarpellary to monocarpellary pistil that has without doubt taken place in *Leitneria*; contrary to *Leitneria*, the carpels have the position typical of monocarpellary pistils, with the dorsal side outwards. The scales occurring around the ovary in *D. Perrieri* do not give the impression of being homologous to the somewhat gland-like scales of *Leitneria*; there occur one or two coarse scales beside each other, which rather appear to have arisen by reduction of a more perfect perianth. The appearance of the stigma also differs considerably from the primitive type of *Leitneria*, and the ovule is furnished at the top with an extended neck, possibly to be regarded as a caruncula (BAILLON, 1894—1896, Pl. 308 A). The author therefore holds it probable that the family is not to be brought together with *Leitneriaceae*, but should be excluded from the *Amentiferae*, though it may be difficult to pronounce an opinion on its true affinities.

Order 4. Fagales.

Family Fagaceae.

Important earlier papers: Örsted, 1867 and 1871; Eichler, 1878; Prantl, 1887 and 1889; Čelakovsky, 1890, Schottky, 1912; Troll, 1926; Camus, 1929; Schwarz, 1936; Barnett, 1942 and 1944.

In respect of the inflorescence the genus *Lithocarpus* shows a greater variation than other genera (this also if *Quercus* and *Cyclobalanopsis* should be regarded as a common genus), and several different types may here be distinguished, to which the structure of the inflorescence in the other genera may directly or indirectly be traced back. Firstly there is the difference that while most species have compound catkins, made up of 3—7-flowered or even more-flowered (Schottky, 1912, p. 625) dichasia, in some species the female catkins are simple, the flowers are arranged one by one in the catkin, — this sometimes also being the case with the male flowers (within the *corneus*-group, Schottky 1912, p. 660, further for instance in *L. Curtisii* [1]). The simple female catkins were given by Örsted (1867, 1871) as a character of his genus *Cyclobalanus*; according to later observations, however, this character is not always (for instance not in *L. Cantleyanus*) united with the others denoting this group, though it is common here. Some *Lithocarpus* species have the female flowers now solitary, now in dichasia, for instance *L. Mayrei* and (Schottky, 1912) *L. corneus*; in the former there are on one hand more than three-flowered dichasia, on the other there occur in the same catkin 3-flowered dichasia, 2-flowered, with the terminal flower and one side-flower, the other aborted, and solitary flowers, obviously dichasia, where both side-flowers have failed (large scale groups may sometimes be observed at their places). Some species have the female flowers in three-flowered

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[1] For species belonging to the genera *Lithocarpus* and *Castanopsis*, which are as a rule not included in Rehder's Manual (1940), the nomenclature follows Barnett (1944).

dichasia, but only the terminal flower develops further; at the fruit stage there are only small rudimentary appendages remaining of the two side-flowers and their cupules; this is the case in several species of § *Cyclobalanus* (KING, 1889). Thus, there may — at least in some cases — be found a development from compound to simple inflorescences. Frequently it may be observed that in the three-flowered dichasia the terminal flower is a little later in its development than the side-flowers. This fact may be due either to the inflorescence not being a true dichasium but a botrytic inflorescence, or — as the mid-flower is sometimes (e.g. in *L. litseifolius*) earlier developed than the side-flowers — more probably to a tendency to reduction of the terminal flower, this reduction being complete in other genera. Further in the genus there is a difference between species whose catkins are separated from each other, issuing from the axils of foliage-leaves, and others where the leaves supporting the catkins are reduced and scale-like, so that the catkins constitute a panicle-like cluster, a condition usual within the genus. In one case a true ramification of the catkins was observed by the author, namely in *L. Henryi*, where male catkins, borne in the leaf-axils, bear dichasia both on the upper part of the primary axis and on a number of branches supported by small scales, issuing from its lower part. Contrary to the panicle-like inflorescence groups just mentioned, there is here, thus, a true terminal spikelet in each cluster. The female catkins are unbranched. A ramification of this kind also occurs according to PRANTL (1887) in *Lithocarpus Beccarianus*, according to SCHOTTKY (1912, p. 666) in *L. Harlandii* and occasionally in other species.

As in *Juglandaceae*, it may sometimes occur that two catkins stand in the same leaf-axil, one above the other.

Also in respect of the distribution of male and female dichasia (or flowers) there are different types:

1) In some species all catkins consist of female flowers in their lower and male flowers in their upper part. The two parts may be well separated, as in *L. concentricus* (n.c., *Quercus concentrica* LOUREIRO, Fl. Cochinch., 1790, p. 572), where there is a stalk between them without flowers, or may show an insensible transition from the one to the other, the common condition.

2) In other species only the upper catkins are androgynous in this way, with female flowers below, male flowers above, the lower catkins are entirely staminate. This is a common condition in the genus. In the androgynous catkins there are not uncommonly a few male flowers

also at the base, not only in the upper part, for instance in *L. rufovillosus* (MARKGR.) REHD.

3) Other species have male and female catkins completely separate, the upper containing only female flowers, the lower only male flowers. Examples of this are *L. dealbatus*, *L. fenestratus*, and according to SCHOTTKY, l.c., also the other species of his *dealbatus*-group; yet there may here not infrequently be seen some few male flowers, often undeveloped, in the top or elsewhere in the female catkin.

There are of course transitions between these three types; in the second type, for instance, the upper catkins generally contain only a few female flowers below, but sometimes they are mainly female, only having a few male dichasia at the top and we thus have a transition to the third type.

Originating from the genus *Lithocarpus* there may now, in respect of the inflorescence, be distinguished different evolutionary lines to the other genera of the family. The genera that are closest to *Lithocarpus* are *Castanopsis* and *Castanea*. These two genera attach themselves perfectly to certain types of *Lithocarpus*. *Castanea* has the male flowers arranged in 3—7-flowered dichasia, as many *Lithocarpus* species; the female flowers generally also form such dichasia; in some species, however, they are solitary in the catkin. The distribution of female and male dichasia (flowers) is that of type 2; yet in the somewhat deviating *C. Henryi* there is a tendency for the upper androgynous catkins to be entirely female (CAMUS 1929). *Castanopsis* has staminate and pistillate flowers grouped one to three together (exceptionally four or five, CAMUS, l.c., pp. 356, 441); when the pistillate flowers are solitary, this position has undoubtedly, on account of the conditions that will later on be described for the cupule, here as in *Castanea* arisen through reduction of several-flowered dichasia; presumably the same of course is true of the staminate flowers. The catkins of *Castanopsis* are as a rule (CAMUS 1929) either entirely male or entirely female as in type 3, and often they are united into panicle-like clusters as in *Lithocarpus*. Just as *Lithocarpus*, both genera have stout, erect or somewhat inclined catkins, this being probably connected with the fact that in all three genera insect pollination is probably prevalent (RENDLE, 1925, p. 33).

The species generally called *Castanopsis chrysophylla* (with *C. sempervirens*), which in my opinion — as will later on be further developed — should be regarded as a genus of its own, *Chrysolepis*, differs also in its inflorescence from *Castanopsis*. Both staminate and pistillate flowers are here arranged in 3—7-flowered dichasia (the male dichasia sometimes even up to 11-flowered) and the flower distribution is that of type 2, the uppermost catkins are thus androgynous with female dichasia below, often a few only. In these respects the genus is similar to *Castanea*, but it differs from the latter and is reminiscent of *Castanopsis* by the fact that the catkins are often clustered panicle-like, and a difference from both genera is that the male catkins may be branched, with small side-branchlets at the place of the dichasia, as occasionally may be the case in *Lithocarpus*.

Another difference is the large number of bracteoles occurring in the male dichasia. While the three-flowered dichasia of *Castanopsis* have two bracteoles only (Fig. 27 *A*, cf. Camus, 1929) and the 7-flowered of *Castanea* have six such bracteoles (Fig. by Eichler 1878), in both kinds of dichasia in *Chrysolepis* there are bracteoles at the flowers of the youngest generation too, secondary, tertiary or even quaternary. They are irregularly developed, often quite narrow scales (Fig. 27); sometimes they seem to grow together, but sometimes their number may also be increased, perhaps through division, something that is of interest owing to the parallel that is formed with the cupular scales of the female dichasium.

The genus *Quercus* and the genus *Cyclobalanopsis*, separated from the former, differ more from *Lithocarpus* than the three previously mentioned genera and represent a special line of development. Both male and female catkins are here simple. An exception is afforded only by a species of *Cyclobalanopsis*, *C. argentata* (Korth.) Oerst., which has 3-flowered dichasia in the male catkins (Schottky, 1912); further, in *C. acuta* (Thunb.) Oerst. there occasionally occur such dichasia in the female catkins; these cases, as well as some intermediate forms described below, form a transition between the compound and simple catkins and indicate a development from the former to the latter. Male and female catkins are in *Quercus* and *Cyclobalanopsis* completely separate and the female ones are placed higher, as in *Lithocarpus*, type 3. At the top of the female catkins of *Quercus robur* a transitional flower with rudimentary pistil and one or two stamens may sometimes be seen (further data on this are given below); this may be regarded as indicating that the female catkins have developed from androgynous catkins by reduction of the upper, staminate portion. Only the female catkins are erect in *Quercus* and *Cyclobalanopsis*, generally short and few-flowered; the male catkins are weak, pendulous, which is undoubtedly connected with the fact that pollination is here effected by wind-agency.

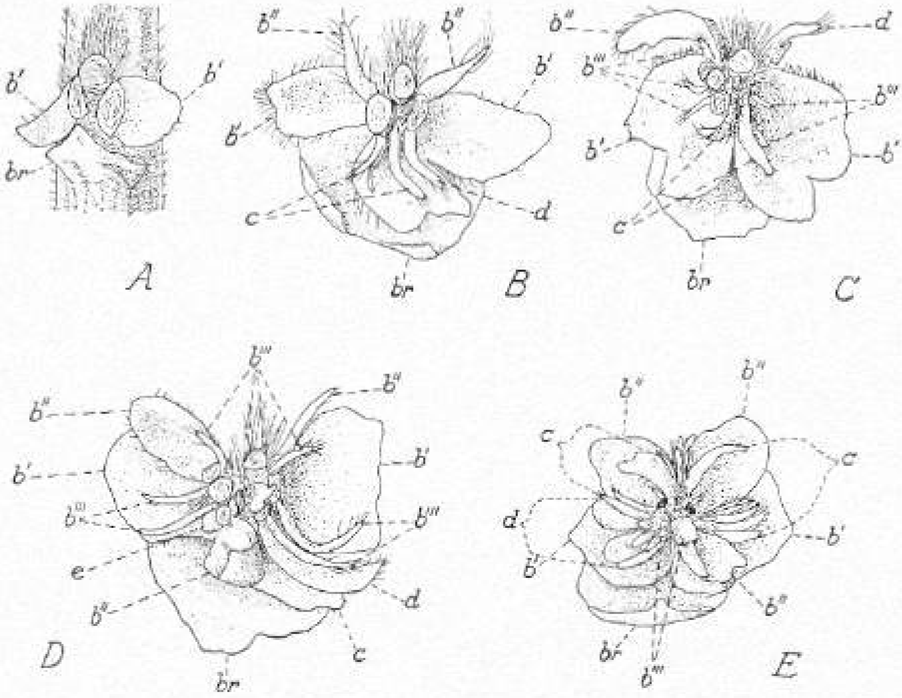

Fig. 27. *A Castanopsis formosana*, male dichasium after removal of the flowers; *B—E Chrysolepis chrysophylla*, male dichasia, the flowers removed, *br* bract, *b′* primary, *b″* secondary, *b‴* tertiary bracteole; *B* 3-flowered dichasium, the one primary bracteole is deeply cleft, the anterior lobe possibly corresponding to an anterior secondary bracteole, in that case *d* is a supernumerary scale, *c* two scales before the left side-flower, probably corresponding to a secondary bracteole; *C* 7-flowered dichasium, *c* erect scales, seemingly bracteoles (tertiary) of the anterior tertiary flowers, while the anterior secondary bracteoles appear to be connate with the primary, *d* a bifid scale apparently composed of a secondary and a tertiary bracteole; *D* 7-flowered dichasium, *c* anterior secondary bracteole, concrescent with the primary, *d* and *e* supernumerary scales, at least *d* has probably arisen through splitting of a tertiary bracteole; *E* 7-flowered dichasium with whole scale groups (*c*) around the posterior tertiary flowers and at the one anterior a group (*d*) that may correspond to an anterior secondary bracteole, while some few scales inside it may correspond to a tertiary. *A* and *E* × 10, *B—D* × 15.

Another line of development — with stronger divergences from *Lithocarpus* — is formed by the genera *Fagus* and *Nothofagus*. Here, the flowers are certainly arranged as a rule in dichasia, but these form no real catkins but stand singly in the leaf-axils. The genus *Nothofagus* never has more than three flowers in the dichasium, not infrequently the number is reduced to two or one. The terminal flower is always present, however. Especially the male dichasia are frequently one-flowered, this being so in *N. cliffortioides* (HOOK. f.) OERST., *N. Menziesii* (HOOK. f.) OERST., *N. Solandri* (HOOK. f.) OERST. etc., while for instance in *N. fusca* (HOOK. f.) OERST. both solitary male flowers and three-flowered dichasia may be observed. Solitary female flowers occur regularly in *N. pumilio* (POEPP. & ENDL.) REICHE and in *N. cliffortioides* they are met with in the rudimentary female inflorescences occurring in otherwise male specimens. In this species they have flattened, 2-winged ovaries, and are obviously the remaining terminal flowers of reduced dichasia. In *N. pumilio*, however, the female flowers (Fig. 28 *B*—*D*) have not only 3 edges and wings, which could be explained on the basis of their having returned to an original state owing to altered space conditions, but frequently four, sometimes even six or seven. The perianth-lobes and the styles may then also be more than is normal in trimerous flowers. Because of these peculiarities possibly a coalescence of two or three flowers into one may be supposed. Perhaps the same is the case with the male flowers of some species which have a large number of stamens (about 30 to 40) and an explanate, many-lobed perianth in the male flower: *N. obliqua* (MIRB.) BLUME, whose deviating male flowers were already mentioned by ÖRSTED (1871, p. 353), *N. Menziesii*, and *N. Moorei* (MUELL.) MAID., which show the same peculiarities (Fig. 28 *E*).

The *Nothofagus* species are in general dioecious. Often, however, there are rudimentary female dichasia in male individuals, such having been observed in *N. cliffortioides* (Fig. 28), where the »dichasia» are one-flowered, further in *N. obliqua, fusca, Menziesii, Solandri, Cunninghamii* (HOOK.) OERST., and *Dombeyi* (MIRB.) BLUME, and sometimes male flowers occur in the female specimens, as in *N. betuloides* (MIRB.) BLUME, where in such a specimen a male flower was observed, apparently normal, but with comparatively small anthers (see Fig. 28 *F*). If male and female flowers occur in the same individual, the male flowers are placed lower down, the female ones higher up on the shoots. Sometimes the flowers or the dichasia are close together and the supporting leaves are at least at anthesis undeveloped: we have then a transition to an androgynous inflorescence, which is staminate below, pistillate at the top, thus the reverse case to the common one in the family (e.g. *N. cliffortioides, N. Solandri*, see Fig. 28 *G*).

In the genus *Fagus* the male flowers are arranged in short, many-flowered inflorescences, the nature of which is somewhat debated.

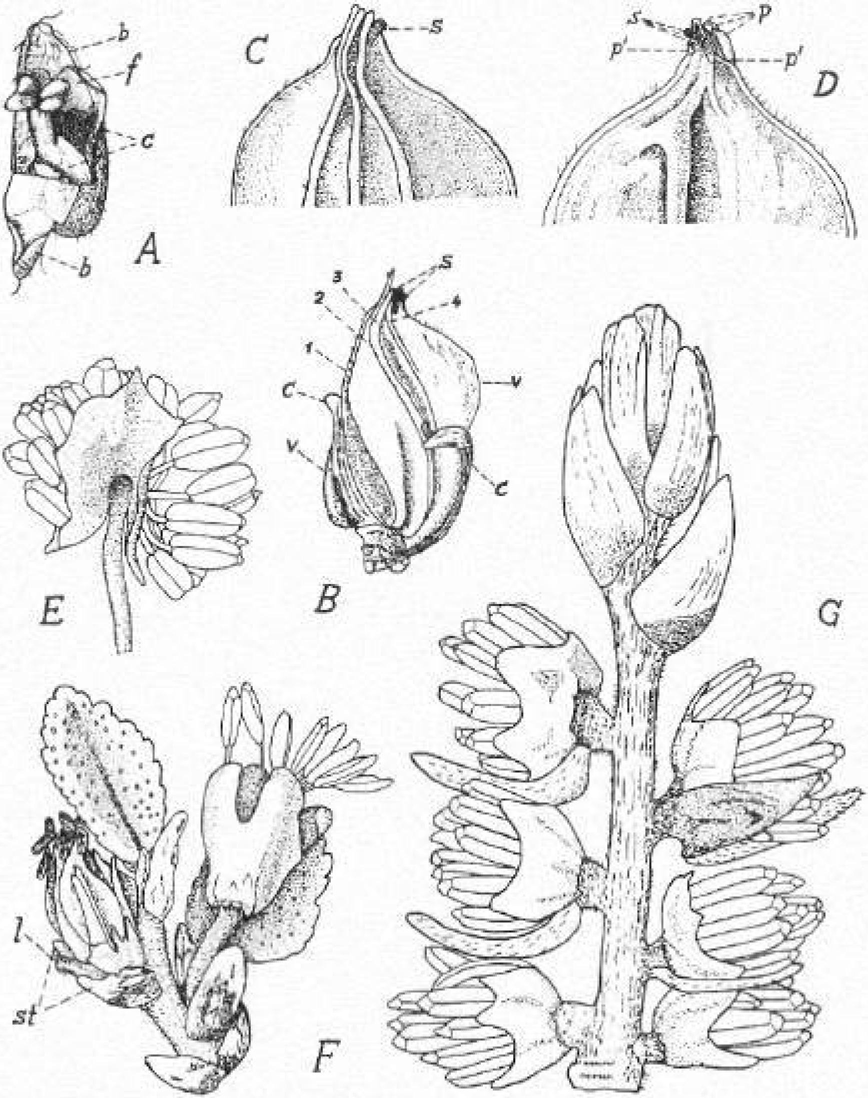

Fig. 28. *Nothofagus*. *A* rudimentary female dichasium from a male specimen of *N. cliffortioides* (*b* primary bracteole, *c* rudimentary cupule, at the one side with some scales [*f*] at the outside); *B* fruit of *N. pumilio* with edges (*v*) upwardly running out in small perianth-leaves and in addition 4 ridges (*1*—*4*), 3 of which (*1*—*3*) run out in perianth-leaves (*c* cupule, *s* stigma); *C*—*D* the same, fruit from two sides with 5 perianth-leaves, 2 small (*p'*) from the edges and 3 larger (*p*) from 3 parallel ridges (*s* stigma); *E* male flower of *N. Menziesii*; *F* branchlet of *N. betuloides* with a male flower and a female dichasium (*st* stipules, *l* broken petiole); *G* branchlet of *N. cliffortioides* with male flowers and above buds with rudimentary female flowers. *A* about × 15, *B* about × 4, *C*—*F* about × 5, *G* about × 6.

According to ČELAKOVSKY (1890), they represent catkins, which have developed from definite inflorescences. He bases this conclusion in the first place on the fact that they are inserted lower on the shoot than the female inflorescences; if male dichasia occur on the same shoot as female ones, they are inserted higher than the latter (for instance in *Lithocarpus* and *Castanea*). PRANTL (1887) is of the opinion that most likely they are dichasia. This author (1887, p. 329—330) found that in *Fagus grandifolia*, a short time before opening of the buds, there might be seen a certain difference between the male flowers in the length of the pedicels and the size of the buds; the development proceeds from the top downwards in two developmental series (in one case three). He also thought that he could always discern a top flower (in some cases observed by the present writer, however, this was lacking). About the same conditions as PRANTL observed in *Fagus grandifolia* may also be found in *Fagus sylvatica* if the beginning of the anthesis is followed in a male inflorescence. A top flower limiting the whole inflorescence is however lacking, at least in most cases. At first two apical flowers open, one in each part of the two-parted inflorescence, and then development proceeds downwards in each part, quite as in a cyme. The inflorescence might then be supposed to be a catkin made up of two dichasia. This is, however, in conflict with the fact that according to PRANTL a terminal flower may exist in *Fagus grandifolia*, which is confirmed by ČELAKOVSKY (1890), who states that he has seen an apparently terminal flower both in *Fagus grandifolia* and *sylvatica* (p. 156). In my opinion there is a complete parallelism with the female inflorescence, where the terminal flower is as a rule aborted, but exceptionally occurs, more or less rudimentary. In the female inflorescence (of *Fagus sylvatica*) the number of flowers is not infrequently larger than two — especially in certain trees — through development of additional side flowers (Fig. 29). Each of the two commonly occurring flowers may be furnished with two side flowers and these in their turn may have one or two side flowers developed, so that the number in the one half of the inflorescence is 5—6, almost as great as in the staminate one, where it is generally about seven or even more. Transitions also occur between male and female inflorescences; the outer flowers of these or some of them are staminate, the inner are pistillate. In the author's opinion, thus, the male flowers as well as the female flowers are arranged in two-parted dichasia, where the terminal flower is as a rule absent. With regard to ČELAKOVSKY's argument as to their position, which seems to be well-founded, the conclusion is to be

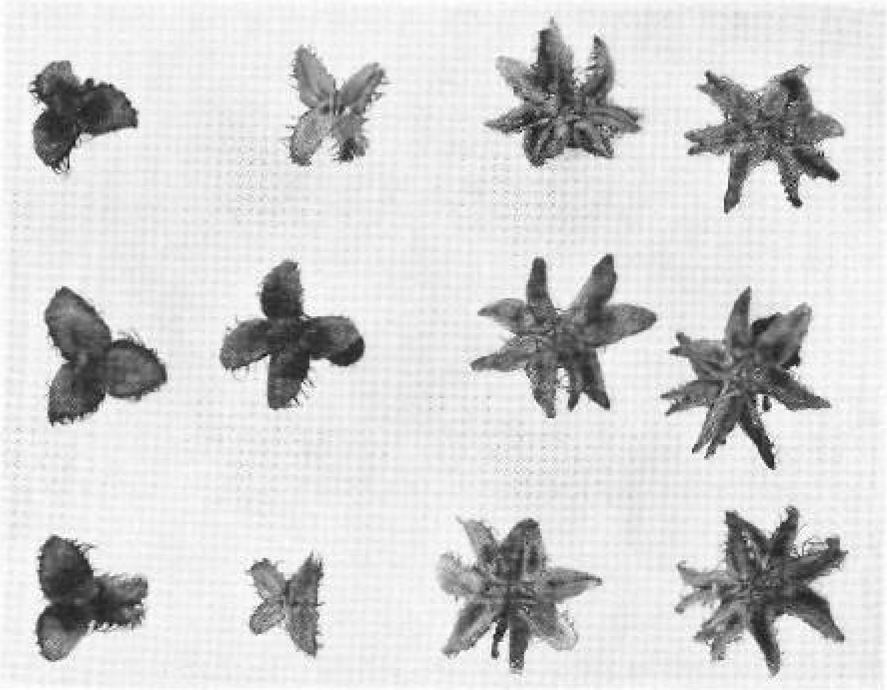

Fig. 29. *Fagus sylvatica.* Cupules with one flower and three lobes (to the left), with terminal flower present, more or less rudimentary (row 2 from the left), with 2 secondary flowers and 4 tertiary flowers and eight-lobate cupule (row 2 from the right), and with a larger number of flowers and lobes (to the right).

drawn that in *Fagus* as well as in *Nothofagus*, where the arrangement of staminate and pistillate dichasia is the same, both the male and the female catkin are reduced into a single dichasium.

The inflorescence of the *Fagus* group thus seems to have arisen through strong reduction from one of the inflorescence types occurring in *Lithocarpus* which have been signified above as types 2 and 3, where the lower catkins are wholly staminate, the upper pistillate or pistillate below. As there sometimes occur in *Fagus sylvatica* some male flowers outside the female ones in the female inflorescence — as also may be the case in *Castanea* —, it seems most likely that the catkin type from which the *Fagus* type derives its origin has been built as in *Castanea*, i.e. the upper catkins have been androgynous and only at the base have they had a few female dichasia (or a single one), above these have they had male dichasia and, at the limit between the male and female, possibly androgynous dichasia, in the same way as such may occur there in *Castanea*.

The cupule characteristic of *Fagaceae* is of two types, between which however there are some transitions. The cupule of *Lithocarpus* and the *Quercus* group is one-flowered, open above and not bursting, that of *Castanea*, *Fagus*, and *Nothofagus* contains more than one flower and opens in a determinate number of lobes at maturation of the fruit. The genus *Castanopsis* forms a transition between the two types: the cupule is here uni- or pluri-florous and opens irregularly. Through PRANTL's (1887) investigations of *Lithocarpus* it was made clear that the cupule is here a stem-structure and is not — as assumed earlier — made up of bracts; the bracts, or bracteoles, may here be observed outside the wall of the cupule. None the less, even in modern works (e.g. KARSTEN, 1936) the view is advanced that the cupule of *Fagus* and *Castanea* is formed by bracts, thus not homologous to the other types. As early an author as ČELAKOVSKY (1890), however, showed by investigations of beech-cupules with supernumerary flowers and lobes that the lobes do not here correspond in number and position to bracts; according to him, the bracts may instead be recognized, in *Fagus* as well as in *Castanea* and *Nothofagus*, among the lowest scales of the cupule, which he regards as a stem-structure. For the stem nature of the cupule there also speaks the fact that flowers and fruits often emanate high up on the wall of the cupule (*Fagus*, *Castanopsis*) or at the tip of the lobes (*Fagus*), which especially happens when the number of flowers is greater than normal, as well as the circumstance that at an early stage in *Fagus* a secondary bracteole may sometimes be observed outside the cupule (see Fig. 33 *d*); in *Castanea* all the four secondary bracteoles are at early stages discernible in the 3-flowered dichasia. There also occur transitions between male and female inflorescences, where the flowers are partly staminate with pistil-rudiments and where the reduced cupule consists only of an enlargement of the peduncle, with scales on the surface, from which the flowers emanate (Fig. 30). Undoubtedly the cupule is a stem structure in the *Fagus* and the *Castanea* groups as well, quite homologous to the corresponding structures in *Lithocarpus* and *Quercus*; as mentioned above, transitions between the two types are also present, viz. in *Castanopsis*.

In *Lithocarpus* and the *Quercus* group the cupule is still undeveloped at anthesis; the flowers are then surrounded only by a crowd of scales and not until after the flowering does the stem part bearing the scales grow up around the ovary as a cup, the scales being then removed to

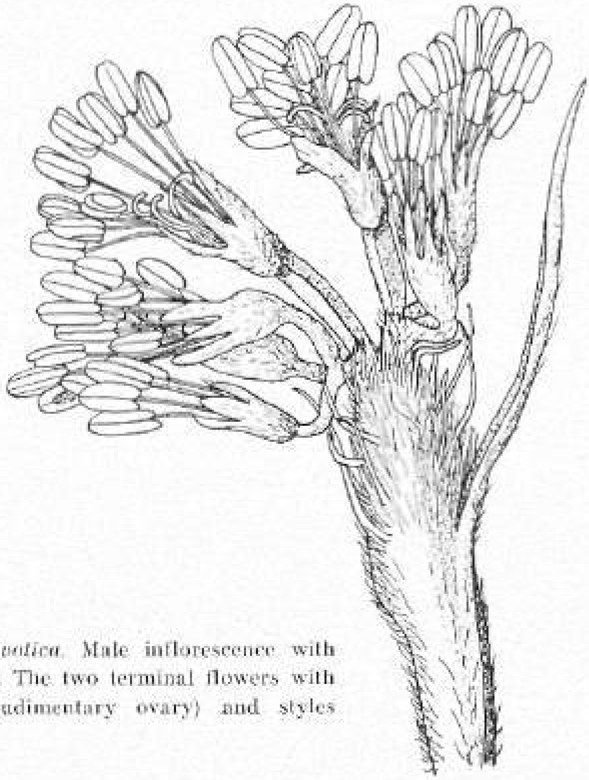

Fig. 30. *Fagus sylvatica*. Male inflorescence with rudimentary cupule. The two terminal flowers with triangular stalk (rudimentary ovary) and styles developed. × 6.

the outer side of this cup. In *Fagus* and *Castanea* the cupule is already developed at anthesis. This must be considered to indicate that the cupule of the latter genera is of a more derived type; the cupule is known to be a special structure for the family *Fagaceae*, developing within the family, and then that type should be more original which is undeveloped at an early stage, that one more advanced which shows a greater differentiation at a corresponding stage.

The primordiality of the cupule type of *Lithocarpus* is also indicated by the great variation occurring within it. Not only is there a difference between species having distinct scales on the cupule and others having annular lamellae, and between species where the cupule covers the fruit completely and others where it only surrounds its base. There is also the important difference that in one group, sect. *Synaedrys*, the cupule is fused with the fruit-wall and in some species of the section (e.g. *L. Maingayi*) is asymmetrically developed. The section *Corylopasania* differs by the cupule being protracted into a long, tubular covering, considerably longer than the glans, reminiscent of certain *Corylus* species.

Other circumstances, too, speak for the cupule type of *Lithocarpus* (which is almost unchanged retrieved in *Quercus* and *Cyclobalanopsis* respectively) being the more original. It is hardly possible to derive the *Lithocarpus* cupule from *Castanea* or *Castanopsis*, whereas it is very easy to imagine a development from *Lithocarpus*, sect. *Pasania*, to the *Castanea* as well as to the *Fagus* group, as was already demonstrated by PRANTL (1887). In the *Lithocarpus* section just mentioned the female flowers are arranged in cymes, generally 3-flowered, sometimes with more flowers, and the cupules are close to each other and frequently coalescent so that the separating walls between the fruits fuse with each other. The separating walls are often thin. Supposing that these walls entirely disappear, then the cupule type arises that is found in *Castanopsis*. That such a development has actually taken place, is shown by the fact that some *Castanopsis* species with two or three fruits in the cupule show, between these, remnants of the walls, which have thus not completely disappeared, e.g. *C. Hullettii* among species with cupule and fruit partly connate (Fig. 31 *b*) and *C. Fabri* (Fig. 31 *a*) among other species.

Hence, as regards the cupule, the genus *Castanopsis* is closely attached to *Lithocarpus*. Some species, as *C. cuspidata* and *lanceaefolia*, are on the border-line between the two genera and have sometimes been referred to the one, sometimes to the other of them. Other species, BARNETT's (1944) »Group of *C. rhamnifolia*«, have the cupule completely fused with the gland, just as the section *Synaedrys* within *Lithocarpus*, while in another group, BARNETT's *C. inermis*-group, the cupule is only partly adnate and the fruits are either partially separated by walls, as in the *C. Hullettii* mentioned, or totally without separating walls, as in *C. inermis*. With regard to the course of development there are however some unexplained details. The cupule is in *Castanopsis* frequently 4-parted, with four spiny areas, a condition that is still more pronounced in *Castanea*, § *Eucastanon* DODE. The cause of this 4-partition has been the object of discussion. According to ČELAKOVSKY (1890), each of the four parts corresponds to an original cupule, in *Castanea* as well as in *Castanopsis* (and the *Fagus* group); he imagines a 7-flowered dichasium as starting-point, the four tertiary flowers of which take part with their cupules in the formation of the common cupule, while the primary and secondary flowers are reduced. The supposition might explain the position of the cupule parts and also appears plausible in other respects, but it does not seem to be supported by the actual transitions that may be observed within the genus *Castanopsis*. In the species *C. cuspidata* and *C. lanceaefolia* of the sect. *Pseudopasania* CAM. the observation may in some cases (Fig. 31 *f*) be made that the cupule, though containing one flower only, is obviously 3-parted. The roundedly triangular cupule has the scales arranged in three systems of curves, above each there is a rounded bump at the mouth, and between the two anterior ones there is a sharp vertical limit. Undoubtedly such a cupule is formed by the union of three, one posterior (mid-)cupule and two anterior (side-)cupules.

The same 3-partition of the cupule is refound in several other species. *Castanopsis Delavayi*, for instance, has two spiny areas on the anterior part of the cupule, each with a separate system of curves, divided from each other by a feeble, vertical border-line (Fig. 31 *e*). At the side of the axis there is a third part with small, fleshy scales, arranged in approximately straight lines (Fig. 31 *d*). In *C. Eyrei* (Fig. 31 *c*) the cupule is rather bilabiate with a shorter, scaly posterior lip and a longer, spiny anterior one, which is 2-cleft at the tip and has the spines arranged in two curve-systems. A similar 3-partition is found in several other species, though the posterior, scaly part is generally still more reduced and as a result the cupule gets a still more irregular shape. In *C. echidnocarpa* DC., which according to CAMUS (1929) belongs to the same section as *C. cuspidata*, *Pseudopasania*, there may now further be observed a transition from the 3- to the 4-parted cupule. It is here still possible to see the 3-division of the cupule, perhaps best in the younger one (Fig. 31 *h*), but also in the older (Fig. 31 *g*). There are a minor posterior part, which bears small scales only, and two larger anterior ones, separated by a sharp boundary. These two anterior parts, however, do not develop quite regularly. At an earlier stage (Fig. 31 *h*) it may be seen that the first spines arise on two separate spots of each part and that the cupule is almost pentagonous. In a later stage (Fig. 31 *g*) the now fully developed spines are arranged in continuous curves at the base of each part, but they are more weakly developed at the middle of the curve, and higher up the curves are bent upwards at the middle and here bear scales instead of spines. The two lateral parts become in this way divided into four; in other species this division is more sharply pronounced, and as the posterior (mid-)cupule becomes more and more reduced, the common cupule becomes more or less 4-divided. The four parts thus correspond to two bipartite, lateral cupules. The partition is probably in some way connected with the

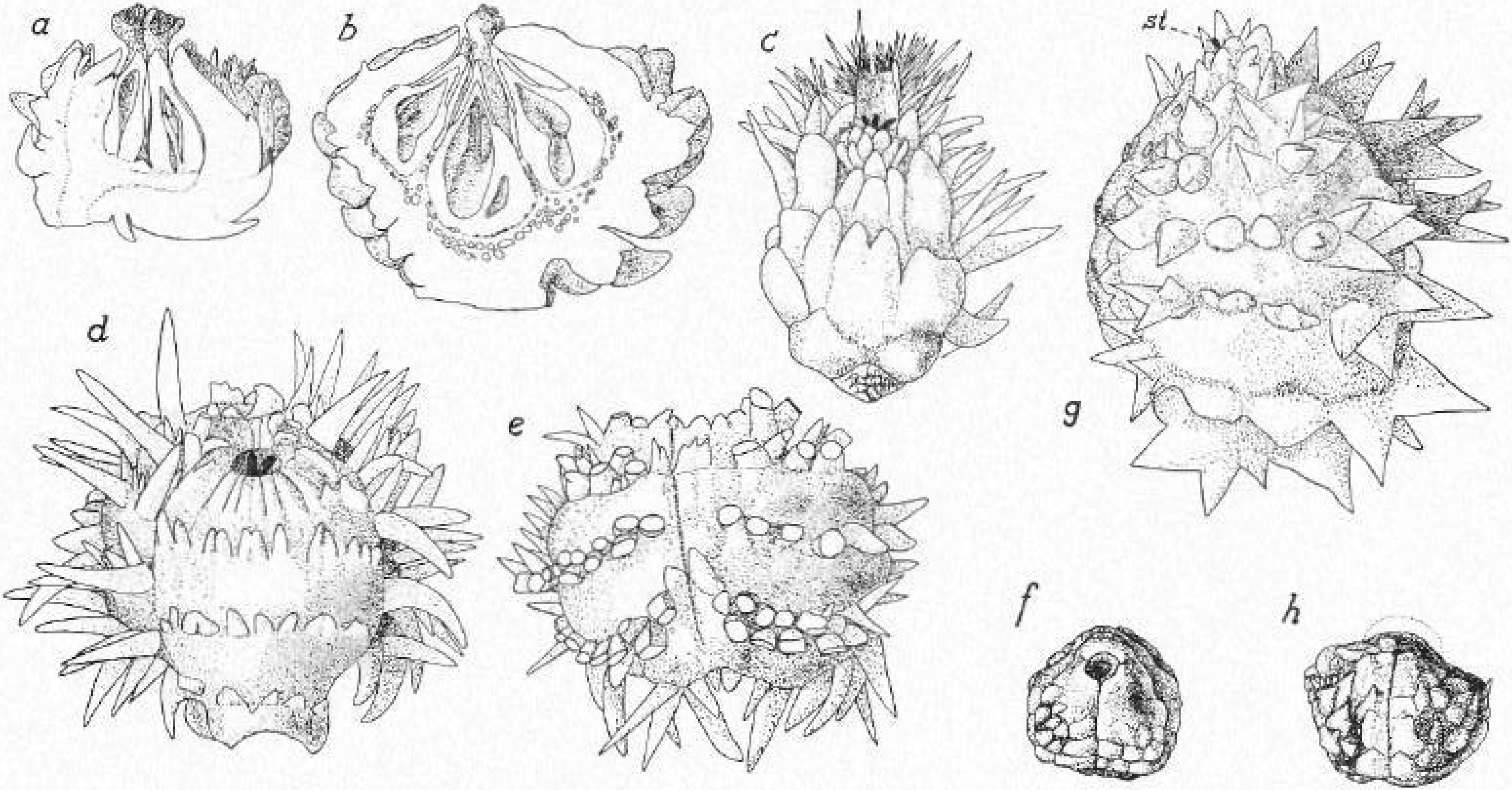

Fig. 31. *a* young cupule of *Castanopsis Fabri* in longitudinal section; *b* the same of *C. Hallettii*; *c* young cupule of *C. Eyrei*, from the axis; *d* cupule of *C. Delavayi*, from the axis; *e* the same in front view; *f* young cupule of *C. cuspidata*, from in front; *g* cupule of *C. echidnocarpa* at fruit stage, from the side (*st*=stigma); *h* young cupule of the same species in front view. × 5.

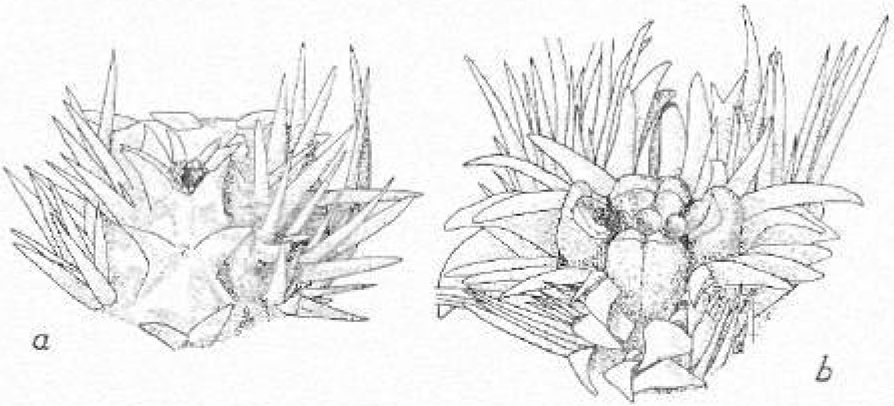

Fig. 32. *a* cupule of *Castanea floridana*, the upper part, from in front; *b* the same of *C. mollissima*. About × 4.

opening of the cupule by longitudinal fissures through the middle of the part-cupules (and in addition at the border between the two anterior ones).

The cupule of the genus *Castanea* resembles strongly that of *Castanopsis* in its structure, but it differs by being symmetrical, whereas that of *Castanopsis* is asymmetrical, which is used as a distinguishing character between the two genera. This is without doubt connected with a somewhat deviating origin.

Firstly, the cupule is here not 3-parted, but 4- or sometimes 2-parted. In the sect. *Eucastanon* there are four diagonal spiny areas that have narrow scaly stripes between them with opening fissures, which has given support to the assumption that four cupules are involved here. In *C. floridana* (Fig. 32 *a*) the cupule consists of four approximately equal parts, two median scaly and two transverse spiny ones, and of a weakly 4-parted swelling at the point of the cupule. In *C. mollissima* (Fig. 32 *b*), which is close to *C. sativa*, the cupule has as in several other species a prolonged, spineless point, which is here very sharply divided into two median and two transverse parts (the posterior median is sometimes a little larger than the anterior). Such a 4-partition is also discernible in *C. sativa* at early stages and then, instead of the narrow, scaly median stripes that later on may be observed, there are two broad median parts, while the two lateral parts are indistinctly divided (Fig. 33 *a*—*c*). In early stages of development, thus, and in a species such as *Castanea floridana*, which is reminiscent of

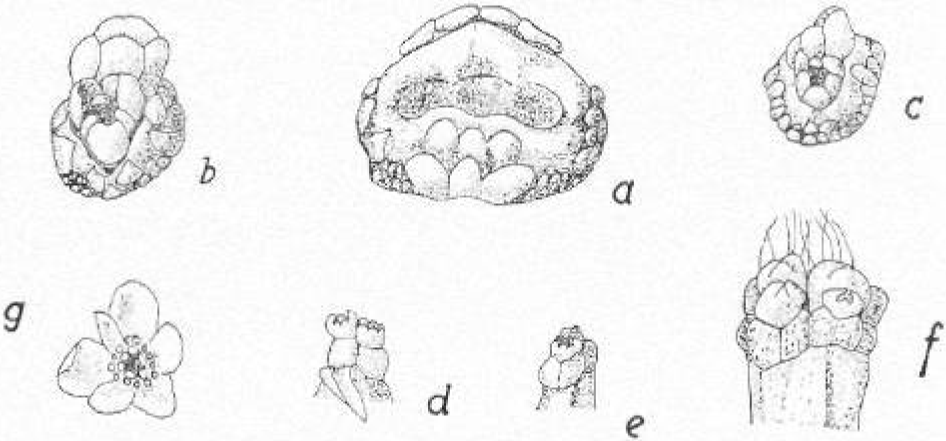

Fig. 33. *a* cupule-primordium of *Castanea sativa* in front view, the 3 flower-primordia and the 7 bracts removed; *b* do., from the side, with remaining flower-primordia; *c* do., a somewhat earlier stage; *d* cupule-primordium of *Fagus sylvatica* at an early stage of development (Aug. 20th), from behind, a secondary bracteole is visible; *e* the same from the side; *f* cupule-primordium with 6 flowers from the same specimen; *g* flower-primordium from a female dichasium of *Castanea sativa* with carpel- and stamen-primordia. About × 20.

Castanopsis, there are two comparatively broad median parts of a nature differing from the two transverse ones, which latter in the course of development are divided into four. The position shows that it cannot be a question of four cupules, but of two lateral ones and a third median, 2-divided (cf. the diagrams in Fig. 35). In the same way as in *Castanopsis* the mid-cupule is more or less reduced, especially below, whereas at the tip it may be very conspicuous (e.g. in *C. mollissima*). If the cupule is 7-flowered instead of 3-flowered, each of the four tertiary flowers is surrounded by a rounded swelling=part-cupule. This condition is figured by Baillon (1876) and may possibly have contributed to Čelakovsky's view of the matter. Yet it is by no means so, that on first being laid down the cupule is always 7-flowered; it is often 3-flowered; and, as stated by Baillon, in the 7-flowered cupules the central part-cupule persists; the part-cupules of the secondary flowers may seemingly do so, too.

The cupule that is found in the genus *Chrysolepis* (Fig. 34 *a*—*e*) differs both from that of *Castanopsis* and from that of *Castanea* by being open above. Further, at an early stage, at flowering time, the separating walls between the part-cupules are rather well developed,

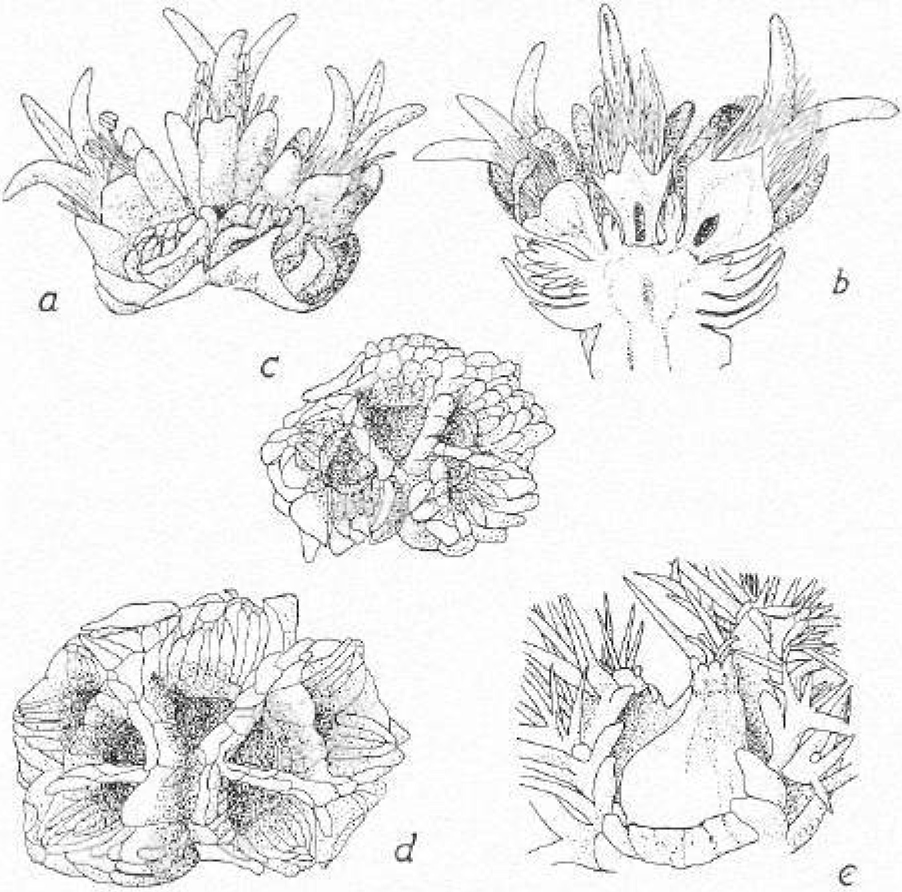

Fig. 34. *Chrysolepis chrysophylla.* *a* 3-flowered female dichasium in front view; *b* the same in longitudinal section; *c* 4-flowered cupule from above, the flowers removed; *d* 7-flowered cupule from above, flowers removed; *e* cupule at fruit stage, longitudinal section. *a*—*d* about × **10**, *e* × 5.

so that the compound cupule is 3—7-chambered, with triangular chambers (Fig. 34 *c* and *d*). A similarity to *Castanopsis* is that the side-cupules of first order meet in front of the mid-cupule (see for instance Fig. 34 *d*). A difference, however, is that the outermost part-cupules (the secondary cupules of a 3-flowered common cupule, the tertiary of a cupule with more flowers) are 2-lobed during the whole development of the cupule, with two lobes that do not shut to the fruit but (Fig. 34 *e*) stand at some distance from it. At maturation only those

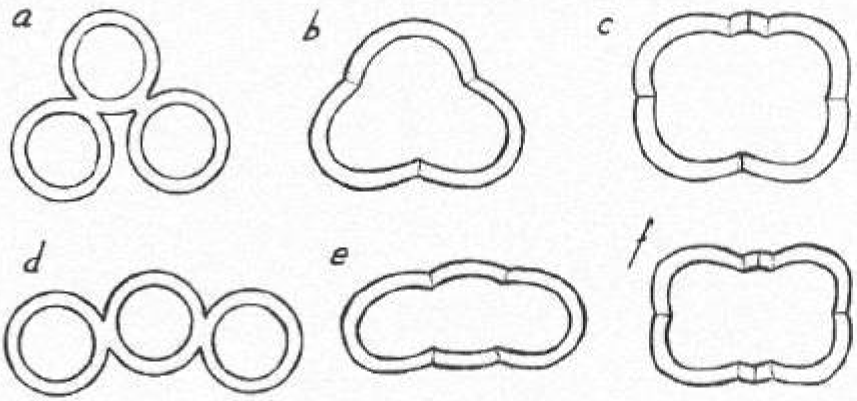

Fig. 35. The derivation of the cupule in *Castanopsis* and *Castanea*, diagrams: *a* and *d* different starting-points within *Lithocarpus*; *b* and *c* development to the cupule-type of *Castanopsis*, either more regularly 3-parted (*b*) or almost 4-parted (*c*) with strong reduction of the original mid-cupule; *e* and *f* development to the cupule-type of *Castanea*, with the reduced mid-cupule divided into an anterior and a posterior part.

valvules appear — in a 3-flowered cupule four — which are formed by the lateral part-cupules; the part-cupule of the mid-flower is here as in other genera strongly suppressed at a later stage. The separating walls between the part-cupules are then also to some extent suppressed; they may partly be grown together with the fruits. Sometimes an undeveloped fruit may be quite encapsulated in the cupule. Characteristic of the cupule of *Chrysolepis* is, further, that the spines are arranged in straight transverse rows and at the lower part of the cupule emanate from lamella-like ridges (somewhat reminiscent of the conditions in some *Nothofagus* species) and that in the margin of the lobes there is a row of scales which are bent inwards over the inner wall (see Fig. 34 *e*). In its cupule *Chrysolepis* thus shows some similarities to *Castanopsis* but also such important deviations from this genus that it must be considered to belong to a parallel line of development.

Within the *Fagus* group (*Fagus* and *Nothofagus*) there might appear to be very good reasons for the supposition that the cupule is formed through the union of four. On the one hand the cupule is here pronouncedly 4-lobed and this 4-partition may also be observed at a very early stage (Fig. 33 *d*—*e*); on the other hand at the appearance of tertiary flowers the cupule lobes of *Fagus* are two-cleft and surround the additional flowers as a bipartite cupule, whereas the secondary flowers then have no other, independent cupule. This may also be observed in both earlier and later stages (Figs. 29 and 33 *f*). It might of course on this account seem well justified to suppose with ČELAKOVSKY that the cupule is built up of the cupules of the four tertiary flowers of a seven-flowered dichasium (such as sometimes occurs in *Lithocarpus* and *Castanea*) and that at the reduction of the tertiary flowers these cupules have been undivided. Yet certain facts speak against such a supposition. Firstly, there sometimes occur more than six side flowers in a cupule of *Fagus sylvatica*: besides the two secondary and the four tertiary flowers there may also occur one to three quaternary ones (Fig. 29, to the right). If we start from a 7-flowered dichasium, we must consequently presume that in some cases there has been an increase, but in most cases a reduction of the number, which does not seem probable. Secondly, both in *Fagus* and in *Nothofagus* it happens that a side flower fails to develop and that the cupule-lobes at the side of the missing flower are united into one, so that the cupule becomes 3-lobed (Fig. 29, at the left); in *Nothofagus pumilio*, as a matter of fact, both side-flowers are regularly absent, the cupule 2-lobed. Thus, if the cupule were formed by four tertiary cupules, this would imply that two such cupules were completely united at the failure of the secondary flowers inside of them, which would not be probable, either. Further, in an early stage of development of the cupule (before it has yet been differentiated, Fig. 33 *d*—*e*) it appears as if there were a greater difference between the two lateral cupule-halves, which may also stand at somewhat different height, than between the two quadrants of the same side; the boundary between these resembles more the longitudinal strip that occurs in the tertiary cupules of a 6-flowered dichasium (Fig. 33 *f*). In the developed cupules, too, it may in *Fagus* and still more in *Nothofagus* be observed that the transverse fissures do not descend so far as the median. All these circumstances (together with the parallelism that exists with the cupule of the *Castanea* group) make it most probable that the cupule of the *Fagus* group is formed by two original cupules, the two secondary cupules, whereas the cupule of the mid-flower, which in the *Castanea* group is reduced, has completely disappeared within the *Fagus* group, just as the mid-flower itself in *Fagus*. Such an interpretation is to a great extent also supported by the similarities that are found to the genus *Chrysolepis*. The *Fagus* cupule may easily be thought to arise from a 3-flowered cupule of this genus through continuing reduction of the central part-cupule and of the separating walls, so that the two lateral, two-cleft part-cupules are left only.

Thus, it appears as if the cupule of the *Fagus* group were a further development of a type that is close to that of the *Castanea* group, especially that occurring in *Chrysolepis*. According to this assumption, the two transverse opening fissures of the *Fagus* cupule would be the mid-fissures of the two part-cupules, and it is then quite a natural thing that these disappear on failure of the flower inside of them. The larger number of flowers and cupules that sometimes occurs would depend upon secondary increase, as a result of which the new flowers, as in *Chrysolepis* (and also *Castanea*), get their particular cupule, here 2-lobed, and the cupules of the mother axis, which in *Chrysolepis* and *Castanea* are more or less reduced, disappear entirely here, in so far as the basal parts of the new cupules, under the attachment of the flowers, should not be considered to belong to these (cf. ČELAKOVSKY, 1890).

A certain reduction of the cupule is noticeable in the genus *Nothofagus*. Thus, in *N. pumilio* it consists of two narrow band-like lobes only, scarcely more than half as long as the fruit (Fig. 28 *B*), and in the rudimentary female dichasia that sometimes occur in male specimens of *N. cliffortioides* the cupule-structures are still more reduced and are smaller than the surrounding bracteoles (Fig. 28 *A*).

The cupule that occurs in the *Quercus* group is closely connected on to that of *Lithocarpus*. The genus *Cyclobalanopsis*, however, is distinguished by the peculiarity that at the point of the fruit there are some annular zones of similar appearance as the lamellae that here occur at the cupule, though more weakly developed (Fig. 36 *a* and *b*). Such structures are generally lacking within *Lithocarpus* § *Cyclobalanus*, which has a similar cupule; only exceptionally were weakly developed rings observed on the fruit of one species, *L. Teysmannii* (Fig. 36 *g*—*h*). At an earlier stage of the fruit development of *Cyclobalanopsis* (Fig. 36 *c*—*d*) it may be seen that these zones are more evenly distributed over the surface of the young fruit; it is not until later that through intercalary growth of the lower part of the fruit they are carried up towards its top. At a still earlier stage, at the flowering itself (Fig. 36 *f*), they are not yet discernible, but the innermost lamellae of the cup are then not developed either. When these lamellae are formed, the zonation of the ovary begins to appear (Fig. 36 *e*). It may accordingly be said that the zones of ovary and fruit form a direct continuation of the lamellae of the cupule in their location and time of development; certainly they are homologous with these. This speaks very strongly in favour of the cupule of *Cyclobalanopsis* being a further development of that occurring within *Lithocarpus* § *Synaedrys*, where

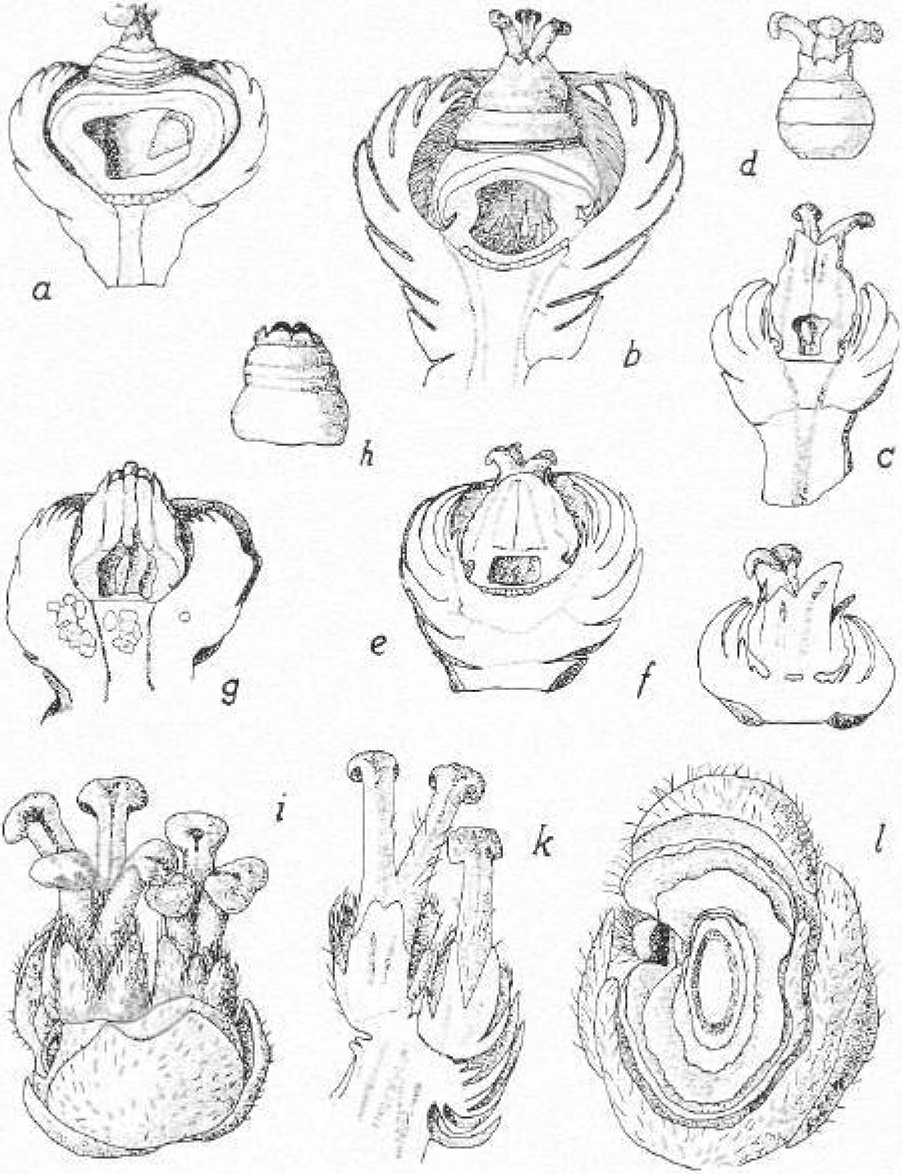

Fig. 36. *a* young fruit with cupule in longitudinal section of *Cyclobalanopsis myrsinaefolia* (somewhat obliquely cut, so that the whole apex of the fruit is visible); *b* the same of *C. acuta*; *c C. Blakei* (SKAN) SCHKY., section of young cupule; *d* the same, flower a little after anthesis in side view; *e*—*f* sections of cupules of *C. glauca*, *e* with young fruit, *f* with flower; *g Lithocarpus Teysmannii*, young fruit with cupule in longitudinal section; *h* the same, the fruit from the side; *i* 3-flowered dichasium of *Cyclobalanopsis acuta* from the base of a catkin, the one flower (to the left) fallen off; *k* the same in longitudinal section; *l* cupule of *C. acuta* from above (at anthesis), the front side below. *f, i, k* × 10, *l* × 15, the others × 5.

the cupule is fused with the fruit, this development having implied that its upper part, still connate with the fruit, is here reduced, while the lower part is carried up by an annular growth of the axis, which surrounds the base of the fruit as a cup without being adnate to it. That such a development takes place within the genus *Lithocarpus* too, is suggested by the conditions mentioned in *L. Teysmannii*. Thus, the cup surrounding the *Cyclobalanopsis* fruit does not seem to be homologous to the cupule of *Lithocarpus* § *Synaedrys* or the cupule of the genera *Castanopsis, Castanea, Fagus*, and *Nothofagus*, but only to its lower part. The same is true about the genus *Quercus*, whose cupule is undoubtedly on the whole a further development of the *Cyclobalanopsis* type; within the section *Erythrobalanus* a feeble ring may sometimes be seen at the point of the fruit (cf. SCHWARZ, 1936), indicating a development from a *Cyclobalanopsis*-similar type through continuous reduction.

In one of the 3-flowered dichasia that sometimes occur in *Cyclobalanopsis acuta* (Fig. 36 *i, k*) it was observed that the three cupules — about equally developed — showed small gaps between the flowers, so that these met with each other. This indicates that in this genus a coalescence takes place of three cupules into one. This is possibly also supported by the fact that *C. acuta* generally has cupules that are much protracted along the length of the main axis, as the base areas of the female dichasia of for instance *Lithocarpus fenestratus*, and that the cupule may be divided into a minor, posterior and a larger anterior part (Fig. 36 *l*).

The perianth of the male flower is within the genus *Lithocarpus* of somewhat varying development, sometimes expanded, with the lobes more free from each other, sometimes more cup-like or campanulate (Fig. 37 *A*) and more strongly connate, sometimes more regularly radial, sometimes protracted in length, somewhat reminiscent of *Juglandaceae* (e.g. in *L. glaber*). The other genera agree more or less completely with these different types. *Castanopsis, Chrysolepis*, and *Castanea* have a little varying perianth with expanded, rather little connate perianth-leaves of regular development. As in *Lithocarpus*, the leaf-number is generally six, and there may often be discerned three outer and three inner leaves, which may also be of different shape and size. The genera *Fagus* and *Nothofagus* on the other hand have a cup-like or campanulate, more strongly connate perianth; a deviating development is only shown by those *Nothofagus* species whose flowers, as mentioned above, have probably arisen through coalescence of three (see page 82).

Within the *Quercus* group the perianth of the male flower is more or less irregularly developed. This irregularity does not only appear within the genus *Quercus*, but — quite contrary to what is generally stated (cf. SCHOTTKY, 1912, SCHWARZ, 1936) — in a high degree also within the genus *Cyclobalanopsis*. In for instance *C. acuta* a well-developed staminate flower may consist of a large number of stamens (at least up to 17) and a somewhat smaller number of scales of varying size, partly amidst the stamens; these may often be observed to spring from the axil of a scale (Fig. 37 *B*). And in *C. myrsinaefolia* (BL.) SCHKY. the scales are frequently also intermingled with the stamens in a way reminiscent of certain *Myrica* species. The origin of these flowers is elucidated by some observed flower forms in *C. myrsinaefolia*. Sometimes it may here be observed (Fig. 37 *D*) that the so-called flowers are composed of three, one mid-flower, which is somewhat higher inserted on the main axis, and two side-flowers, thus a typical *Fagaceae*-dichasium. The boundaries between the part-flowers disappear, however; Fig. 37 *D* shows that the one side-flower (at the right of the figure) has a strongly reduced perianth, Fig. 37 *E* illustrates the coalescence of the mid-flower with the one side-flower (at the left of the figure), Fig. 37 *F* shows that a corresponding union takes place with the other (at the right of the figure), and in the flower reproduced in Fig. 37 *G* there is only an inconsiderable remnant left of the perianth leaves that have separated the original part-flowers from each other. Undoubtedly the flower of *C. acuta* is the result of a similar development, though at the same time a certain recombination of the floral parts apparently takes place here. At a greater reduction there may appear in those same species flowers of the simple type that is reproduced in Fig. 37 *C* and *H*. In other species, e.g. *C. glauca* (THUNB.) OERST., all flowers are of a similar simple structure, in the species mentioned often with 5 perianth leaves and 5 stamens (Fig. 37 *I*). Within *Quercus* the staminate flowers do not, either, show any transitions to dichasia as in the two *Cyclobalanopsis* species mentioned, but certain conditions argue in favour of these flowers — as well as the simply-built *Cyclobalanopsis* flowers — representing a further step in the development that is observed in these species. In *Qu. semecarpifolia* (Fig. 37 *K*—*L*), *castaneaefolia* (Fig. 37 *M*), and *serrata* (Fig. 37 *N*) the perianth is divided into a few, often three, large lobes, which are somewhat incised in the margin and which, if three in number, sometimes have a position cor-

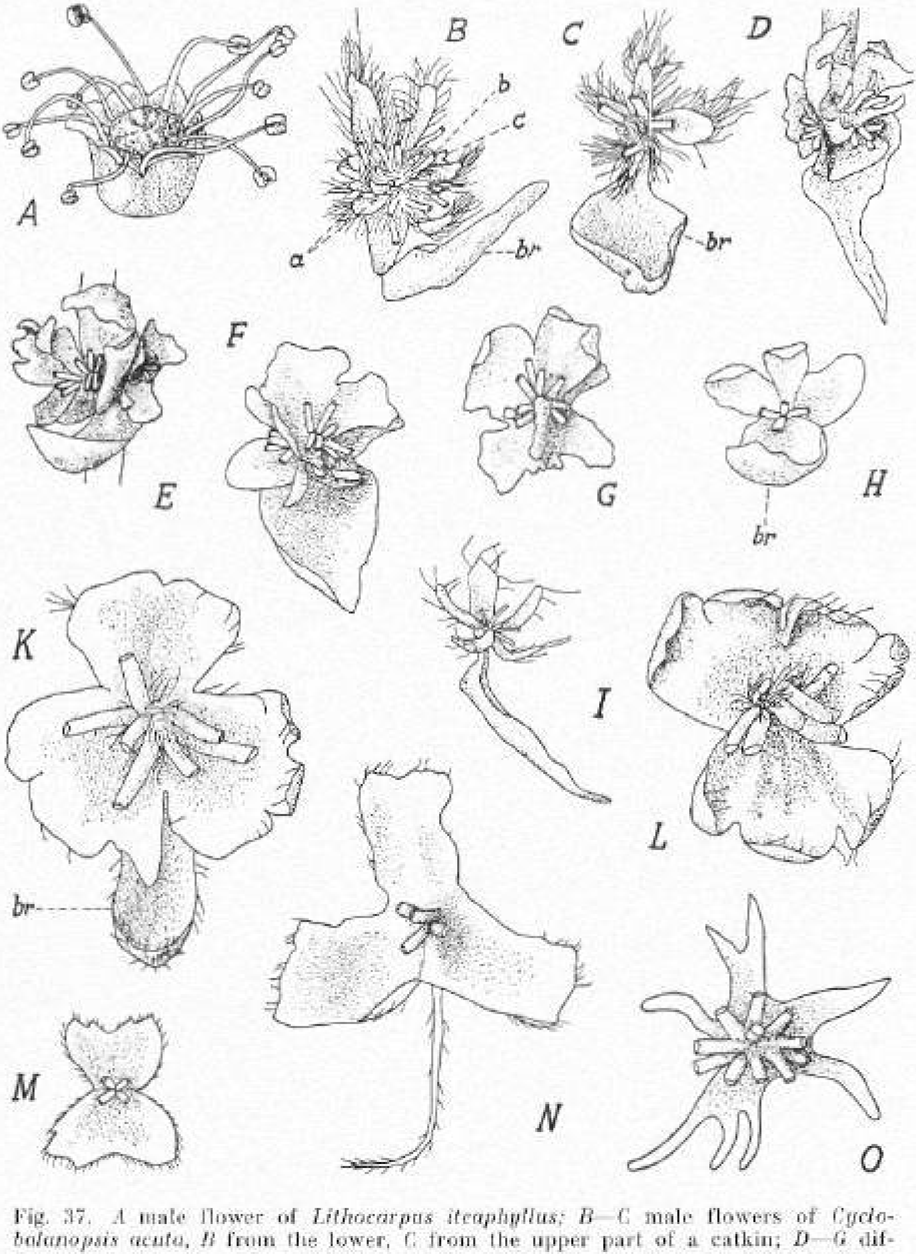

Fig. 37. *A* male flower of *Lithocarpus iteaphyllus; B—C* male flowers of *Cyclobalanopsis acuta, B* from the lower, *C* from the upper part of a catkin; *D—G* different stages in the coalescence of the male flowers in a dichasium of *C. myrsinaefolia*; *H* flower from the upper part of a catkin of the same; *I* male flower of *C. glauca*; *K—L* male flowers of *Quercus semecarpifolia*; *M Qu. castaneaefolia*, *N Qu. serrata*, *O Qu. Frainetto*, male flowers. *br* bract, *a, b, c* stamens springing from the axils of adjacent scales. About × 10.

responding to the flowers of a three-flowered dichasium (Fig. 37 *K* and *N*). These flowers are very reminiscent of the type occurring in *Cyclobalanopsis myrsinaefolia*. Other species have a larger number of narrower lobes, of varying number, shape, and size, often lobed in their turn (e.g. *Qu. Frainetto*, Fig. 37 *O*, also the above-mentioned *Cyclobalanopsis glauca*), and are more reminiscent of *C. acuta*; as in this species, the number of stamens is frequently somewhat larger than that of lobes, though not twice as large. Thus it is highly probable that, on the whole, the male flower of *Cyclobalanopsis* and *Quercus* has arisen through the development that may be followed in for instance *Cycl. myrsinaefolia*, viz. through coalescence of the flowers of a 3-flowered dichasium, such as occurs within the genus *Lithocarpus* and also in a *Cyclobalanopsis* species, *C. argentata*.

The morphology of the stamens has not been considered to have any great importance for the systematics of *Fagaceae*. Örsted, thus, who gave an elegant demonstration of the differences in the structure of the pistil in different genera, is of the opinion that the stamens, like the male flowers on the whole, do not show any essential distinguishing features (1867, p. 42; 1871, p. 353). Closer examination reveals, however, that between the larger systematical groups there are very characteristic differences regarding the stamens as well, forming an almost complete parallel to the different types of development of the pistil.

In the genus *Lithocarpus* the anthers (Fig. 38 *a*, *b*) are very small (ca. $^1/_4$ mm long), about as broad as long, emarginate at the base, and the filaments are far projecting, with the tapering top fixed at about the middle of the dorsal side of the anther. The anthers are versatilely attached to the filament; frequently the apex is turned downwards (Fig. 38 *a*). The genera *Castanopsis*, *Castanea*, and *Chrysolepis*, which as to structure of the styles agree almost completely with *Lithocarpus*, have also stamens of the same type (Fig. 38 *c*, *d*, *e*). The anther is here of the same form, dorsifixed, versatilely attached to the far projecting, upwards thinner filament. The only difference, as a matter of fact, is that it is or may be a little larger; yet also here it is very small, scarcely more than a $^1/_2$ mm long. The filament may also be a little broader upwards (cf. Fig. 38 *e'*, *e''*).

In the genera *Fagus* and *Nothofagus* the stamens have quite a different structure. The anthers are here much larger, oblong in form, and basifixed. In *Fagus* they are cordate at the base (Fig. 38 *f*, *g*), in *Nothofagus* (Fig. 38 *h*), where they have a very characteristic

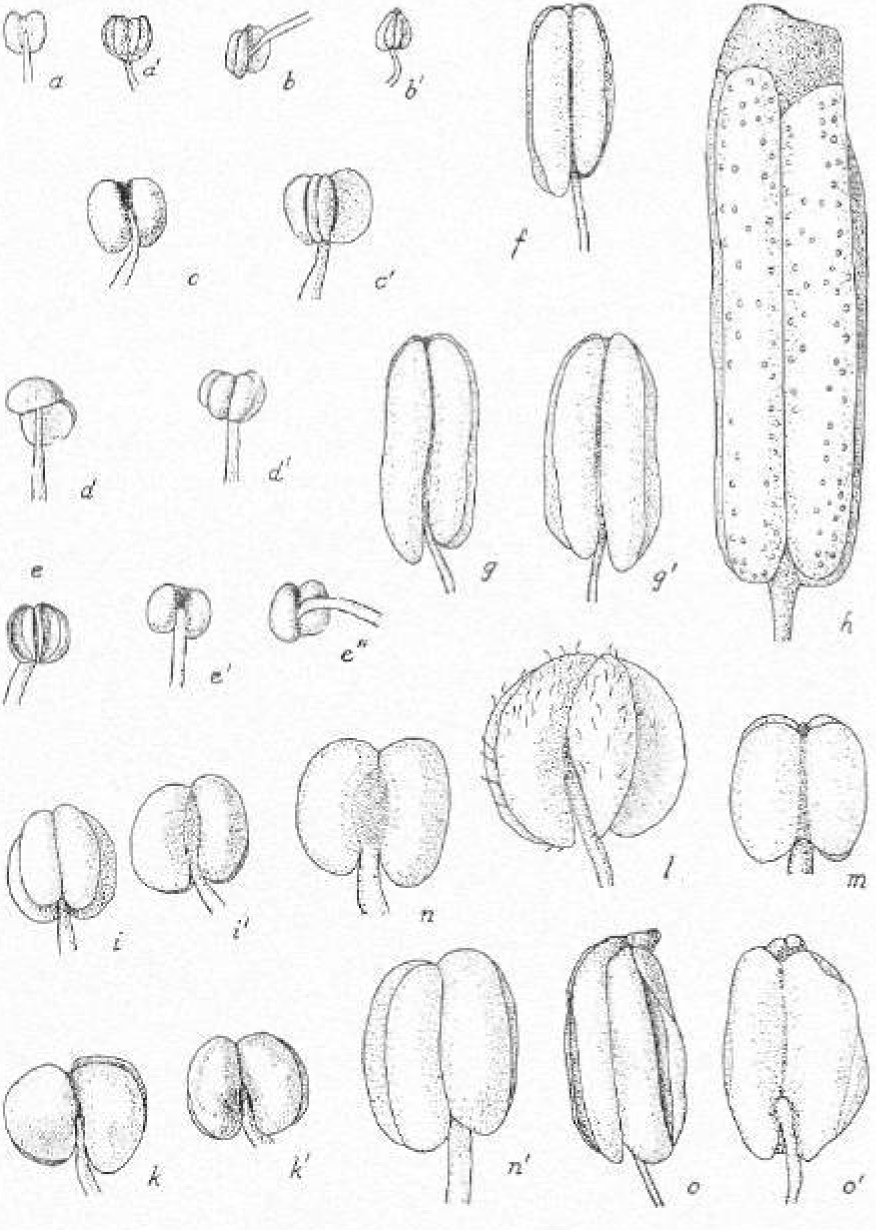

Fig. 38. Anthers of various *Fagaceae*. *a Lithocarpus iteaphyllus*; *b L. Henryi*; *c Castanopsis hystrix*; *d Chrysolepis chrysophylla*; *e Castanea sativa*; *f Fagus grandifolia*; *g F. sylvatica*; *h Nothofagus truncata*; *i Cyclobalanopsis acuta*; *k C. myrsinaefolia*; *l Quercus castaneaefolia*; *m Qu. Frainetto*; *n Qu. robur*; *o Qu. Sadleriana*. The apex of the anther is turned downwards in *a*, *a'*, *c'*, *d'*, *e*. × 20.

appearance, they are rounded at the base, much protracted in length and possess a large connective-appendage at the top. They reach here a length of nearly four mm in some species.

In the genera *Cyclobalanopsis* and *Quercus* the anthers (Fig. 38 *i—o*) are, as in the *Fagus* group, basifixed and comparatively large, whereas the filaments are short in proportion to the perianth. The form, however, is generally broad-rounded with cordate base and in this respect is somewhat reminiscent of *Lithocarpus*, especially in *Cyclobalanopsis*, where the size is somewhat smaller too. Within *Quercus* there occurs some variation as regards the stamens — as is the case with the pistil —; sometimes the shape of the anthers is more prolonged, reminiscent of *Fagus* (*Qu. Sadleriana*, Fig. 38 *o*), and sometimes the anthers are pilose (e.g. *Qu. castaneaefolia*, Fig. 38 *l*), and, further, more or less developed connective-appendages may occur in some species (*Qu. Sadleriana*, Fig. 38 *o*; *Qu. Frainetto*, Fig. 38 *m*).

There are thus very characteristic differences between the development of the stamens in different genera, differences that to a great extent certainly depend upon a transition from insect- to wind-pollination (sometimes connected with dioecism) and from this resulting changes in inflorescence structure and greater quantitative demands for pollen. (The pollen grains are also larger in *Fagaceae*, it is true, when the anthers are larger, but not in the same proportion; the number consequently increases too.)

While the stamens in the family are generally about twice as many as the perianth leaves, partly superposed, partly alternating, their number within the *Quercus* group is reduced. In *Cyclobalanopsis acuta* the number of stamens may rise to 17, but as the flower is undoubtedly formed by coalescence of three, this number already means a reduction, and this is still more marked in the flowers of this and other species of the *Quercus* group, where the stamens are only, for instance, five or four. Sometimes it is possible, both in *Quercus* and *Cyclobalanopsis*, to see how two or three stamens are united with each other (Fig. 39); perhaps the reduction may partly be due to such a coalescence.

Within *Quercus* there is generally no obvious relation between stamens and perianth leaves, but within *Cyclobalanopsis* the stamens may sometimes be observed to be clearly superposed to certain perianth leaves (cf. Fig. 37 *B*). In *Lithocarpus*, moreover, the stamens are not always clearly divided into superposed and alternating, every other of each kind, but there may occur two stamens above one perianth leaf, whereas there is none in one of the adjacent interspaces (e.g.

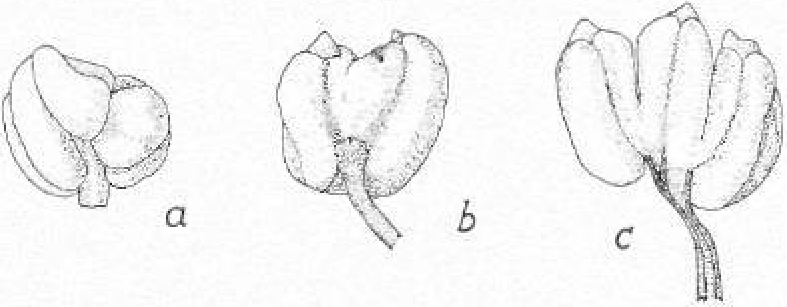

Fig. 39. *a* fusion of two stamens of *Cyclobalanopsis acuta*; *b*—*c* fusion of two and three stamens respectively in *Quercus Sadleriana*. *a* about × 20, *b*—*c* × 15.

L. edulis). It seems very probable that the superposition is the primary condition and that some stamens for the sake of space have been displaced secondary to the interspaces. This is also confirmed by BAILLON's (1876, p. 6) observations on the first formation of the stamens in *Castanea*, where the six superposed stamens are formed first — and sometimes only these appear — and later on (possibly) their number increases by one or more younger stamens being formed at each side of them.

The perianth of the female flower in the genera *Lithocarpus, Castanopsis, Chrysolepis*, and *Castanea* is regularly developed, inconspicuous, more or less high connate, generally with six perianth leaves, three outer and three inner, though the number may vary to some extent. Within *Lithocarpus* the perianth lobes are thick, firm and stiff and resemble bracts, this especially when, as for instance in *L. tubulosus* (Fig. 40 *A*), they are to their greater part free from each other. (In *L. densiflorus* [HOOK & ARN.] REHD. they are rather thin, but this is also the case with the cupular scales.) Within *Castanopsis* the perianth lobes are rather thick and fleshy, but not so stiff and firm, being more soft and flexible. *Chrysolepis* has a thin-lobed perianth, and this occurs within *Castanea* too. In the *Quercus* group *Cyclobalanopsis* is closest to *Lithocarpus*; the perianth lobes are here regularly developed, generally six in number, rather thick and fleshy. Within *Quercus* the perianth lobes of the female flower are however thin and soft and frequently of somewhat irregular development. The size often varies irregularly and some of the perianth lobes are incised. In *Quercus petraea* (Fig. 40 *B*) it is still possible to see that there are twice as many perianth lobes as styles (in the reproduced case, five in number), every other one larger (a small perianth lobe in this case is replaced by a rudimentary stamen). In *Qu. coccifera* (Fig. 40 *C*) there is scarcely any clear relation between the styles and the irregularly narrow-lobed perianth. There are thus some similarities to the perianth of the staminate flower, though the irregularity is greater in this.

SCHWARZ (1936) has called attention to some differences in the basal part of the perianth of the female flower within the *Quercus* group: within *Cyclobalanopsis* the perianth gradually passes into the ring-lined »perianthopodium» (the stalk-like prolongation of the ovary upwards), in § *Erythrobalanus* of *Quercus* it is sharply and more or less umbilicately delimited from the cylindric perianthopodium, in other *Quercus* groups it shows a gradual transition into the indistinct perianthopodium, which sometimes may have almost entirely disappeared. Similar differences as those observed by SCHWARZ may also be found within the genus *Lithocarpus*, which also in this respect shows a great variation, though they are not distributed on certain groups. *L. fenestratus* has thus a well-developed cylindric perianthopodium (Fig. 40 *D*). Other species lack such, and some have the square, umbilicate perianth base that is found in § *Erythrobalanus*, for instance *L. Reinwardtii* (Fig. 40 *E*). The genera *Castanopsis* and *Castanea* generally have a narrow, stalk-like part which shows an even transition into the ovary downwards and bears the rounded perianth at the top (see Fig. 31 *a* and *b*, Fig. 40 *F*); in the genus *Chrysolepis* such a structure is totally lacking, however; the perianth is directly inserted at the broad ovary (Fig. 40 *G*).

The *Fagus* group differs rather much from other groups concerning the perianth of the female flower. A perianthopodium is here quite absent, and as the connate part of the perianth is also very weakly developed, the perianth lobes seem to emanate directly from the ovary. In *Fagus* all six are well developed, long, narrow, soft, though the three at the edges of the ovary are somewhat larger than the other three (Fig. 40 *H*). In *Nothofagus* the perianth is obviously reduced. Sometimes there are three (or in the mid-flower two) comparatively large outer perianth-leaves, which form a prolongation upwards of the edges of the ovary, and alternating with these there are smaller inner perianth-leaves, which are generally much reduced (Fig. 40 *I*). In other cases the inner leaves are not at all discernible and the outer ones are not very conspicuous either (e.g. Fig. 40 *K*). In one case it was observed that one of the outer perianth-leaves of a mid-flower was two-cleft, which perhaps is to be regarded as evidence that it has arisen through union of two in an originally trimerous flower. In *N. pumilio*, where

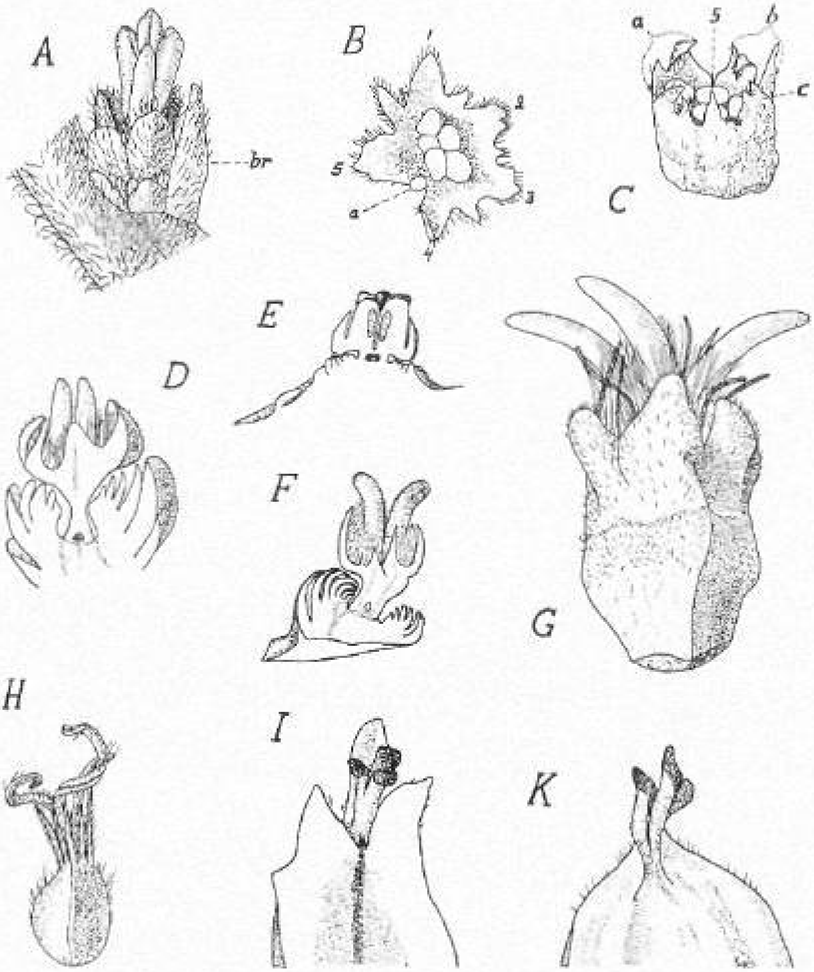

Fig. 40. Female flowers of various *Fagaceae*. *A Lithocarpus tubulosus*, flower with cupule (*br* bract); *B Quercus petraea* (*1—5* larger perianth-leaves, *a* rudimentary stamen, the styles cut off); *C Qu. coccifera* (*a—c* larger, lobate perianth-leaves, *s* off-cut style between two leaves); *D Lithocarpus fenestratus*, section; *E L. Reinwardtii*, do.; *F. Castanopsis cuspidata*, do.; *G Chrysolepis chrysophylla*; *H Fagus grandifolia*; *I Nothofagus truncata*; *K N. antarctica*. *B*, *C*, *G* × 15, *H* × 5, the others × 10.

the ovary often has more than three edges, there is usually a perianth leaf at the point of each of them (Fig. 28 *B—D*).

The different structure of the pistil was already demonstrated by Örsted (1867, 1871), who in a very perspicuous way has shown the systematically important differences of style and stigma and especially the distinction between the cylindric style, with pore-like stigma, of *Lithocarpus* and the *Castanea* group and the flattened style, with extended stigmatic surface, of the *Quercus* group, a type that — with certain changes — is also found in the *Fagus* group. He has also shown the variation that is found between smaller systematical units within the *Quercus* and *Fagus* groups. To this there is not much to add. It may only be mentioned that SCHOTTKY (1912) has shown that some *Castanopsis* species have the stigmatic surface extended over the whole — in these species flattened — top; perhaps it may also be pointed out that some *Nothofagus* species have a style- and stigma-type, that does not differ very much from the *Lithocarpus* type. There are, thus, transitions between the different types, and with SCHOTTKY (l.c.) we may assume a development towards a dilated stigmatic surface in connection with biological conditions, viz. transition to wind pollination.

The carpel number is generally three, though even in species that as a rule have this number it often rises to four or five (see Fig. 40 *A* and *B*). Some groups have regularly a larger number. The genus *Castanea* has for instance 6 carpels (e.g. *C. pumila*) or even 7—9 (in *C. sativa* up to 12), and certain *Lithocarpus* species of § *Cyclobalanus* have 5—6 such, which in both cases comes to expression in the ovary as well, which acquires a larger number of cells. In the genus *Cyclobalanopsis*, too, the styles are as a rule more than 3, often 4—5, sometimes even 7 or 8 (CAMUS, 1934, Pl. 4). Reductions and fusions of carpels are here common (Fig. 41 *A*—*C*); apparently there is a transition from a primary larger number to the trimery common in *Quercus*. That a larger number is present here is of a special interest with regard to the indications suggesting that the cupule has arisen through fusion of three, as well as the union of the three staminate flowers of a dichasium to one. Possibly such a fusion has also taken place between the pistillate flowers, although no proof of this is educible from the large number of carpels, in as much as such a number likewise occurs in species of *Castanea*, where the flowers are arranged in dichasia. There are however other reasons arguing for the view that such a fusion has taken place. Sometimes it may be observed that there are three chambers in the ovary lying at the side of each other in the same position as the flowers in a dichasium (Fig. 41 *F*), and in other cases, when there is a regular trimerous pistil, it may be seen that each carpel at the inside bears two ridges=carpel edges (Fig. 41 *G*), which is probably without correspondence in *Lithocarpus*.

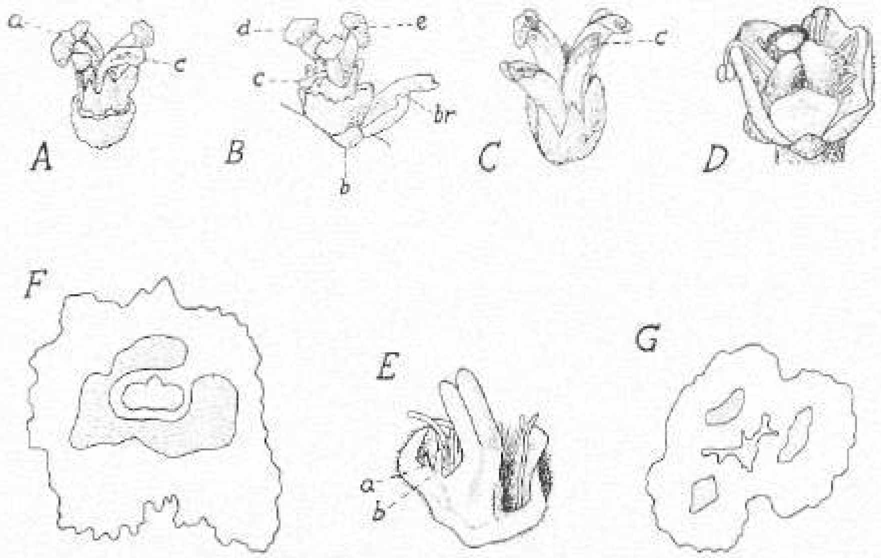

Fig. 41. *A Cyclobalanopsis glauca*, female flower with 5 styles, two of which are coalescent (*d*) and one deviating (*e*); *B* the same, female flower with a small, rudimentary style (*c*), two coalescent styles (*d*) and a style with a longitudinal stripe that may indicate a fusion (*e*), *br* bract, *b* bracteole; *C C. species*, female flower without cupule, 4 styles, one of which is smaller (*c*); *D* flower transitional between male and female flower in *Lithocarpus iteaphyllus*; *E* the same of *L. dealbatus*, *a*, *b* scale-like structures inside the perianth; *F* cross section of ovary of *Cyclobalanopsis acuta*; *G* the same of another flower of the same species, somewhat higher up in the ovary. *A*—*E* about × 10, *F*—*G* more enlarged.

The assumption of a flower fusion seems to be in opposition to the statements that rudimentary side-flowers may occur in the cupules of some *Quercus* species (SCHWARZ, 1936, *Qu. rubra* and *Cerris*; LENDNER, 1916, p. 165, with reference to BAILLON 1876, here a Figure of *Qu.* «*hybrida*», which has apparently given cause for the statement). In *Quercus rubra* and *Cerris*, however, the rudiments seem to be undeveloped cupule scales, homologous to the other scales, which at some sections may look like flower rudiments, and if *Qu. hybrida*, figured by BAILLON, is identical with *Qu. lusitanica*, as it probably is, the densely clustered flowers here belong to separate cupules, though this is not evident from the Figure.

The question of the origin of the flower and cupule within the family *Fagaceae* attracts great interest. As in several genera, *Castanea*, *Castanopsis*, *Chrysolepis*, and *Lithocarpus*, there occur rudimentary

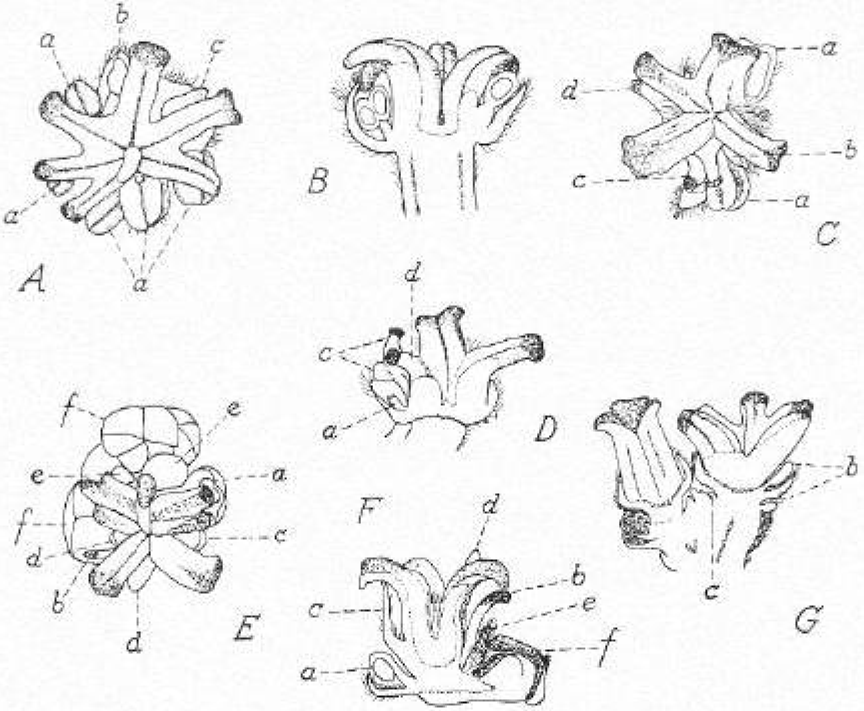

Fig. 42. *Quercus robur*, bisexual or otherwise deviating flowers at the top of the female catkin. *A* flower with 6 styles and 4 stamens (*a* anther, *b* appendage that is apparently a transition between stamen and carpel, *c* the same, more carpel-like); *B* the same flower in longitudinal section; *C* flower with 4 larger styles and two smaller ones (*a* anther, *b* structure apparently transitional between stamen and carpel, *c* transitional structure, partly stamen-like, partly carpel-like, *d* lower inserted style); *D* the same flower in longitudinal section (*a* filament of normal stamen, *c* = *c* in *C*, *d* a small style-branch); *E* flower with 5 higher located styles, 2 of which probably correspond to each 2, and a small, lower inserted, *b* (*a* anther, *c* and *d* longer perianth-leaves, glabrous at the tip, *e* shorter perianth-leaves, hairy, *f* scale-groups); *F* the same flower in longitudinal section, the designations the same; *G* a deviating flower together with a normal, longitudinal section (*b* structures probably transitional between scales and stamens, *c* scale probably belonging to the deviating flower). × 10.

pistils in the male flower, the rudiment being especially large in the primitive genus *Lithocarpus*, it has been supposed that the flower has developed from an originally bisexual one. Another possibility, however, is also conceivable: the flower may have arisen through reduction of an inflorescence with a whorl of staminate flowers around one or more central pistillate flowers. The perianth-leaves would in such case in reality be bracts, which they also undeniably strongly resemble. Some elucidation of the question which of the two possibilities has been the one actually occurring is given by the cases in which bisexual or intersexual flowers appear. This happens sometimes in *Quercus*, e.g. in *Qu. robur*, where above the female flowers there may occur another flower with both stamens and pistil developed (Fig. 42). The pistil is here of unusual development, both in form and in carpel number (cf. for instance the normal and the deviating flower in Fig. 42 *G*). Besides the frequently about 5—6 connate carpels there may in several cases be observed one or two others, small and thin, free from the former (Fig. 42 *C*, *d*; *E*, *b*). Transitions between stamens and carpels occur, too (Fig. 42 *A*, *b* and *c* probably; *C*, *c*). These flowers are now sometimes surrounded by a simple whorl of scale-like perianth-leaves (Fig. 42 *A*), but in other cases (Fig. 42 *E*—*F*) the number is larger and two different kinds may be distinguished, on the one hand inner leaves, narrow, glabrous upwards, on the other hand outer, shorter and broader, pilose. Of special interest is now that the stamens may be inserted outside the inner perianth leaves, as is shown by Fig. 42 *F* (to the left, *a* outside of *c*) and spring from the axil of an outer leaf. As shown in Fig. 42 *G* (to the right of the figure), there may also occur small clavate structures, apparently transitions between stamens and scales (*b*), outside as well as inside the perianth-leaves.

Also in the genus *Lithocarpus* there are not infrequently flowers transitional between staminate and pistillate, which are often located in the border region between the male and female part of a catkin. In these flowers there are some deviations too. Thus, the cup-like perianth of *L. iteaphyllus*, rather reminiscent of that of the male flower, may be dissolved (Fig. 41 *D*) into several free lobes of different size, and in *L. dealbatus* it was observed that small, pilose scales appeared inside the coarse perianth leaves (Fig. 41 *E*). These scales sometimes resemble staminodes, and sometimes (*L. iteaphyllus*, Fig. 41 *D*), as a matter of fact, there may be observed a stamen quite outside another.

The increase in number of perianth-leaves or scales that occurs in the bisexual flowers of *Lithocarpus* and *Quercus* is, of course, due to a tendency to cupule-formation beyond the perianth proper. Judging from the conditions in *Lithocarpus* just mentioned, the perianth of the male flower is not directly homologous to that of the female flower but to a whorl of cupular scales further out.

Another instance of bisexual and intersexual flowers is given by an abnormal variety (in reality a chimaera, cf. HJELMQVIST, 1944) of

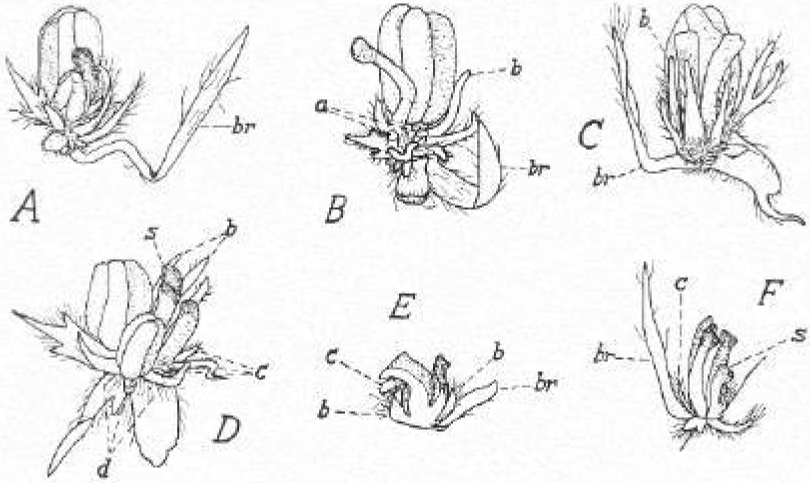

Fig. 43. *Quercus robur* var. *heterophylla*. Bisexual or otherwise deviating flowers. *A* flower with 1 style, 1 large and 1 small stamen (*br* bract); *B* flower with 1 style and 3 stamens (*a* 2 stamens, cut off, *b* narrow, curved scale, glabrous, *br* bract); *C* flower with 2 styles and 1 stamen (*b* narrow leaf between the pistil and the stamen, glabrous upwards, *br* bract); *D* flower with 3 styles and 2 stamens (*s* 2 coalescent styles, *b* 2 scales united below, from the axil of which the large stamen most nearly emanates, *c* 3 small scales around the free style to the right, *d* 3 small scales around the smaller stamen); *E* flower with 4 styles in longitudinal section (*br* bract, *b* perianth—cupular scales, *c* structure apparently transitional between stamen and perianth-leaf — cupular scale); *F* flower with 4 styles (*br* bract, *c* narrow scale, inserted just below the adjacent style, *s* style that below in the one margin passes over into a hairy scale). × 10.

the common oak, *Quercus robur* var. *heterophylla*. The flowers here have a very deviating structure (Fig. 43), possibly owing to different nutritional conditions. They generally contain 1—4 styles, usually free, and 1—4 stamens of varying size, all of very irregular arrangement. In addition there is a small number of surrounding scales, of varying shape, size, and height of insertion. These scales are either undivided or 2- or 3-parted, and often there are two or three narrow scales side by side, certainly corresponding to one 2- or 3-divided scale. Sometimes a stamen or a pistil may be observed to spring from the axil of a scale, and in other cases a pistil (Fig. 43 *D*, *c*) or a stamen (Fig. 43 *D*, *d*) may be enclosed by three small scales, undoubtedly corresponding to one three-lobed scale. In some cases there occur transitions between carpels and scales (Fig. 43 *F*, *s*), in other cases apparently between stamens and scales (Fig. 43 *E*, c).

The flowers described show transitions between a simple perianth and a perianth with an additional cupule-structure. The surrounding leaf-structures may be regarded as intermediate between tepals and cupular scales. The free carpels or stamens, which may often be seen to spring from the axil of a scale, are, *inter alia* through their irregular arrangement at different heights of the axis, very reminiscent of small flowers of simple organization, which spring from the axil of a bract, in the same way as this is the case with those stamens in the first-mentioned *Quercus* flowers which (see Fig. 42) are inserted in the axil of a scale outside an inner perianth leaf.

That the flower of *Fagaceae* is a reduced inflorescence is confirmed by the conditions at the formation of the male flower within the genus *Cyclobalanopsis*. The staminate flowers may here, as was earlier shown, arise through fusion of three, and then in *C. acuta* a large number of the perianth leaves may subsist, with one or two stamens in their axils, though their arrangement becomes different. This surely must be considered as a proof that the coalescing flowers are in reality inflorescences with a number of small flowers uniting into a new inflorescence, a circumstance that facilitates the union both in this and the other cases when it occurs in the family.

The inflorescence nature of the flower seems also to be proved by BAILLON's above-mentioned observations on the development of the stamens in *Castanea*, where first a stamen is laid down inside each perianth-leaf and later one or two younger ones may be developed at each side of it. Thus, there is formed a small group inside each leaf; within the outer ones there often seem to be three, inside the inner leaves one—two (in Fig. 33 *g* it is evident that two are developing inside one of the leaves).

As regards the origin of the cupule there is reason to notice the above-mentioned cases with double whorls of scales around the flower, where the outer also bear stamens (sometimes rudimentary) in their axils, as well as the transitions found between stamens (or carpels) and scales. These conditions may surely be taken as an indication that the pistillate flower forms the upper part of an inflorescence, where the lower part only consists of bracts, whose flowers (probably staminate) have either disappeared or been transformed into scales, so that the whole forms the leaf structures of the cupule. The lower bracts of the presumed original inflorescence, thus, would at the female flower give rise to the cupular scales, the upper ones to the perianth of the flower, whereas — as is evident from above-mentioned examples for

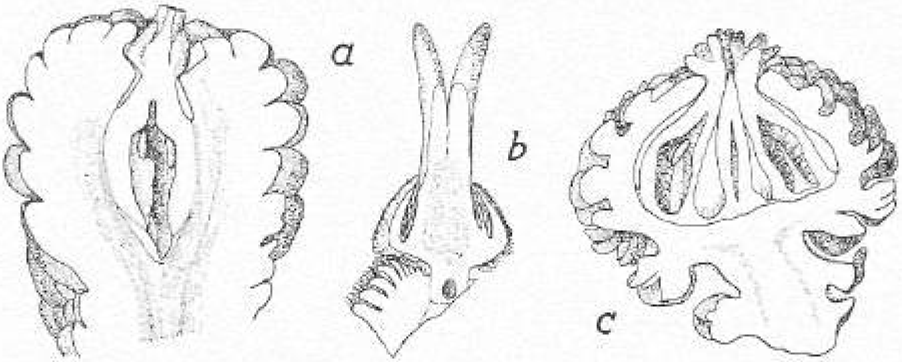

Fig. 44. *a Lithocarpus castanopsisifolius*, cupule and fruit in longitudinal section; *b* the same, female flower and young cupule in longitudinal section; *c* cupule with young fruits of *Castanopsis inermis* in longitudinal section. *a* and *c* × 5, *b* × 10.

Lithocarpus — in the male flower only some outer scales would remain and form its perianth.

As the ovary of the female flower is inferior, the perianth-leaves thus connating with it, it is of course not surprising that in a group of *Lithocarpus* which is apparently very primitive (*Synaedrys*) the cupule scales are partly so too. This is probably a very original condition, presumable also because the union of the cupule with the ovary is discernible at a very early stage (Fig. 44 *b*).

The development of the fruit undoubtedly affords some conditions of interest, more perhaps however with respect to the relations to other families than to the intra-family relationships. As was already pointed out by Örsted (1867), in the genus *Lithocarpus* there are some similarities in the fruit structure to *Juglandaceae*; some species have a very thick fruit wall, two-layered, and in the inner part there are lacunae in the wall as for inst. in *Juglans*, some species have false partitions in the fruit, so that the total number according to Örsted (1871) may rise to 12 or still more. Sometimes there are (e.g. in *L. cyrtorhynchus*, *L. platycarpus*) a large number of irregular indentations of the fruit wall, so that the conditions are quite reminiscent of *Juglandaceae*. The *Fagus* group, on the other hand, shows some similarities to the family *Betulaceae* in the fruit structure. The fruit is here strongly edged and somewhat alate upwards; if the pistil is dimerous, as in the mid-flowers of *Nothofagus*, the fruit is thin and flattened and is then suggestive of the fruit of, for instance, *Alnus*.

The ovules are two in number in each cell of the ovary, thus generally six in the ovary, only one of which is as a rule further developed. BENSON (1894) has investigated the embryology of the three genera *Fagus*, *Quercus*, and *Castanea*. The ovules are pendulous and epitropous, with two integuments. BENSON points out several peculiarities which are reminiscent of primitive groups, though they are not only found there. Thus, in *Fagus* there is formed an axile sporogenous tissue in the nucellus, consisting of several parallel cell-rows; from this tissue the embryo-sac develops, apparently at rather varying places; sometimes two embryo-sacs arise, and not infrequently there occur cells with more than one nucleus, which do not develop further but are probably to be regarded as an incipient embryo-sac formation. In the axile cellrows of *Castanea* and *Quercus* there is one that is deviating and that can only be designated as sporogenous tissue; the embryo-sac originates in this. A point of special interest is that in *Castanea* there may be formed one or more tracheides at the base of the embryo-sac; according to BENSON, these cannot have any actual function but must be a vestige of tissues that have disappeared in the phyogenetical development, possibly to be compared with the tracheides that in *Casuarina* are formed from the sporogenous tissue. A common feature to all genera is the formation of a long, chalazal protuberance (caecum) from the embryo-sac, also a certain similarity to *Casuarina*; the pollen-tube, however, does not enter through this but through a large epidermal cap lying over the micropyle. Thus, there does not occur chalazogamy here as for instance in *Juglandaceae* and *Betulaceae*; as in these families, the pollen-tube may however — at least in *Quercus* and *Fagus* — send out blind branches. The time between pollination and fertilization may be very long, in species of *Quercus* with biennial fruit ripening over a year (SCHNARF 1929, p. 273, with references to several authors).

The evolutionary lines and relationships existing in the family *Fagaceae* have already been elucidated in the main in the morphological account. Both with respect to inflorescence and to cupule there is clear evidence that the genus *Lithocarpus* is the most original genus, from which two separate lines of development emanate, the one to *Cyclobalanopsis* and *Quercus*, the other to the *Castanea* and *Fagus* groups. In the structure of the flower itself there are certain conditions arguing for the same course of development, while other circumstances at least are compatible with such an assumption.

Of the two genera *Cyclobalanopsis* and *Quercus*, which form the one evolutionary line, the former is more closely connected with *Lithocarpus*. In the flower structure and cupule of *Cyclobalanopsis* it is still possible to follow the transition from the *Lithocarpus* type to the *Quercus* group, as the catkins are here also more reminiscent of this type. It does not, however, seem to be derived from § *Cyclobalanus* of *Lithocarpus*, which has a similar cupule structure, with lamellae instead of scales, but from the type of § *Synaedrys*. This view is supported, as mentioned above, by the lamellae occurring at the surface of the fruit and further by the fact that also the pistillate flowers were here originally quite certainly arranged in threes, as still occurs in some cases. This is often the case within § *Synaedrys*, whereas in § *Cyclobalanus* the pistillate flowers occur as a rule one by one in the catkin. Sometimes, besides, there is also a lamellate cupule within the section *Synaedrys*.

The genus *Quercus* may on the whole be regarded as a further development of the *Cyclobalanopsis* type, as was shown above in regard to flower structure and cupule. On this account there is perhaps no very good delimitation between these genera, and, indeed, they are often united into one. *Cyclobalanopsis* is distinguished, however, by several important morphological characteristics that separate it from *Quercus*, e.g. lamellae at the cupule, the lamellae or rings also regularly occurring at the upper part of the fruit itself, the form of the female flower and its regular, fleshy leaves, the erect inflorescences, to some extent the shape of the stigmas, the greater number of carpels, the more primitive structure of the male flowers. Such prominent investigators as ÖRSTED (1867, 1871) and SCHOTTKY (1912) separate the two genera from each other; SCHOTTKY also on the ground that they seem to have different derivation. It is of course also quite possible that *Quercus* has some direct relation to *Lithocarpus* as well as to *Cyclobalanopsis*; it goes perhaps back to some *Lithocarpus* group with scaly cupule. It thus seems justifiable to regard *Quercus* and *Cyclobalanopsis* as separate, though related, genera. Any further subdivision of *Quercus* into a number of genera in accordance with SCHWARZ (1936) seems however scarcely justified in view of the less marked differences in the floral morphology and the circumstance that these groups probably form a single evolutionary series.

With the *Castanea* group there begins another line of development from *Lithocarpus*, characterized by the flowers being independently developed and structurally very like those of *Lithocarpus*, while the cupules of a dichasium coalesce into one, and some other changes take place. In the genus *Castanopsis* the coalescence is effected in such manner that the cupules of the two side-flowers directly grow together at the abaxial side, while the mid-cupule forms an adaxial part; in *Castanea* the original side-cupules are at both sides separated by wall-parts formed by the mid-cupule. With regard to this and the existing differences in the inflorescence, the two genera should probably be regarded as parallel lines of development with different points of departure and on this account — in spite of several similarities — as clearly distinct. Within *Castanopsis* there is a rather great difference between the sect. *Callaeocarpus* A. DC., characterized by fusion between cupule and ovary, and other species. One might be inclined to think that here it was a question of two groups that had different derivation, the one from the section *Synaedrys*, the other from the section *Pasania* or *Chlamydobalanus* of *Lithocarpus*. However, in view of the fact that there are all sorts of transitions within *Castanopsis* between adnate and free cupules (for instance, the cupule of *C. inermis*, almost free at an early stage, see Fig. 44 *c*), and that there are great agreements between the sections in other respects, it seems more probable that the sections have a common origin and are consequently referable to the same genus. Somewhat different conditions are presented by the species that is called *Castanopsis chrysophylla* (with *C. sempervirens*). It differs from the other species in several essential characters. Firstly the inflorescence is different: the pistillate flowers occur in androgynous catkins and the dichasia are 3—7-flowered instead of 1—3-flowered. These are characters which are to be found within *Lithocarpus*, and also within *Castanea*, but which can scarcely have arisen through some development from the *Castanopsis* type. Further, the cupule is of a very deviating type, open and lobate, with transverse rows of spines at the lobes, the rows below partly uniting into lamellae, and with scales in the margins, which bend inwards over the inner surface. These characters are to some extent reminiscent of the *Fagus* group, especially of *Nothofagus*, while the walls between the part-cupules, well-developed at early stages, are reminiscent of *Lithocarpus*. The absence of perianthopodium in the female flower may be a mark of resemblance both to *Lithocarpus* and to the *Fagus* group, the sharply triangular ovary to the latter. Fruits that are somewhat triangular may however occur in *Castanopsis* too, as well as walls between the fruits, and a parallel with the *Castanopsis* type is the meeting of the primary side-cupules at the abaxial side, as the bilobate side-cupules also form some correspondence to the two-parted ones of many *Castanopsis* species, the parts being separated at the opening. Without doubt *Castanopsis chrysophylla* is to some extent connected with the other *Castanopsis* species — and, above all, belongs decidedly to the *Castanea* group with respect to styles, stamens, cupular spines etc. — but it shows considerable deviations in important characters, in some respects reminiscent of *Lithocarpus*, in others of the *Fagus* group, and must, as far as the writer can understand, belong to a separate evolutionary line. The species should on this account be detached as a genus of its own, for which I suggest the name *Chrysolepis*[1]. I am inclined to regard the three genera belonging to the *Castanea* group as representing parallel lines of development, originating from *Lithocarpus*-like types.

The *Fagus* group, with the genera *Fagus* and *Nothofagus*, stands rather isolated from other groups. The resemblances found to the genus *Castanea* in the cupule are held both by ÖRSTED and SCHOTTKY not to mean any real close kinship to this genus. It is possible, too, that there is no direct relationship of this kind, but a certain degree of affinity with the *Castanea* group must nevertheless certainly exist owing to the great agreements in, among other things, the organization of the cupule. Especially I would emphasize the resemblances that are found to the genus *Chrysolepis*, which were already to some extent pointed out by ČELAKOVSKY (1890). The cupule lobes that surround the side-flowers of a 3-flowered dichasium in this genus are very reminiscent of the cupule lobes within the *Fagus* group, which are sometimes also here separated from the outset (for instance — to a high extent — in *Nothofagus pumilio*). And when the cupule is 4—7-flowered, the tertiary flowers are surrounded each by a two-parted cupule, just as in *Fagus* in corresponding cases. In *Chrysolepis*, it is true, the cupule of the mid-flower is also developed, as well as walls between the part-cupules, but these parts undergo considerable retrogression in the ontogenetic development and may have quite disappeared in a later phylogenetic development. Other resemblances between *Chrysolepis* and the *Fagus* group are the similar lamellae of the cupule in *Chrysolepis* and certain

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[1] *Chrysolepis, gen. nov. Fagacearum; amentis masculis vel androgynis; floribus 3—7(—11)fasciculatis, masculis omnibus bracteolatis; cupulis apertis, locolos triangulares circa flores formantibus, margine circa flores exteriores quosque bilobis, frugiferis extra spinosis-lamellosis et margine quoque squamosis; perigonio floris feminei tenui sine stipite ab ovario trigono exeunte.*

Typus generis: Chrysolepis chrysophylla n. comb. [=Castanopsis chrysophylla (HOOK.) DC.].

Nothofagus species, the broad ovary without perianthopodium and the pronounced triangularity of this, while the mid-flower may sometimes have an elongately 4-edged ovary (though still with three styles). Especially regarding the inflorescence there are some deviations in the *Fagus* group that separate it sharply from all others, but these may be due to a far advanced reduction, and it seems possible to imagine that this group has arisen through reductions and other changes as a branch from the evolutionary line whose first part is represented by the *Castanea* group, the genus *Chrysolepis* in this development forming an important link of union.

Of the two genera belonging to the *Fagus* group, *Nothofagus* appears to be more primitive in some characters, such as the occurrence of a terminal flower in the dichasia, the comparatively few flowers of the male dichasia, the structure of the styles, while in *Fagus* the aborted terminal flowers, the many-flowered male dichasia and the style structure imply greater deviations from the original *Fagaceae*. On the other hand, in some cases *Nothofagus* shows a far advanced reduction in comparison with *Fagus*, as in the perianth of the pistillate flower and the development of the cupule in some species. Also in such a character as the thin, normally epigeal cotyledons it appears to be more advanced than *Fagus*, whose peculiar cotyledons form a transition to the other genera. The two genera should probably most appropriately be regarded as parallel lines of development from a common ancestral group, at which development one genus has become more advanced in some respects, one in others.

The genus *Lithocarpus*, which according to the previous exposition should be regarded as the most original, has with reference to its great variation been divided into several sections, occasionally regarded as subgenera. According to BARNETT (1944), there are five sections; this author includes subg. *Oerstedia* of HICKEL and CAMUS (1921) in § *Synaedrys*, which seems to be a justifiable proceeding, in spite of the peculiar cupules of the only species belonging to this group.[1] Some of these sections have not only in older time but also by later authors been

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[1] The species *L. Balansae*, by HICKEL and CAMUS referred to subg. *Oerstedia*, seems to be identical with *L. lithocarpaeus* (OERST.) n.c. (*Pasania lithocarpaea* OERST. in Vid. Medd. Naturh. For. Kjöbenh. 1866, 1867, p. 76, Tab. I—II) and the subg. *Oerstedia* with subg. *Lithocarpaea* of ÖRSTED (l.c.). Material (fruits) of this species in Herb Copenhagen (very good figures also by ÖRSTED, l.c.) shows great agreements with the figures (not so good) of DRAKE DEL CASTILLO (1890) of *L. Balansae*; material determined as belonging to this species has not been seen by the writer.

regarded as independent genera. Thus the sections *Cyclobalanus* and *Synaedrys* are regarded by SCHWARZ (1936) as genera, the former with the same name, the latter with the name *Lithocarpus*, while the other species are referred to a genus *Pasania*. Especially *Cyclobalanus* also undoubtedly shows several deviating characters. When ÖRSTED in his time (1867) proposed the genus, he did not found it only on the qualities of the cupule (lamellate), but also on important characters in the inflorescence (single pistillate flowers), styles (erect, short, high up connate), and fruit (6—9-chambered). Partly owing to the enlarged material that has become known, however, it is clear that this species group — and likewise the others considered as sections — do not show any sharp limits and are not unitary either in the more important characters; on this account they cannot be regarded as proper genera. There occur transitions between lamellate and scaly cupule as well as between adnate and free; some species of § *Synaedrys* have lamellae on the cupule (for instance *L. Maingayi*); within § *Cyclobalanus* there may occur styles of the common type (for instance in *L. Cantleyanus*); false partitions occur not only there (but also for instance in *L. costatus*, belonging to *Synaedrys*). Further, as mentioned above, *L. Teysmannii* has rings at the fruit like the genus *Cyclobalanopsis*, while they are lacking in other species of *Cyclobalanus*; hence in this character too the section is not unitary; the genus *Cyclobalanopsis* has a considerably more uniform organization.

Which section of *Lithocarpus* is the most original, is not easily decided. The small § *Corylopasania*, which has the cupule protracted into a long covering reminiscent of *Corylus*, must surely represent a special line of development; this is probably also the case with the section *Chlamydobalanus*, in which the cupule encloses the whole fruit without being united to it. The sections *Cyclobalanus* and *Synaedrys* both show original features. The simple female catkins of *Cyclobalanus* are held by SCHOTTKY (1912) to be a more primitive character than the compound ones, and it might of course also be thought that the fusion of cupule and fruit that is met with in *Synaedrys* was a lately developed character, so that this section was not as original as *Cyclobalanus*. There occur however in *Lithocarpus* examples of reduction of 3-flowered dichasia into one-flowered — the former thus appear more primitive —, and, as mentioned above, on morphological grounds it is probable that the fusion of the cupule with the ovary is a primitive feature, which is confirmed by observations of the development of the flower. Further, in one case there was observed in *Cyclobalanus* a development of the cupule which, like that occurring in *Cyclobalanopsis*, must trace its origin from the *Synaedrys*-type. It must consequently be assumed that § *Cyclobalanus* is less original than § *Synaedrys*, and probably the same is then also true of § *Pasania*, though there are some original features in this also.

Taking then into consideration the affinities which the family *Fagaceae* — and hence the order *Fagales* — show to other groups, and especially to those treated earlier here, stress should in the first place be laid upon the agreements that in several cases may be observed with the order *Juglandales*. Especially in the fruit structure there are some features reminiscent of *Juglandaceae*, such as the thick walls, occasionally with lacunae, and the numerous wall projections and correspondingly incised cotyledons of some *Lithocarpus* species, and also in the structure of the male flower a certain resemblance may sometimes be recognized. These similarities however scarcely have any great importance; they are to be regarded as parallel phenomena, natural in related orders. More important are the essential agreements found in the general floral organization of very original types in both orders. In some primitive *Myricaceae* it may be observed that the pistillate flowers are pseudanthia made up of central female flowers and — usually reduced — male flowers around them, the bracts of which may — owing to phenomena of coalescence — emanate from the surface of the ovary. The conditions within *Lithocarpus* § *Synaedrys* seem to be a clear parallel to this: here, too, we have a pistillate flower which is evidently of pseudanthic character, with a number of empty bracts surrounding the flower and partly emanating from the ovary. In this case there is a superior perianth, according to the writer's opinion formed by the highest bracts; no such is as yet developed within *Myricaceae*, which family on this account should probably be held to have a somewhat more primitive position.

With the order *Balanopsidales* there are in *Fagales* some agreements which at the first glance appear rather great. The fruit and the cupule are exteriorly of similar appearance, and there may be a resemblance, too, between the circle of male flowers sometimes occurring in *Balanops* and a staminate flower in *Fagaceae*. As earlier pointed out, there are nevertheless also considerable differences, which are of greater importance than the rather superficial characters mentioned, as for instance the different nature of the cupule in the two cases, the absence of perianth in the female flower of *Balanopsidales*, the different structure of stigmas and fruit, etc., and the *Balanopsidales* seem for this reason to be closer to *Juglandales* than to *Fagales*. There are however some agreements of real importance — deserving special mention is the fact that the flowers of *Fagales* seem to have arisen through a similar development from simply-built inflorescences that may be followed within *Balanopsidales* —, and for this reason it seems probable that a certain degree of affinity exists, though it is not certain that there is a direct line of development.

An indubitable and rather close relationship exists to the order *Betulales*, which as a matter of fact is usually included in *Fagales*. Before the relation between these two orders is discussed, the order *Betulales* must however first also be treated.

Order 5. Betulales.

(*Betulaceae* A. BRAUN in ASCH. Fl. Prov. Brand. I, 1864, p. 62; PRANTL in ENGLER-PRANTL Nat. Pfl.-fam. III, 1, 1889, p. 38; WINKLER, Das Pflanzenreich IV, 61, 1904, p. 1; *pro familia*.)

Family 1. Betulaceae.

(*Betulaceae* BARTLING Ord. nat. pl., 1830, p. 99; REGEL in DC. Prodr. XVI, 2, 1868, p. 161; *Betulaceae* trib. *Betuleae* WINKLER, Das Pflanzenreich IV, 61, 1904, p. 19, 56, et auctt. plur.)

Important literature: EICHLER, 1878; PRANTL, 1889; BENSON, 1894; WINKLER, 1904; WOLPERT, 1909; ABBE, 1935, 1938.

The inflorescence is within *Betulaceae* as a rule a catkin composed of dichasia, but both in the arrangement of the catkins and in the structure of the dichasia there occurs some variation, so that some lines of development are discernible within and between the genera. In the arrangement of the catkins the genus *Alnus* shows the greatest variation. A species that in this respect appears very original is *A. nepalensis*, belonging to the section *Clethropsis*. Here the catkins (Fig. 45 *a*) form large panicle-like clusters in the branch tips (reminiscent of some *Lithocarpus* species), with several catkin-bearing branchlets, the upper with male, the lower with female catkins. At the limit between the male and the female part of the compound inflorescence there occasionally occur branchlets with superior male and inferior female catkins. Anthesis takes place here (cf. PRANTL, 1889) in the first year of development of the catkins, as well as in the other species belonging to section *Clethropsis*, *A. nitida*. This species, however, differs by the number of catkins being considerably smaller; there is only a simple cluster of male catkins in the top, and in the leaf-axils lower down there are solitary, stalked female catkins; evidently a reduction has taken place here of the large, panicle-like catkin-cluster.

The species *A. nitida* forms a transitions to the sect. *Gymnothyrsus*, in which the male catkins are arranged in a simple raceme in the top and the female catkins are either solitary (e.g. in *A. japonica*) or some few together on a catkin-bearing branchlet (examples *A. glutinosa* and *A. rubra,* usually) in the axils of leaves that are frequently somewhat reduced (Fig. 45 *b*—*c*). In some species, as *A. maritima,* anthesis takes place in the autumn, thus as in § *Clethropsis* in the same year as the catkins are first developed, but in most species not before the following spring, undoubtedly a more advanced condition, biologically understandable in a temperate climate with a short period of vegetation and pronounced winter-rest.

A further step of development may be observed in the section *Alnobetula.* The catkins have here on the whole the same arrangement as in *Gymnothyrsus.* They however do not all pass the winter without protection as in this section, but the lateral shoots that bear female catkins are enclosed in buds during the winter, and the female catkins are consequently located in the leaf axils of the year's shoots (Fig. 45 *d*), thus also a development that is biologically explicable. While the female catkins in this section are generally two or more together at the same shoot, in one species, *A. firma,* they are solitary and emanate higher up on the main branch than the male catkins (Fig. 45 *e*). Sometimes however the male catkins are here, too, located in the top (Fig. 45 *f*), but also in this case they are more widely separate than in other species.

The most remarkable deviation with respect to the arrangement of the catkins is shown by the section *Cremastogyne* with the species *A. cremastogyne* and *lanata.* All catkins here spring from the leaf-axils of the year's shoots, the female catkins higher up, the male lower down (Fig. 54 *g*). The male and the female catkins are thus here arranged at the same shoot. It might be assumed that this was an original condition, and that by reduction of it those types had arisen which have male and female catkins at different branchlets. This is however in opposition to several conditions in the inflorescence (buds around the young catkins, inverted relative order of male and female catkins as against *A. nepalensis*), and also by the strongly reduced flower structure in the section. Instead, the inflorescence arrangement of sect. *Cremastogyne* should probably be held to be the most derived type in the genus. Most closely it is connected with *Alnobetula* by the development of buds around the young catkins. With respect to the mutual arrangement of male and female catkins the *Alnus firma* mentioned may possibly form a transition from *Alnobetula* to *Cremastogyne.* As mentioned above, in this species there are often female catkins above male catkins on the same

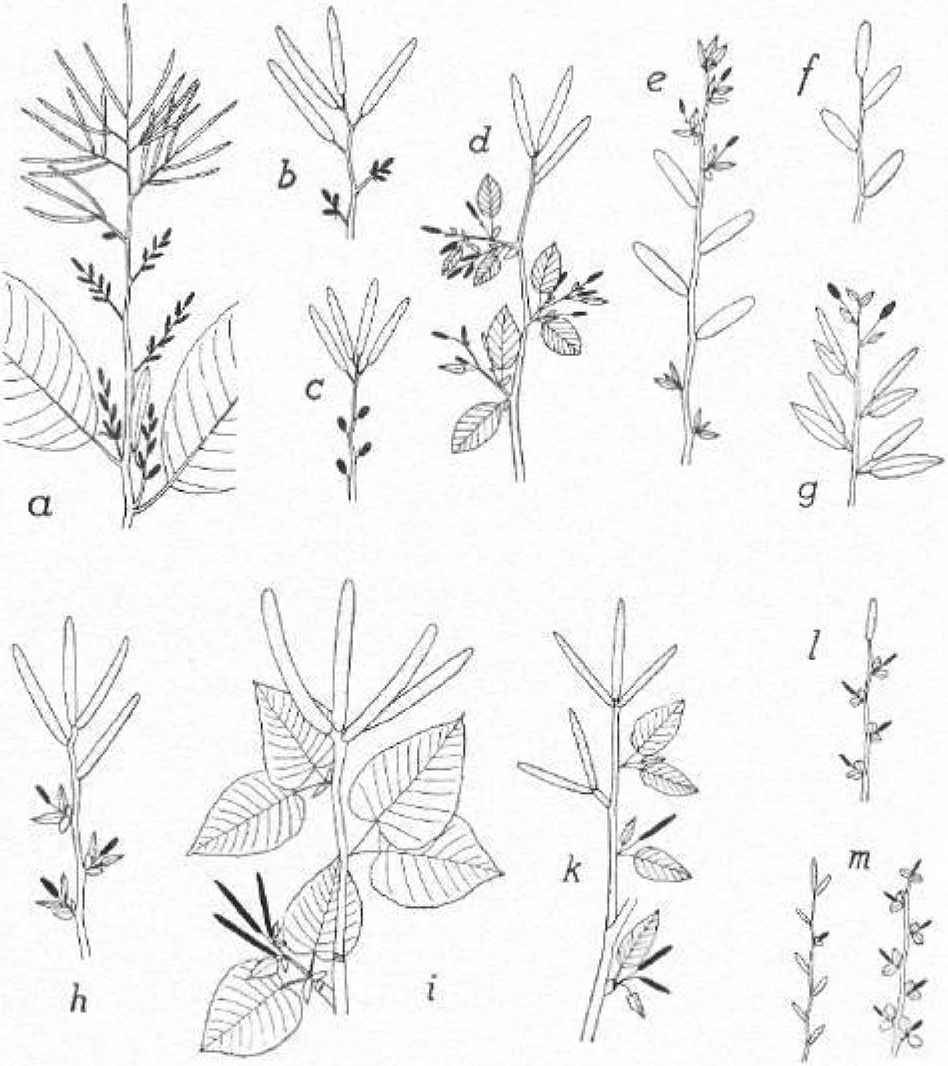


Fig. 45. The arrangement of the catkins in *Alnus* and *Betula*, schematically. *a Alnus nepalensis*; *b A. rubra*; *c A. japonica*; *d A. viridis*; *e—f A. firma*; *g A. lanata*; *h Betula lutea*; *i B. Maximowicziana*; *k B. papyrifera*; *l B. glandulosa*; *m B. pumila*. Female catkins black, male catkins dotted.

branch, though it is not a shoot of the year but a one-year old branch. The first foundation of the catkins takes place in the same year as the branch develops, and if it be presumed that the development of the catkins was accelerated, so that they were also fully developed that year, we should have a transition to the *Cremastogyne* type.

The genus *Betula* is in the arrangement of its inflorescences more derived than *Alnus,* on one hand not showing so great a variation, on the other attaching to — and further developing — more advanced types of *Alnus,* in the first place those occurring in § *Alnobetula.*

The series that in the arrangement of its catkins is most closely connected with *Alnus* seems to be § *Costatae.* Here (Fig. 45 *h*) the male catkins are somewhat separate from each other in the branch tops, and the female catkins are arranged as in *Alnus,* § *Alnobetula*; they are only solitary at the shoots, contrary to the usual condition in this section. A resemblance to *Alnus,* further, is that the female catkins of several species belonging to this series are short and erect, with persistent catkin-scales.

The series *Acuminatae* and *Albae* have (Fig. 45 *i, k*) the male catkins closely agglomerate in the tops, and long, more or less pendulous catkins with deciduous scales, characters that must be regarded as more derived. Two species of ser. *Acuminatae, B. Maximowicziana* and *alnoides,* have several female catkins together at the same shoot, a condition in some degree reminiscent of *Alnus,* especially in the last-mentioned species; in *B. Maximowicziana* the conditions are not quite the same, as the catkin group is not located at a shoot that springs from a leaf-axil, but terminally at a short lateral shoot (Fig. 45 *i*), a position more corresponding to that of the male catkins. In *B. papyrifera,* belonging to ser. *Albae,* similar groups of two—three female catkins may also be observed at shoots from older lateral shoots of the branches (Fig. 45 *k*); in addition there are however here side-shoots from the one-year-old branches with solitary female catkins, and this arrangement becomes the predominant one in other species.

The series *Humiles,* finally, as in several other respects, also shows proof of strong reduction in the arrangement of its catkins. Here, the groups of male catkins are reduced to a terminal catkin (or possibly two together), and these catkins are either located in the branch-tops only as in *B. glandulosa* (Fig. 45 *l*), while the female catkins emanate lower down, or the male catkins are arranged along the branch-sides in the same place as the female catkins. This latter arrangement occurs for instance in *B. pumila* (Fig. 45 *m*) and *B. nana* and is probably connected with a tendency to dioecious flower repartition that occurs here, undoubtedly a derived character too.

The organization of the dichasia -- as well as of the flowers —

was recently thoroughly investigated by ABBE (1935; 1938). One of the most interesting observations made by this author (1938) concerning deviating structural conditions is that in *Betula papyrifera* the dichasia may sometimes contain an additional flower that is median, abaxial, and must thus be a third side-flower to the primary flower. It seems to me as if this fact should be compared with the cases mentioned earlier (e.g. *Myrica Faya*) in which a terminal flower is surrounded by more than two lateral ones and should be interpreted as favouring the view that the dichasia of the *Amentiferae* had arisen from an inflorescence in which the lateral flowers were either more than two or also of varying number, and that the number had not been fixed at two until later in the course of development.

With respect to the female dichasia there might be reason for assuming *Alnus* to be a more advanced type than *Betula*, since the former genus has constantly only the two side-flowers developed, the mid-flower aborted, whereas *Betula* as a rule has all three flowers. Such an assumption, however, is in conflict with the fact that the bracteoles are more completely present in *Alnus*, generally two primary and two secondary, than in *Betula*, where there are not more than two primary, which, besides, are more strongly connate with the bract. It is very possible that the abortion of the primary flower in *Alnus* should be traced back to a type outside the family; the same thing occurs both in *Fagaceae* and *Corylaceae*, in the former family within the *Fagus* group, which shows several other points in common with *Betulaceae*.

In favour of the view that the dichasia of the genus *Betula* represent a more advanced type there also argues the fact that this genus not infrequently shows reductions of the numbers usually present, both with respect to flowers and bracteoles. Within the series *Costatae Betula corylifolia* and *B. globispica* (Fig. 46 *A*, *B*) have solitary female flowers in the dichasium; the same thing occurs according to ABBE (1935) in § *Humiles*, constantly in *B. nana* var. *Michauxii*, in some cases in other species. In *B. chinensis* the same specimen may have dichasia with three and two flowers in each, as well as with only one. When two flowers are present, the mid-flower and one side-flower, the latter is often somewhat reduced, sometimes (Fig. 46 *C*) sterile and scale-like; and sometimes there are two small scales only at the place of the side-flowers, which are undoubtedly reduced flowers (Fig. 46 *D*). These conditions clearly show that also in the series *Costatae* the solitary flowers arise through reduction of three-flowered dichasia. Like the side-flowers, the bracteoles may also be reduced

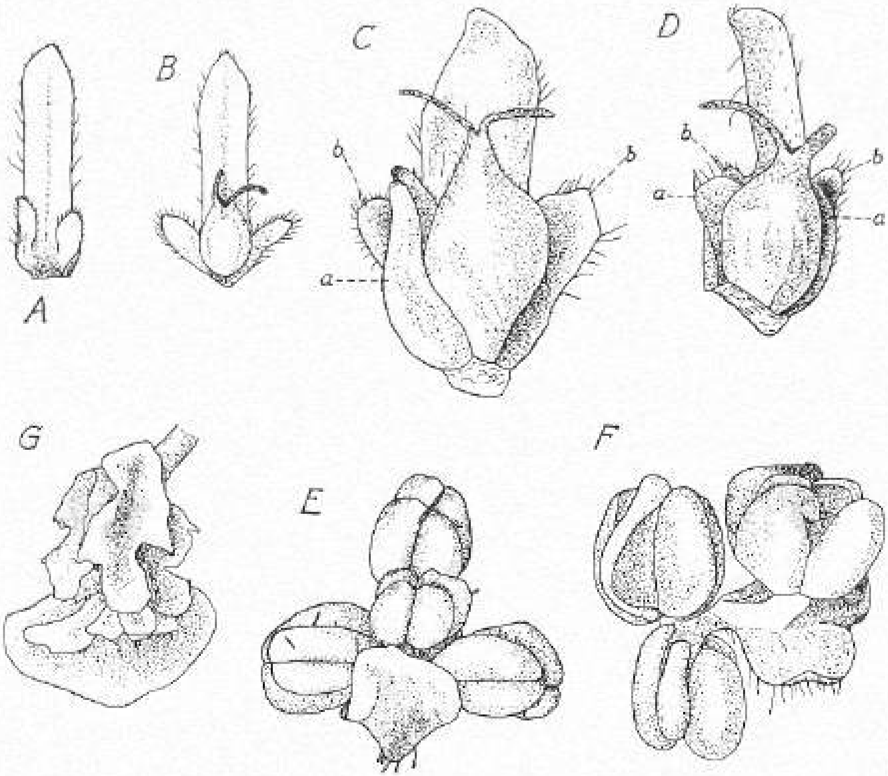


Fig. 46. *A Betula globispica*, catkin scale from female catkin; *B* the same, uniflorous female dichasium; *C—D B. chinensis*, transition to uniflorous female dichasium, in *C* a sterile side-flower (*a*), in *D* two scales (*a*) at the place of the side flowers (*b* bracteoles), *E* male dichasium of *Alnus cremastogyne*; *F* the same of *A. lanata*; *G* the same of *A. firma*, the stamens removed. *A—B* × 5, *C—D* and *G* × **10**, *E—F* about × 15.

within *Betula*. This was shown by Abbe (1935) for § *Acuminatae*; the same thing occurs within *Costatae* in *B. chinensis*, where in the same catkin there may be dichasia with two bracteoles, one bracteole, or no bracteole at all, and within § *Humiles*, in *B. nana* var. *Michauxii*, where also a change occurs between three-lobed and entire catkin scales (Rehder, 1940, p. 133; Abbe, 1935).

The invariably three-flowered male dichasia have a development that in *Alnus* shows a considerably greater variation and in general more original conditions than in *Betula*. In *Alnus* there are either found four bracteoles, the common condition, or there is — within § *Alnobetula* —

a number changing from two to four, often varying even in the same individual, or the bracteoles are totally lacking; this is the case in the section *Cremastogyne* (Fig. 46 *E*, *F*). In *Alnus nepalensis*, according to ABBE (1935), first the secondary and later also the primary bracteoles disappear towards the top of the catkins. In *Betula* there are as a rule two primary bracteoles; only within § *Acuminatae* is there some variation, as *B. luminifera* and *B. alnoides* var. *pyrifolia*, belonging to this section, have no bracteoles according to ABBE (1935). In *B. alnoides*, however, two small, low-inserted bracteoles were observed in the male dichasium by the present writer; probably here, as in the female dichasia of the same section, there is a gradual reduction of the bracteoles.

Concerning the perianth of the staminate flower I may refer to ABBE (1935) for details and merely point out that here, too, a line of development may be followed from the genus *Alnus*, which for one thing generally has a more original organization, for the other a greater variation, to *Betula*, which does not vary as much and shows a further development of more advanced types within *Alnus*. Most species of *Alnus* have a well-developed, four-leafed perianth in the staminate flower, as the sections *Clethropsis* and *Gymnothyrsus*; in these species only exceptionally is some perianth-leaf or other suppressed; yet a certain tendency may be discerned within *Gymnothyrsus* to the suppression of the posterior perianth-leaf of the side-flowers and the lateral ones of the top-flower. In the section *Alnobetula*, however, the perianth-leaves are more weakly and irregularly developed (and more strongly connate to each other), for instance in *A. firma* (Fig. 46 *G*), where the flower is also cymbiformly elongated. In the two species belonging to § *Cremastogyne* a perianth is totally lacking in the staminate flower (Fig. 46 *E*, *F*).

The genus *Betula* attaches itself most closely to § *Alnobetula* of *Alnus* with regard to the perianth of the male flower as well as in the arrangement of the catkins. *B. Maximoviczian*a shows in this respect as well a more original character; as a rule it has four well developed perianth-leaves. *B. alnoides* however, which belongs to the same series, has a somewhat reduced perianth. In the series *Albae* and *Costatae* there may sometimes be four perianth-leaves present, but generally they are fewer, often two, and of irregular shape. The reduction has reached farthest in ser. *Humiles*, where there generally occurs one perianth-leaf only in each flower, viz. the outer transverse one of the two side-flowers and the anterio-median of the terminal flower.

The perianth of the female flower does not show any obvious lines of development within the family, but its morphology is of great interest in comparison with other families. According to earlier authors, a perianth was lacking in the female flower. The occurrence of a reduced perianth was however already pointed out by WOLPERT (1909), for *Alnus viridis,* and ABBE (1935) is of the opinion — no doubt correct — that both in *Alnus* and *Betula* there is a rudimentary perianth, usually fused with the ovary wall. Among the reasons assigned by the author mentioned for this opinion is the fact that in some exceptional cases more or less free perianth-leaves may occur in *Betula* as well as in *Alnus.* Such structures may also be very prettily observed in *Betula lutea* (Fig. 48 *A, B*), where they are not uncommon, and further in some pistillate flowers of the androgynous catkins that in some cases occur both in *Alnus* and *Betula.*

In *Alnus glutinosa* — and also in *A. viridis* — catkins may sometimes be found that are male below, female at the top and that in a transitional zone show dichasia with intermediate forms between stamens and carpels, sometimes three to four in one flower (cf. ZIMMERMANN, 1922). Higher up in the catkin the terminal flower becomes more or less reduced and the number of carpels in the side-flowers limited to two, transverse. In the lower female flowers, however, there is a perianth, which towards the top becomes smaller, the two lateral perianth-leaves showing a tendency to become larger than the median ones. There is, thus, a certain similarity to the genus *Nothofagus,* where three of the lobes in the pistillate flower are longer and form a prolongation of the edges of the ovary; especially this similarity is evident in comparison with the terminal flowers in the dichasia of *Nothofagus,* which are not trimerous, but dimerous.

Androgynous catkins are also found in an abnormal *Betula*-form, var. *urticifolia* (SPACH) of *Betula pendula*×*pubescens,* which in reality is a periclinal chimaera (HJELMQVIST, 1944). In the same catkin there may here be observed all possible transitions between female and male flowers and dichasia. In Fig. 47 *A* a dichasium is shown which is almost normally female; yet the side-flowers have poorly developed wings and in the central flower the wings run out into free perianth-like points (*p*). Fig. 47 *B* shows that at one side in the mid-flower there occur a transition between carpel and stamen and a lobe, free in its upper part (*p*); one of the side-flowers also has such a lobe, while the other is partly reduced. In another case (Fig. 47 *C*), at either side of the pistil of the mid-flower, which had two median styles but no

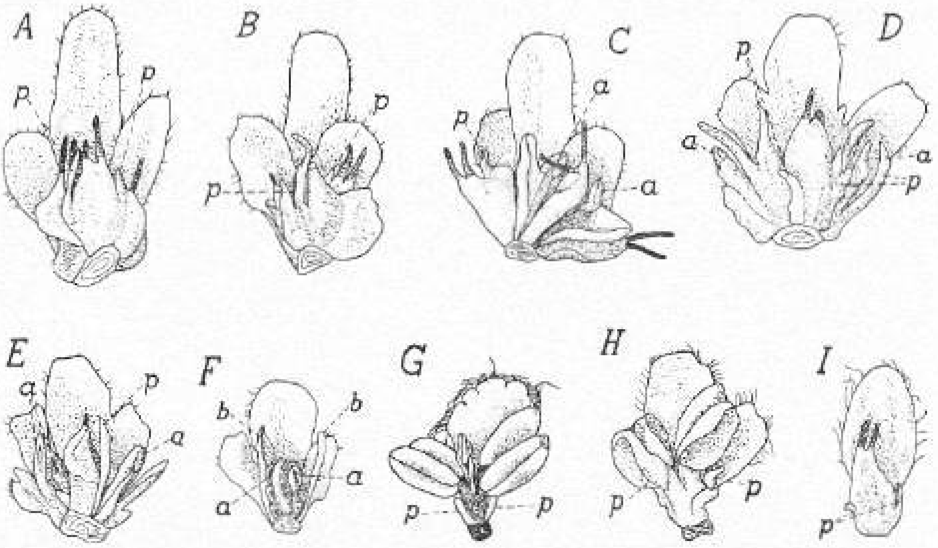


Fig. 47. *Betula pendula* × *pubescens*, var. *urticifolia*. Transitions between male and female dichasia. *p* perianth segments, *a* stamens or stamen-like structures, *b* scales. See further the text. About × 10.

wings, there was a stamen-like structure (*a*) that at its edge was united with a large tepal-like wing, forming a fold beside the stamen, and one of the side-flowers had a very tepal-like lobe (*p*), at the base passing into a wing. In Fig. 47 *D—E* a continued reduction of the side-flowers is very conspicuous; in them there appear stamen-like structures and free lobes, which in some cases are to be regarded as perianth-leaves; in the terminal flower there are also such. In the dichasium reproduced in Fig. 47 *F* the terminal flower consists of a carpel with a stamen-like structure at either side, with a wing at the edge, and the side-flowers have here almost disappeared, being reduced to narrow scales. From this it is no great step to uniflorous dichasia, either with two stamens in the flower and a rudimentary pistil, a rather common condition (Fig. 47 *G*), or with two stamens only (Fig. 47 *H*), occasionally with a pistil only (Fig. 47 *I*). (One or two of the bracteoles often also disappear in these uniflorous dichasia.) In all the cases perianth-like segments may be observed at the place of the fruit-wings.

In some of the above-mentioned instances a distinction may be seen between the upper free point of the fruit-wing and the lower adnate part of it (Fig. 47 *A*, *p*, to the right in the central flower); sometimes the upper part is also flattened in the opposite direction to the fruit-wing (Fig. 47 *C, p*). It appears as though similar conditions were here met with as in the genus *Nothofagus*, where the fruit-wings pass upwards into perianth-leaves, only forming erect points in their prolongation. The reduction is only stronger within *Betulaceae*. As the perianth-leaves of *Nothofagus* may bear a gland on their top, in several *Alnus*- and *Betula*-species there occur, as demonstrated by ABBE (1935, 1938), glands at the ovary in the same position as was to be expected of the perianth-leaves, according to this author representing the points of the perianth-leaves, the rest of which are fused with the ovary wall.

With respect to the stamen-number there is a similar variation and a similar line of development as in the perianth of the staminate flower. The great majority of *Alnus*-species have regularly four stamens. In exceptional cases, however, strong deviations occur: thus *A. cremastogyne* and *A. lanata* of the section *Cremastogyne* have only four stamens in the dichasium, two in the central flower and one in each of the side-flowers (ABBE, 1935, cf. Fig. 46 *E, F*). In *Betula B. Maximoviczianа* shows about the same conditions as those predominating in *Alnus*; most *Betula* species, however, have a reduced stamen-number, generally two in each flower, and in ser. *Humiles* the number is often only one. With regard to the shape of the stamens a development may be followed from almost undivided stamens in *Alnus* to deeply cleft ones in *Betula*; *B. Maximowicziana* however has, as *Alnus*, an undivided filament. Only the anther is more or less divided in *Alnus*, the filament is entire, except in abnormal forms like that reproduced in Fig. 48 *E—F*, where some of the stamens are more deeply cleft, indicating that the tendency is also present in *Alnus*. Within § *Humiles* of *Betula*, for instance *B. glandulosa* has undivided filaments, but they are here very short, almost unexisting; in *B. pumila*, which has somewhat longer filaments, they are obviously cleft at the top, and the fact that a cleavage is not observable in other cases is no doubt due to the reduction characteristic of the series. In § *Clethropsis* of *Alnus* the stamens are furnished with far-projecting filaments.

The pistil consists as a rule of two carpels, but, as demonstrated by ABBE (1935, 1938), trimery not infrequently occurs, which makes this author assume trimery to be the original state and the dimery to have arisen through reduction. The opinion seems well-founded, but I cannot endorse ABBE's assumption that the oblique position of the carpels in the side-flowers is due to the disappearance of the adaxial (transverse) carpel. When *Betula lutea* gets a trimerous pistil, which

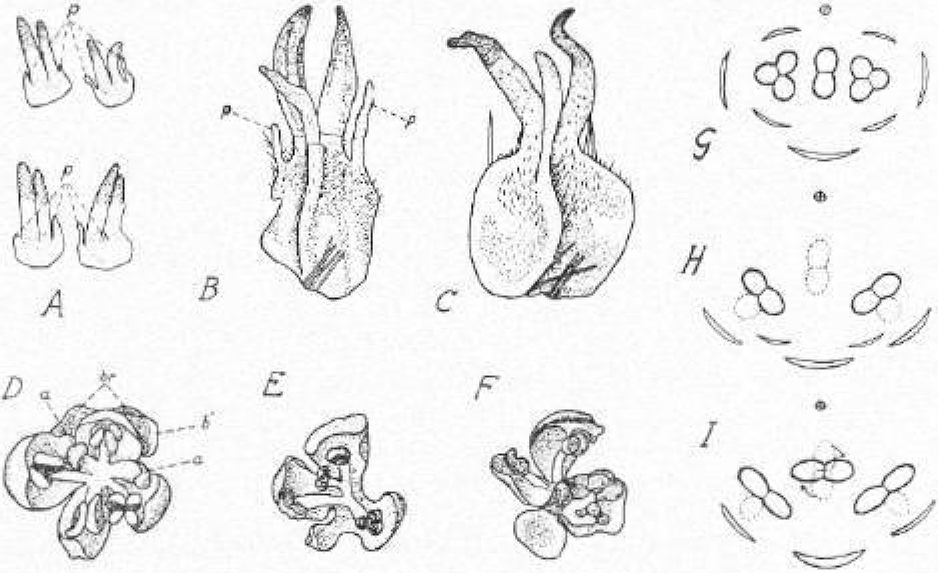


Fig. 48. *A* female flowers of *Betula lutea* with perianth-segments (*p*); *B—C* trimerous female flowers of the same at a later stage, *B* side-flower seen from the abaxial side, *C* terminal flower seen from the axis (*p* perianth-leaves); *D* male flower of *Alnus glutinosa* in a uniflorous dichasium with two small bracteole-like structures (*a*) at one of the stamens; *E—F* male flowers of a laciniate *Alnus incana* with divided stamens, one of them with a rudimentary pistil; *G* theoretical diagram showing the original organization of the female dichasium; *H* change for reaching the *Alnus* type; *I* change for reaching the *Betula*-type. *A—C* about × 20, *D—F* × 10.

not infrequently happens, the side-flowers have their third carpel on the abaxial side (Fig. 48 *B*). This must, as far as I can understand, be interpreted to the effect that it is the median of the three original carpels which is usually absent, while the two remaining, originally transverse ones have assumed a diagonal position (Fig. 48 *I*) as a result of torsion under the pressure of the surrounding leaves. If the terminal flower in *Betula lutea* gets a third carpel, this becomes — in the rather numerous cases I have observed — adaxial (Fig. 48 *C*). Abbe (1938) however states that this additional carpel may be abaxial in other species. In *Alnus* a terminal flower sometimes occurs with two median carpels (Abbe 1935). For these reasons it seems probable that the original condition was that occurring in *Nothofagus*, with two median carpels in the terminal flower, which in *Alnus* have totally disappeared, in *Betula* have been turned by the strong pressure into a transverse position (cf. Figs. 48 *G—I*). When the third carpel, which also here was once present, again appears, it may consequently be both adaxial and abaxial.

We come, then, to the question of the origin of the flower in *Betulaceae*. The stamens are here markedly superposed. Thus, for instance, it is stated by WOLPERT (1909) that when in certain flowers the number of stamens increases exceptionally to 5 or 6, a 5th and 6th perianth-leaf also appear, supporting the additional stamens (WOLPERT, 1909, Taf. I). This strong connection between perianth-leaf and stamen above it may of course suggest a pseudanthic nature of the flower, but it is no proof of it. Such should especially be sought within the genus *Alnus*, which as shown above, has proved to be the most original. It appears as though there is at least a strong support for the pseudanthic theory in a structural aberration that I observed in *Alnus*. In a flower of *A. glutinosa* (Fig. 48 *D*), and likewise in one of *A. incana*, two narrow leaves occurred above a perianth-leaf, one at either side of the stamen. They thus had exactly the same appearance as the bracteoles of a flower and argue strongly in favour of the view that the present flower corresponds to a whorl of simply built flowers, its perianth to a whorl of bracts. Possibly the same thing may be substantiated by the fact that in the cases where the stamens are branched, which occurs in laciniate forms, this ramification may take place in different planes, so that a small bushy group is formed above a perianth-leaf (Fig. 48 *E*, *F*).

In the development of the fruit there is the difference between the two genera that as a general rule *Betula* has a well-developed fruit-wing and good fruit-dispersion by the wind, whereas *Alnus* generally has a poorly developed wing and little effective wind-dispersion. Sect. *Alnobetula* of *Alnus* also in this respect is transitional to *Betula*, and in this genus the series *Costatae* in conformity with *Alnus* has a poorly developed fruit-wing. It may thus be said that *Betula* has a fruit development that biologically viewed is more appropriate, which is a further reason for regarding this genus as more advanced. In its fruit-wing, too, § *Humiles* gives proof of reduction.)

In an embryological respect the family is primitive, with several peculiarities that are reminiscent of the Gymnosperms or otherwise are original. According to the investigations of WOLPERT (1909), the ovules in *Betulaceae* were originally four in number, issuing from two parietal placentas, two from each of them. Two of these ovules, however, are as a rule suppressed, and of the two remaining only one is developed into seed. The two placentas grow together into one, and the pendulous, epitropous and unitegminous ovules then take up a position that should not need to change very much for the arising of the common type of *Juglandales*. The development of the embryo-sac (BENSON, 1894; WOLPERT, 1909) proceeds without any great deviations; there is no true sporogenous tissue, nor any *caecum*-structures, as in *Fagaceae*. In contradistinction to this family however a typical chalazogamy occurs here (NAWASCHIN, 1893; BENSON, 1894), and the pollen-tube also shows — compared with *Fagales* — the peculiarity that it forms blind ramifications (BENSON, 1894).

The relationships within the family will be quite clear from the preceding account. Of the two genera *Alnus* is the more original, *Betula* more derived. Some conclusions may also be drawn with regard to the sections of the genera. § *Alnobetula* of *Alnus* forms in several respects a transition to *Betula*, whereas § *Clethropsis* is probably very original. Within *Betula*, § *Costatae* is the most original, § *Humiles* the most derived and reduced. A more uncertain position is occupied by § *Cremastogyne* of *Alnus*; it is in some respects more reduced than *Alnobetula*, but also exhibits some original features. Within *Betula* § *Acuminatae* also has a somewhat uncertain position compared with *Albae* owing to the variation that is found within the series; on the whole, however, it may doubtless be regarded as more original.

The relation of *Betulaceae* to other families and orders may appropriately by discussed first when the whole order has been treated.

Family 2. Corylaceae.

(*Corylaceae* A. DC. Prodr. XVI, 2, 1864, p. 124; *Betulaceae* trib. *Coryleae* WINKLER Das Pflanzenreich IV, 61, 1904, p. 18, 19, et al. auctt.)

Important earlier literature: EICHLER, 1878; PRANTL, 1889; BENSON, 1894; WINKLER, 1904; ABBE, 1935 and 1938; BOBROV, 1936; HAGERUP, 1942.

With regard to the arrangement of the catkins the genera *Carpinus* and *Ostryopsis* form a special type: the male catkins spring here from the axils of last year's leaves and the female catkins are terminal on leafy side-branchlets generally emanating higher up at the one-year old branches (Fig. 49 *a*). *Carpinus* sometimes has — on small branches — the male catkins placed right up to the branch-points, but the uppermost, seemingly terminal, catkin also springs from a leaf-axil, and a

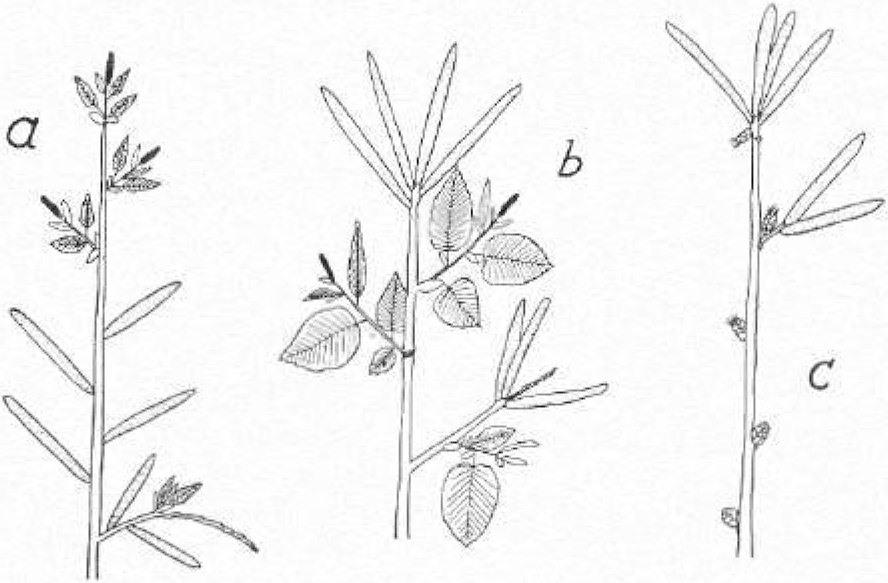


Fig. 49. The arrangement of the catkins within *Corylaceae*, schematically. *a Carpinus* (about the same in *Ostryopsis*), *b Ostrya*, *c Corylus*.

small tip may be observed on the opposite side, representing the point of the main axis; the catkins are thus all lateral. In this respect, accordingly, there is a deviation from *Betula* and *Alnus*, § *Alnobetula*, to which groups the type otherwise shows great resemblance. In the literature it is usually stated that the male catkins of *Carpinus* pass the winter enclosed in buds. This, however, is not quite correct. It is true that in some individuals of *Carpinus Betulus* these catkins are almost entirely covered with bud-scales, only the outermost point being visible, but often a large part of the catkin projects and the basal part only is surrrounded by bud-scales. And in *Carpinus Tschonoskii* the male catkins pass the winter without protection, as in *Ostryopsis*; there are certainly some empty catkin-scales at the base of the catkin, but this is also the case in for instance *Ostrya* and *Corylus*.

The genus *Ostrya* (Fig. 49 *b*) has the male catkins gathered in dense clusters at the branch-tips, where they pass the winter without protection, whereas the female catkins are developed as in *Carpinus*. Exceptionally there are lateral male catkins below the female catkins of the last year, generally only one, sometimes (Fig. 49 *b*) more. The *Ostrya* type is very reminiscent of *Betula*, though there are certain differences which make it more closely attached to the *Carpinus* type, to which it certainly should be traced back. The male catkins are here developed on short summer-shoots which appear at the branch-tips in June—July and besides these catkins only bear strongly reduced leaves. The catkins spring from the axils of these leaves; as there is also such a leaf close to the uppermost catkin and as the main axis is zigzag-curved right up to the tip, all catkins are certainly lateral. Such a summer-shoot corresponds undoubtedly to a catkin-bearing year's shoot of *Carpinus*, which has been reduced and contracted owing to a proleptic development.

The catkin arrangement of *Corylus*, finally (Fig. 49 *c*), belongs to a third type. Here, the male catkins are clustered on side-branchlets emanating from the axils of last year's leaves. These branchlets are sometimes long, with a larger number of catkins (*C. colurna*), sometimes shorter, with some few catkins (*C. avellana*), and bear strongly reduced leaves; only exceptionally was it observed that in *Corylus avellana* a leaf with assimilating lamina occurred at the lowest catkin of a branchlet. The lower catkins emanate from the axils of the reduced leaves; the uppermost is seemingly terminal. A difference from the catkin-bearing shoots of *Ostrya* is that in *Corylus* there often occurs a branch with a female catkin (or two to three such branches) below on these side-shoots; in addition, however, such branches with female catkins — as in other genera leafy and with terminal catkins — emanate from the one-year old branches. The branches with male catkins appear in summer from buds surrounded by bud-scales; as in *Ostrya* it is surely also here a case of proleptic development.

While in *Betulaceae* and even *Juglandaceae* a development may be followed from catkins that pass the winter without protection to female, possibly also male, catkins enclosed in buds, the development seems in *Corylaceae* to proceed in the opposite direction: the family may be traced back to a type where all catkins are — as in *Fagaceae* — enclosed in buds during winter, and development advances towards unprotected male catkins. These different conditions might be explained by the fact that two different tendencies assert themselves for biological reasons, one working for winter protection of the catkins, especially of the delicate female catkins, the other working towards a full development of the catkins already in the autumn, so that anthesis becomes so early that the pollination (by wind agency) may take place before leaf development and also the longest possible time is obtained for fruit development. The former tendency appears in *Betulaceae* and

Juglandaceae, the latter in *Corylaceae*, where the interests of protection are already satisfied in the original types and a beautiful combination of both biologically advantageous factors is attained in *Corylus*, where anthesis may entirely take place before leaf development by the stigmas of the female catkins projecting between the bud scales, while the female catkins, thanks to this arrangement, are nevertheless enclosed in buds.

The organization of the dichasia and flowers was recently investigated by ABBE (1935, 1938), who as in the case of *Betulaceae* has made penetrating morphological and anatomical examinations. Through elucidation of the course of the bundles in the staminate flowers he has shown that these are in reality formed by three flowers, i.e. are reduced dichasia of the same type as occurs elsewhere in the order. That this is the fact is also confirmed by the cases in which additional bracteoles and perianth-leaves occur in the genus *Corylus*. ABBE (1935, 1938) reports instances of this for *Corylus americana, maxima* and *Vilmorinii*. In *Corylus colurna* similar conditions occur in the bisexual flowers that are sometimes found in the male catkins, with one or two carpels, formed through transformation of one or two stamens (Fig. 52). In these cases there are as a rule one or two or even (Fig. 52 *c*) three extra scales in the flower, on the adaxial side. At least the middle of these scales, which is higher inserted than the others, must be a perianth-leaf; judging from their lower position the two other scales are probably secondary bracteoles. In any case the number and position of these leaves argue in favour of the view that we have here three flowers that have fused with each other, a fact that, as previously mentioned, is confirmed by the anatomical examinations of ABBE. In contradistinction to the female dichasia the male dichasia are thus furnished with a terminal flower, as in *Alnus*.

The involucre formed by the bracteoles is developed in the family as a separate covering round each fruit, undoubtedly a biologically more advantageous and a more derived condition than when all bracts and bracteoles of the dichasium, as in *Betulaceae*, fuse into one scale. In the genus *Carpinus* the involucre in such a species as for instance *C. Betulus* is without doubt of an original organization, a three-lobed scale with a larger mid-lobe formed by the bract and two smaller side-lobes formed by the bracteoles. Even within the same genus, however, there are different variations of this organization: *Carpinus japonica* has the one, adaxial, bracteole split off as a free leaf, while the other is quite connate with the bract, and several species have a more marked

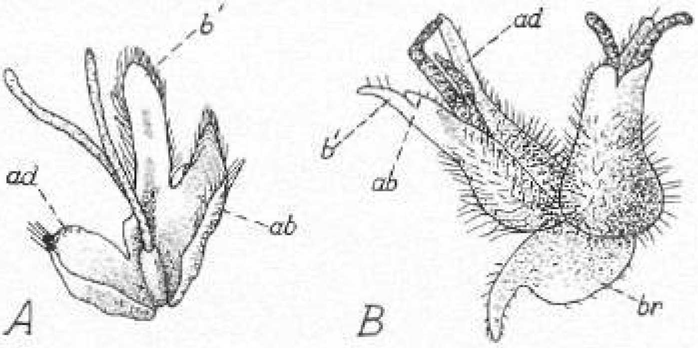


Fig. 50. *Ostryopsis Davidiana*. *A* female flower with involucre; *B* dichasium with two young fruits. *br* bract, *b'* primary bracteole, *ad* adaxial, *ab* abaxial secondary bracteole. *A* about × 20, *B* about × 8.

lobe at the side of the axis, often folded in round the fruit, whereas on the abaxial side there is no distinct lobe, only a serrate border, which may sometimes (*C. erosa*) also be folded in round the fruit. In some species no lobes are discernible.

Those types that occur in *Ostryopsis* and *Ostrya* may easily be thought to have arisen out of this variation series. *Ostryopsis* has at an early stage (Fig. 50 *A*) an involucre that is rather much reminiscent of *Carpinus Betulus*, though the adaxial lobe is somewhat more separated from the other involucre, but at a later stage (Fig. 50 *B*) it becomes pronouncedly bipartite in a way somewhat reminiscent of those *Carpinus* species which have a more distinctive adaxial lobe. The bag-shaped involucre of *Ostrya* shows attachment to the type within *Carpinus* where the involucral leaves unite into a single lobe, as also to such a type as occurs in *C. erosa*, where the involucre surrounds the nut.

In the genus *Corylus* the involucre is stated by some authors, e.g. VAN TIEGHEM (1906) and ABBE (1935), to be composed of two secondary bracteoles, while the primary bracteole is suppressed. VAN TIEGHEM comes to this result mainly through a discussion of the different orientation of the carpels in *Corylus* and *Carpinus*; in the latter genus he thinks the secondary bracteoles are lacking. From observations of the involucre of a *Corylus* species as *C. avellana*, however, where the two leaves of the involucre are usually distinct, it appears that the abaxial leaf is distinctly larger than the adaxial, and further that at the outside of the dichasium it regularly surrounds the

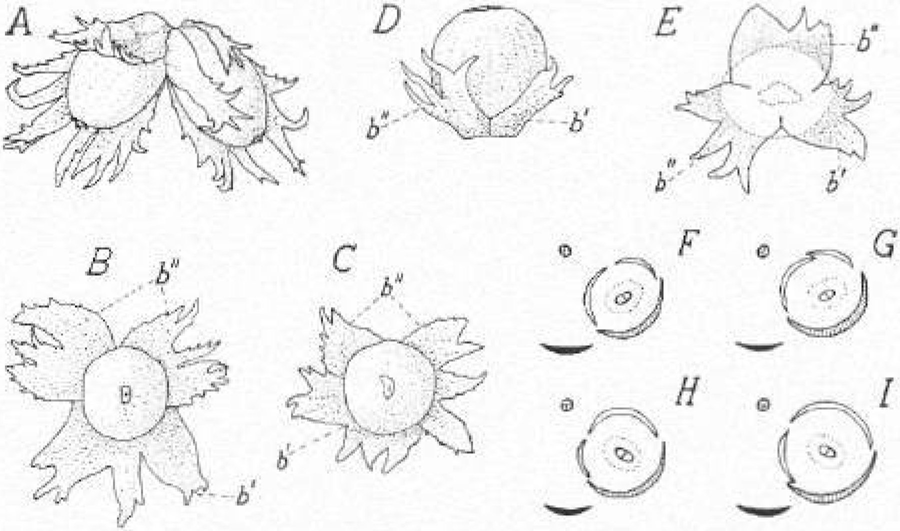


Fig. 51. *Corylus avellana.* *A* two fruits, one of them with two-leafed, the other with three-leafed, involucre; *B—C* fruits with three-leafed involucre; *D—E* involucre, in which one of the secondary bracteoles is somewhat connate with the primary, from the side (*D*) and from above (*E*); *F—I* diagrams showing the development, only one flower of the dichasium designated, the bract black, the primary bracteole streaked. See further the text. *A—E* nat. size.

latter, whereas the condition varies on the opposite side. This gives rise to the supposition that not only two secondary bracteoles are participating. The matter is more closely elucidated by the conditions in the 3-leaved involucres which not uncommonly occur, especially on certain individuals. The three leaves, the primary bracteole and the two secondary ones, may here have the position relative to the carpels that is shown in Fig. 51 *B*, where the two carpels — which are arranged in the longitudinal direction of the fruit — are very nearly median to the primary bracteole and the two secondary bracteoles stand one on each side of the somewhat flattened fruit. In other cases (Fig. 51 *A*) the carpels are nearly transverse to the primary bracteole, and the secondary bracteoles are both placed on the same side of the greatest diameter of the fruit. The most common condition, however, is probably that the carpels are more or less oblique in relation to the primary bracteole (Fig. 51 *C*); the secondary bracteoles are then arranged as in the first case (in this the carpels are, indeed, not exactly median, but a little diagonal, as is shown by the margin of the primary bracteole reaching somewhat further backwards on one side of the fruit than on the other). These different positions are, as is shown by the diagrams Fig. 51 *F—I*, due to the varying position of the carpels, while the bracteoles have about the same position in the different cases in relation to bract and main axis. It may however now sometimes also be observed that two of the three involucral leaves grow together, so that they are still free in their upper part and a feeble suture below denotes the line of coalescence (Fig. 51 *D—E*). Such a coalescence may take place either between the primary bracteole and one of the secondary (Fig. 51 *D—E, I*), or between the two secondary (Fig. 51 *G*), depending on whether the secondary bracteoles are placed on different sides or on the same side of the greatest diameter of the fruit.

These actually occurring cases argue in favour of the two-leaved involucre being formed by participation of the primary bracteole too, which either together with a secondary bracteole forms the one leaf, while the other is formed by the other secondary bracteole, or also alone forms the one leaf, while the two secondary bracteoles form the other. In the former case we get a parallel to the conditions found in *Ostryopsis*, possibly also in some *Carpinus* species, in the latter case there is a certain similarity with *Ostrya* and for instance *Carpinus Betulus*. By the anatomical investigations undertaken by ABBE of the *Corylus* dichasium it is certainly shown (reproductions in ABBE, 1935, p. 20, Figs. 110—117, of *Corylus cornuta*) that no bundles branch off to a primary bracteole (secondary bract according to ABBE) below the ramifications to the secondary; on the contrary, the branching takes place later, higher up, at the point where the primary bracteole might be expected. This, however, is also completely the case in *Ostrya* (ABBE, l.c., Figs. 125—134) and might be accounted in the same way as ABBE explains it here, viz. by the primary bracteole being grown together with the shoot emerging from its axil.

A perianth is lacking in the male flower of *Corylaceae*. Only in abnormal cases has it been observed, and then only in the genus *Corylus*, which is also deviating from the others by the regular occurrence of bracteoles in the staminate flower. Some examples of a perianth in the male flower of this genus are — as mentioned above — reported by ABBE (1935, 1938), who observed up to five scale-like perianth-leaves in a (part-)flower, and in Fig. 52 another instance is shown, though it is not quite a comparable one owing to the flowers not being pure male flowers but bisexual. Within the genus *Carpinus* there may, as is shown by Fig. 53, also occur flowers that only contain

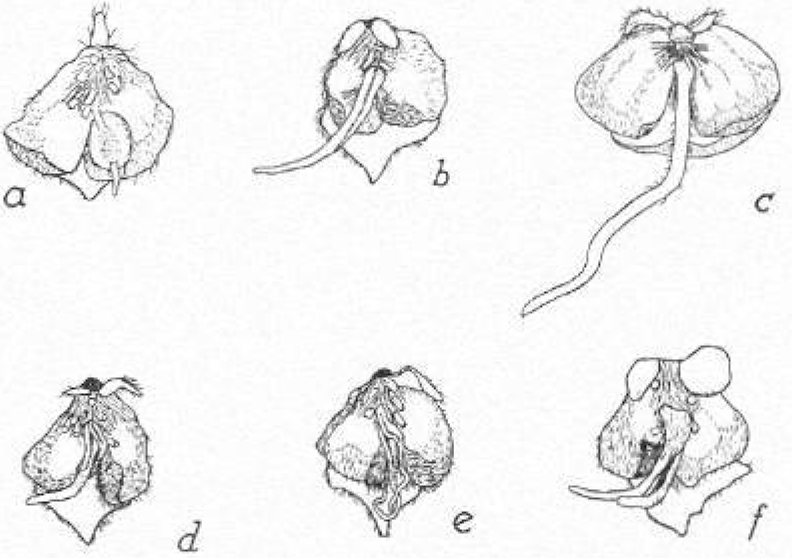


Fig. 52. *Corylus colurna.* Transitions between male and female flowers, with structures intermediate between stamens and carpels (*a*), one carpel (*b*—*c*), or two free carpels (*d*—*f*). One extra scale in *a* and *e*, two in *b*, *d*, *f*, three in *c*. The stamens cut off. About × 10.

stamens and yet have a perianth; also in this case however the flowers are transitional between staminate and pistillate; on a further development towards staminate flowers the perianth-leaves disappear more and more; they are transformed — in any case to a great extent — into stamens.

In contradistinction to the staminate flower the pistillate flower has a perianth, though weakly developed, present in all genera. In some cases, for instance in *Carpinus* and *Ostrya*, it may be seen that two transverse and two median perianth-leaves are favoured, though great irregularities occur. The original condition, at least in *Carpinus*, is however certainly not a tetramerous perianth. This is evident for one thing from the transitions between male and female flowers that sometimes occur, especially frequently in *Carpinus Betulus* var. *incisa* (Fig. 53). In these flowers the perianth-leaves are detached from the ovary and form free, sometimes two- or three-parted lobes. It is evident from this that they are of both indefinite number and indefinite position; they are reminiscent of the irregular scale circles surrounding the flowers of many other *Amentiferae*.

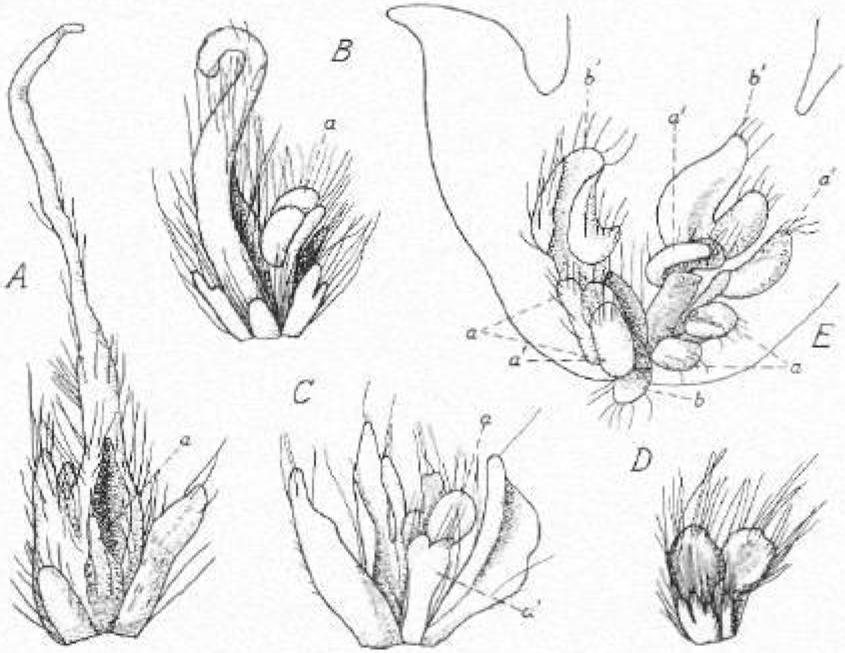


Fig. 53. *Carpinus Betulus* var. *incisa*, transitions between male and female flowers. *A* flower with a carpel open below and a transition between carpel and stamen (*a*); *B* flower with a similar carpel and one stamen (*a*); *C* flower with two somewhat stamen-like structures (*a* and *a'*); *D* flower with two small stamens; *E* flower with two large transitions between scales and stamens (*b'*), three stamens with a half anther each (*a'*), 2 stamens with complete anthers (*a*) and a small scale (*b*). In *A* two perianth-leaves are adnate to the ovary, two free; in the other flowers the perianth-leaves are free. About × 20.

Some *Carpinus* species, as *C. Tschonoskii*, have a strongly reduced perianth in the female flower, and in the genus *Corylus* it is also much reduced. As is shown by HAGERUP (1942), in early stages the perianth is inserted at the base of the ovary; first in the later development it is raised through intercalary growth to the top of it. A similar change of position was earlier mentioned for *Juglandaceae* (*Oreomunnea*).

The stamens are as a rule deeply cleft in the family, in the same way as within *Betulaceae* in most *Betula* species. According to an old record (PRANTL 1889), the filaments in the genus *Ostryopsis* are undivided; other authors state that they are divided, and this is also the common condition, though occasionally undivided filaments may occur, which are as a rule particularly short; probably it is a matter of an occasionally occurring reduction (cf. *Betula* § *Humiles*). An exception is constituted by *Corylus ferox* in the section *Acanthochlamys* of *Corylus*, where the filaments are entire, only the anther being more or less divided. (Probably the condition is the same in the other species belonging to the section, *C. tibetica*.) In other species, as *C. avellana*, however, they are very deeply split, down to the base. It must be assumed that the tendency to this is also present in § *Acanthoclamys*, which is regarded by BOBROV (1936) as the most original in the genus, though it does not appear until in more derived forms (cf. *Alnus*).

The number of the stamens in the genera *Corylus* and *Ostryopsis* is considerably smaller than in *Carpinus* and even smaller than in *Ostrya*. Frequently there are in the former genera only four stamens in a — compound — flower, i.e. two stamens in the original terminal flower and one in either side-flower (cf. ABBE, 1935). This must be interpreted as a proof of reduction of the male flowers in these two genera.

The two carpels in the family have a somewhat varying position. According to ABBE (1935), they are transverse in *Ostrya* and *Carpinus*, diagonal in *Ostryopsis* and *Corylus*. The transverse position in *Ostrya* is very clearly evident from the anatomical investigations of this author, but it may be questioned whether the carpels do not have the same oblique position in some species of *Carpinus* as in for instance *Ostryopsis*. In for instance *Carpinus laxiflora* the fruit at maturation is obviously obliquely placed in relation to the primary bracteole, and for *C. japonica* it seems to be evident from the anatomy as well, as this is represented by ABBE (1935, Figs. 140—151), that the carpels stand in a plane that is not quite parallel to the primary bracteole and directed towards the secondary ones, but at the axis side is somewhat inclined towards the primary bracteole. However, other species of *Carpinus*, for instance *C. Betulus*, have carpels that must be regarded as transverse; the position varies within this genus, and both the type occurring in *Ostrya* and that in *Ostryopsis* may apparently be traced back to different orientations occurring there. The genus *Corylus*, like *Ostryopsis*, has obliquely placed carpels, but, as previously pointed out (cf. Fig. 51), they do not only stand in the same plane as in *Ostryopsis*, i.e. at the outside of the dichasium inclining towards the adaxial side (Fig. 51 *F, G*), but it may also occur that at the outside it inclines towards the side of the primary bract (Fig. 51 *H, I*).

ABBE (1935, 1938) assumes that the diagonal position of the carpels in *Ostryopsis* and *Corylus* has arisen through the suppression of a third, adaxial carpel, placed inside the adaxial secondary bracteole, whereas in *Ostrya* and *Carpinus* a median carpel has disappeared. As regards *Ostryopsis*, however, the assumption is in conflict with the conditions when a third carpel occurs, which is exemplified by ABBE himself (1938). This third carpel is median to the primary bracteole, and the carpels generally occurring must consequently be the two transverse ones; the conditions cannot be altered by the fact that one of these (the abaxial) becomes sterile in the trimerous ovary. Thus, in the same way as in *Ostrya* and *Carpinus* the median carpel seems also to be suppressed in *Ostryopsis*, in direct correspondence to the conditions in the side-flowers of *Alnus* and *Betula*, the carpel opposite the primary bracteole disappearing as here and the two remaining carpels in *Ostryopsis* — in my opinion also in many *Carpinus* species — forming an ovary that as a result of the strong pressure of surrounding organs gets a diagonal position. In *Corylus* the conditions are probably the same. Certainly there are here different positions, which might easily be accounted by the suppression of in one case the median, in the other case the adaxial carpel, but, of course, it is very improbable that these different cases could occur in the same species, as would then have had to be the case. The different positions are therefore presumably only due to a more or less strong torsion of the originally transverse carpels.

Owing to the close relationship with *Betulaceae* and *Fagaceae* it is very probable that, as there, the flower has arisen from an original inflorescence. There are however scarcely any sure proofs of this in the family. Still, there are certain reasons arguing in favour of a parallel being present to the conditions within other *Amentiferae* families. Thus, it has been mentioned that in *Carpinus Betulus*, in the transitional flowers previously mentioned, there occur round the pistil an irregular whorl of scales that are partly transformed into stamens (Fig. 53), this being reminiscent of the pseudanthia described for various families. Further, the easy coalescence of three male flowers into one that takes place in the family is in good agreement with the assumption that the flowers are pseudanthia; such flowers are easily fused with one another, as is evident from earlier instances.

With regard to the development of the fruit special emphasis should perhaps be laid on the difference that exists between *Corylus* on one hand, with its large, rounded, comparatively thin-walled fruit, and on the other hand the other genera, especially *Carpinus*, where the fruit is small, flattened, with a comparatively thick and very hard wall.

Corylus is in this respect somewhat reminiscent of *Quercus*, perhaps also of *Comptonia* in *Myricaceae*, whereas *Carpinus* is more reminiscent of *Betulaceae* and *Pterocarya* in *Juglandaceae*. *Corylus* also differs from the other genera by its hypogeal germination, another similarity to the *Quercus* group within *Fagaceae*.

The inner organization of the ovary resembles that of *Betulaceae*. There are two ovules having the same position and structure as in that family, one of which in normal cases develops further. In at least *Corylus* it has been observed (WOLPERT, 1909; HAGERUP, 1942) that four ovules are primarily laid down, as in *Betulaceae*. In the development of the embryo-sac there are some very peculiar features. According to BENSON (1894), there is in *Carpinus* as well as in *Corylus* a true sporogenous tissue, in which a number of cells get more than one nucleus and — especially in *Carpinus* — several embryo-sacs may develop. As in *Fagaceae*, the embryo-sacs send out *caecum*-structures downwards; in *Corylus* there is generally one such, but in *Carpinus* there are more, and the pollen-tubes, which as in *Betulaceae* take their course through the chalaza, grow by way of these into the embryo-sac.

These conditions differ rather much from those occurring in *Betulaceae* and are, like corresponding peculiarities in *Fagales*, to some extent reminiscent of *Casuarina*, as a matter of fact more so than in this order.

The relationships within the family are quite clear as regards the three genera *Carpinus*, *Ostrya*, and *Ostryopsis*. Among these genera *Carpinus* must be regarded as the one showing the most primitive features, and likewise the greatest variation, and the two others represent a further development of certain different types in this genus with respect to inflorescence-arrangement, involucre, the position of the carpels, etc. The development has also brought about a certain reduction, as, for instance, in the number of stamens. The genus *Corylus* shows some divergence from the other evolutionary line. In several respects it agrees most with the more advanced forms of this, but it also shows some deviating features that appear original, for instance the occurrence of free bracteoles in the staminate flower and also the hypogeal cotyledons. These deviations, however, surely need not mean that the genus has another origin and should be referred to a particular family; there are also great agreements with the other genera and it seems very probable that *Corylus* may also be traced back to a type that is close to *Carpinus* and that the deviating features — or the tendency to these — have been present in the original type common for the family.

On a comparison between the families *Corylaceae* and *Betulaceae* it must be said that in its floral morphology the family *Betulaceae* on the whole represents a more primitive type. Especially is this evident as regards the male flowers, which in *Corylaceae* are strongly reduced and coalesce in threes. The development of an involucre round each fruit must certainly also be regarded as a more derivate feature, biologically advantageous, than the common catkin scale in for instance *Alnus*, which is without significance for fruit dispersion. The two families are without doubt closely related, and have also often been united into one. It seems however scarcely possible that the genera belonging to *Corylaceae* have directly developed from the types of the *Betulaceae* genera; the involucre has for instance quite too different an organization, and in the embryology, considerably more primitive features must be said to prevail in *Corylaceae*, indicating a more direct connection with *Fagales*. The two families, thus, have probably rather developed separately from a common origin and should consequently be kept apart from one another.

The order *Betulales* is most closely related to *Fagales*, with which it is generally united. Several morphological features may have arisen through a further development of characters occurring in *Fagales*, there being, as mentioned above, an especially close attachment to the *Fagus* group. Yet there are also considerable differences. There is no stem-cupule in *Betulales*, whereas bract and bracteoles develop in special ways that are not found in *Fagales*. In the male flower there are phenomena of coalescence that are reminiscent of *Juglandales*, the female flower in for instance *Carpinus* has a perianth whose irregularity is certainly not solely due to reduction, a typical chalazogamy occurs. Some of these characters are reminiscent of *Juglandales*, others of *Casuarinales*. To the latter group there is also a similarity as regards the stamens, which here as in *Betulales* show a tendency to splitting, and in the bracteoles, which here as in *Alnus* are lignified at fruit stage, the inflorescence thus being cone-like. How the phylogenetic lines are running that connect *Betulales* with other groups than *Fagales*, is not easy to say; we must confine ourselves to the statement that there must certainly exist some such connection, which justifies *Betulales* being regarded as an order of its own. This order should therefore be considered as having arisen through some changes of the *Fagales* type and some contributions from other sides.

Order 6. Salicales.

Family Salicaceae.

Important earlier literature: EICHLER, 1878; HEGELMAIER, 1880; VELENOVSKY, 1904; NAKAI, 1920, 1930; GRAF, 1921; GOMBOCZ, 1924—1925; RAINIO, 1926; FISHER, 1928; KIMURA, 1928, 1938.

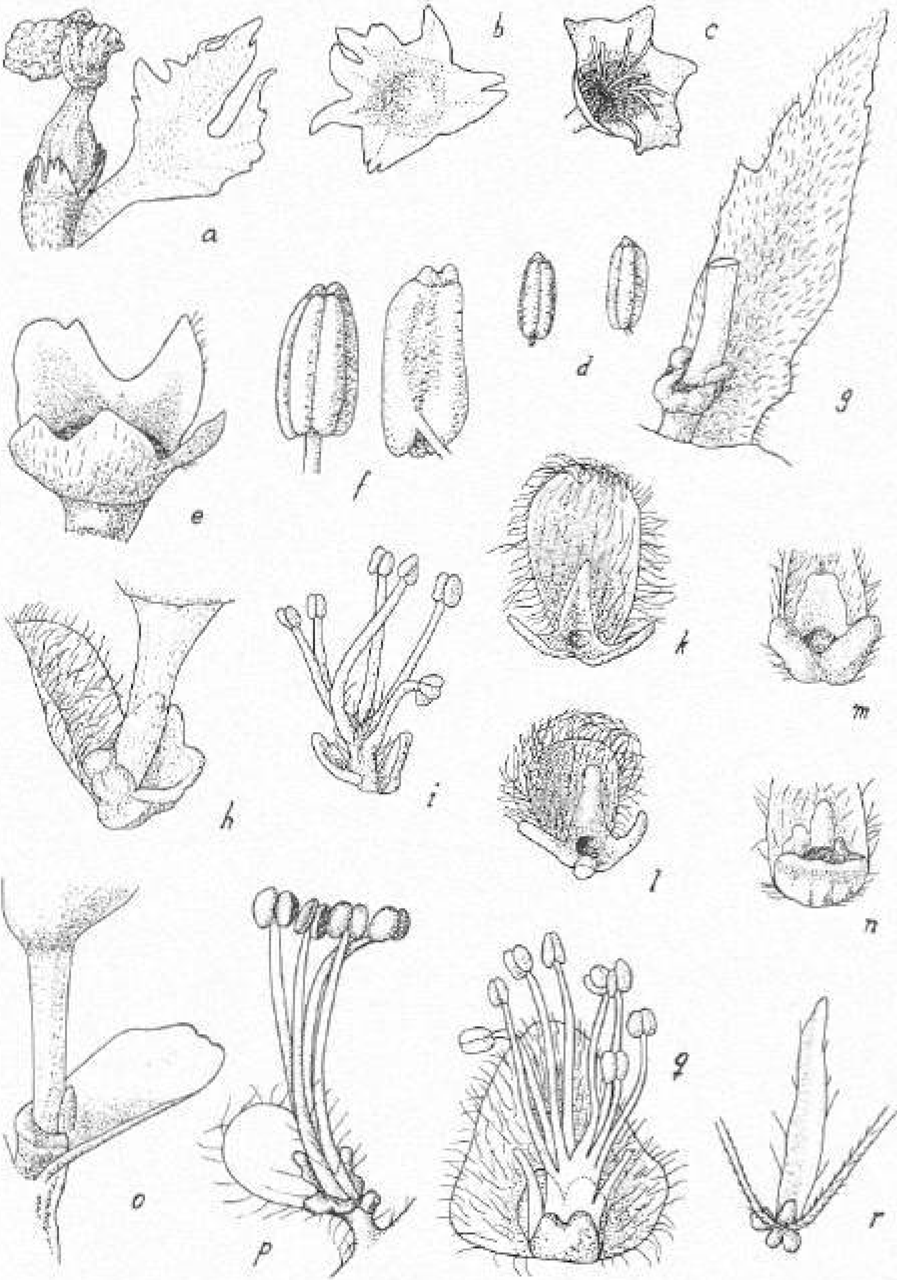
The inflorescence is in *Salicaceae* a simple, unisexual catkin. In *Populus* both male and female catkins, which in the family always occur on separate individuals, are slack and pendulous, in *Salix* they are generally stiff and erect; some species, however, have more or less overhanging catkins and in *S. bracteosa*, which is sometimes referred to a genus of its own, the male catkins are pendulous and slack as in *Populus*, whereas the female ones are erect. The development of the catkins is of course associated with the fact that wind-pollination takes place in *Populus*, whereas insect-pollination prevails in *Salix*; an exception is formed only by the *S. bracteosa* mentioned (NAKAI, 1930, p. 48—49), and possibly by some other species (FISHER, 1928, p. 388).

The organization of the flower has — in comparatively recent times — been elucidated in a meritorious manner by FISHER (1928), who made thorough-going anatomical and morphological examinations of a large number of *Salix* and *Populus* species. Regarding the bract, this author points out the great agreements between the thin, incised bract of *Populus* and the generally coarser, undivided of *Salix*. This must indicate that they are homologous to each other, in contrast to the supposition of NAKAI (1930), but FISHER is of the opinion that they are not the true bracts of the flowers at which they are situated, as they not only spring from the pedicels but also the supporting vascular bundles are not detached from the main axis but from the bundle that runs to the flower. That the bracts of *Salix* and *Populus* are homologous, may also be considered to be confirmed by the fact that in some *Salix* species (*S. dictyoneura* BOCK & ROSTH., *S. Humboldtiana* WILLD., ANDERSSON, 1867, and others, cf. Fig. 54 *g*) there occurs a somewhat incised bract, while in *Populus* there may occur an almost entire one (*P. alba,* Fig. 56 *i*; in *P. lasiocarpa* the bract is shallow-lobed, but of a different shape from *Salix,* broader upwards). As regards the position, it is known that in many other *Amentiferae* the bract may grow together with the flower supported by it, and it is probable that also here we have such a coalescence, which in this instance has advanced so far that the two vascular bundles have also been partly united. From the investigations of ABBE (1935) on *Betulaceae* it is evident that here the bundle of the bract very often issues from the vascular tissue running to the flower; only in exceptional cases, as in the original *Alnus nitida,* does it apparently occur (ABBE, l.c., Fig. 42) that it already detaches itself at the common point of departure of the vascular tissue.

A matter that has been the object of great attention by several investigators of the flower is the so-called disc that is found in *Populus* as a plate- or cup-like structure in both male and female flower, in *Salix* generally as one or a few glands, often of unequal development in staminate and pistillate flower.

There has been some uncertainty whether this disc of *Populus* and these glands of *Salix* are in reality homologous structures (cf. HEGELMAIER, 1880). As pointed out by GOMBOCZ (1924—1925) and others, in the section *Turanga* of *Populus* (e.g. in *P. pruinosa,* cf. Fig. 54 *a*—*c*) there is a deeply lobate disc (especially in the female flower), which forms a transition to those *Salix* species that have a complete whorl of glands in the flower which are united below (see for instance Fig. 54 *h*). The structures are consequently regarded as homologous. Also within the section *Leucoides* of *Populus* the disc is lobate (Fig.

Fig. 54. *a* female flower of *Populus pruinosa* with lobate disc; *b* the disc from above; *c* male flower of the same species, disc not so deeply lobate; *d* the same species, two anthers; *e P. Wilsonii,* disc of female flower, from in front; *f* two anthers of *P. lasiocarpa*; *g* female flower of *Salix* sp. related to *S. Safsaf* from Senegal (PERROTTET 1825 as *S. coluteoides*) with lobulate bract and slightly 5-lobate nectarium, open towards the bract; *h* female flower of *S. australis* with cup-like nectarium, a more profound incision towards the bract; *i* the same, male flower from the side, with the stamens in a column; *k S. oritrepha,* female flower (the pistil removed) with three glands; *l* the same, male flower with four glands, the stamens removed; *m*—*n S. elegantissima,* two female flowers, the pistils removed, from the axis; *o S. Warburgii,* nectary of a female flower with a thick wall towards the axis and two thin scales towards the bract; *p* the same, male flower with four nectary-lobes, the adaxial somewhat deviating; *q S. senegalensis,* male flower with two lobate nectaries and the stamens in a flattened column; *r* proleptic male flower of *S. caprea* with four glands. *a, c*—*f* about × 10, *b, g*—*r* about × 15.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54 *e*), though not so deeply and in the female flower not so irregularly (in *P. Wilsonii*, Fig. 54 *c*, often regularly two lobes towards the axis and three towards the bract); on this account and because the disc is not deciduous as in § *Turanga*, it does not appear to be quite so original as here. FISHER (1928), with the support also of her anatomical observations, arrives at the conclusion that the nectary of *Salix* forms a homology to the disc of *Populus*, or to its peripheral parts. She has demonstrated that in some *Salix* species (e.g. *S. Safsaf* FORSK.) the small internode that bears the flower is upwards extended into a cup-like, oblique receptacle, on which the nectary (cup-like in *S. Safsaf*) is located, and has pointed out the great similarity of this receptacle to the disc of *Populus*. The alternative mentioned, viz. that the nectary of *Salix* possibly corresponds to the peripheral parts of the *Populus*-disc, doubtless means that the author thinks the central part of the disc corresponds to the cup-like stem-part of *Salix*, which here passes without demarcation into the nectary, a supposition that in any case also appears very probable in view of the more vigorously developed vascular bundles in the *Populus* disc. By NAKAI (1930), however, it has been supposed that the bract of *Salix* on account of its different nature on the outer and inner side, is — as a rule — formed through coalescence of a proper bract and a part of the nectary; consequently, the nectary structures present in the two genera would then only partly correspond, the disc of *Populus* being homologous to not only the nectary of *Salix* but also to a part of its bract. As a matter of fact, however, even though there is often no nectary above the bract in *Salix*, such is also often present, sometimes even more vigorously developed than at the adaxial side (e.g. *S. capensis* THUNB., FISHER, 1928). In these cases the bract must surely be a bract and nothing more, and it is then also highly probable that this is the condition in other cases too and that the frequent absence of the nectary here is only due to the narrow space at the side of the bract.

With the reservation that some central parts of the *Populus* disc seem to be axial structures, the various »nectaries» may thus be regarded as homologous.

Several suppositions have been made on the real nature of the disc- or nectary-structures. FISHER (1928) gives a survey of these and rejects with good reasons the theories that they are only nectar-secreting emergences or rudimentary stamens. Instead they must be leaf-structures. This is evident among other things from the observations made by that author on the vascular bundles that also in *Salix* may sometimes run to the nectaries, in other cases are only found as reduced vestiges of an earlier vascular tissue to them. VELENOVSKY's (1904) observations on summer catkins (probably proleptic) of *Salix aurita*, where instead of nectaries three free leaves may occur, also argue in favour of their leaf-nature. On the other hand, it is a debatable point whether they should be regarded as bracts or perianth-leaves. Both GOMBOCZ (1924—1925) and FISHER (1928) regard them as a reduced perianth; VELENOVSKY (l.c.), on the other hand, is of the opinion that the posterior gland of *Salix aurita*, which in the summer-catkins is divided into two leaf-like structures, corresponds to two fused bracteoles and that the third leaf, which corresponds to an anterior gland, is to be regarded as a perianth-leaf. He compares the organization with that of the male flower of the *Juglandaceae*, where, besides the two bracteoles, there may sometimes be found a reduced perianth of few leaves. There are reasons arguing both in favour of VELENOVSKY's assumption and against it. On the one hand, in most *Salix* species there can hardly be seen any difference in development between the glandular structures, and nor any regularly deviating position of certain glands, which might justify some of them being regarded as bracteoles. Also in the proleptic *Salix* catkins, observed by the present writer in *Salix caprea*, the number of glands or leaf-structures does not only rise to three but there may also be found four glands of rather irregular arrangement (Fig. 54 *r*). On the other hand, there are sometimes two lateral glands at the adaxial side, often of an obliquely backwards-oriented position, for instance in *Salix oritrepha* SCHNEID. (Fig. 54 *k*) and *S. elegantissima* (Fig. 54 *m*), and, when a solitary adaxial gland occurs, it is often emarginate or bifid. In *Salix Warburgii* SEEM. the adaxial part of the nectary is often thick and coarse, of other nature than the thin abaxial lobes (Fig. 54 *o—p*). A special importance seems to attach to the conditions in *Salix bracteosa* TRAUTV., often referred to a genus of its own, *Chosenia*. The glands have here as a rule disappeared by way of reduction, but exceptionally the female flower contains two small lateral glands (Fig. 58 *a*, cf. also KIMURA, 1938), somewhat displaced towards the axis, thus occupying the same position as the bracteoles in e.g. *Leitneria*. These conditions — that lateral glands are sometimes present and that they at reduction seem to disappear later than the others — indicate that there really are two lateral glands of a special nature, corresponding to bracteoles. In their development, however, they agree with other glands, at any rate in most cases. Perhaps they might all be regarded as a perianth where the bracteoles — as in some other cases — take part in the perianth formation. For a decision on this question certain conditions in the nature of the flower should be taken into consideration. Sometimes it happens in *Salix amygdaloides*, according to FISHER (1928), that the nectaries not only surround the flower exteriorly, but that some small structures are also found around the base of the middle of the three stamens. This argues of course strongly in favour of the flower being a pseudanthium in which each stamen corresponds to an original flower. The same is confirmed, as far as *Populus* is concerned, by certain circumstances that will be discussed later. Those pseudanthia which are found in other *Amentiferae* are surrounded by leaves of bract-nature, which sometimes develop into cupular scales, sometimes into perianth, sometimes to both. To this »bracteal envelope» the disc or nectary of *Salicaceae* probably forms a correspondence, this also in respect of the irregular arrangement, at which small protuberances may be formed considerably further in than the larger outer structures, and to the sometimes occurring emergences also on these (in *Salix amygdaloides*, FISHER, 1928, Fig. 6, also by the present writer observed in an abnormal flower of *S. alba* × *babylonica*). Without doubt they form a correspondence to the perianth in the staminate flowers of *Juglandaceae*, in agreement with the assumption of VELENOVSKY, and likewise to the »bracteoles» of *Myricaceae* and the perianth in the female flower of *Leitneria*. They are however apparently formed by reduction of such undifferentiated a bracteal envelope that it is perhaps not quite appropriate to denote them as perianth. This bracteal envelope has now developed in different ways: from the original type with several leaves around the flower a development has taken place in *Populus* to a uniform plate-like structure and in *Salix* a reduction of varying extent has occurred. Sometimes this reduction brings about the total disappearance of the glands: this is as a rule the case in *Salix bracteosa*. In other cases there seems to be a certain tendency favouring two median and two transverse glands, for instance in the male flower of *Salix Warburgii* (Fig. 54 *p*), conditions that are somewhat reminiscent of, for example, the perianth of *Corylaceae*. With respect to the great irregularity that generally marks the arrangement of the glands — when these are more numerous — these organs seem originally to have been of varying position and number like the members of the bracteal envelope in other *Amentiferae* and not to have developed from a perianth with definite cycles, as is sometimes assumed (NAKAI, 1930, as well as the diagram of VELENOVSKY, 1904, suggests the same assumption, though this author does not apparently regard this plan as the sole ancestral type).

The stamens in the genus *Salix* are either quite few, 1—2, this in the groups *Diandrae* and *Synandrae* of ANDERSSON (1867, 1868), or of a larger number, the group *Pleiandrae* of ANDERSSON. The latter group includes many forms with original characters, among others also a more developed nectary, and on this account the smaller number may certainly be regarded as having arisen through reduction. Sometimes the stamens are united below, either into a bushlike ramose column (e.g. in *S. australis* HILS. et BOJ. ex FR., Fig. 54 *i*), which is very reminiscent of some *Myrica* species, or there are (the group *Synandrae*) only two stamens united below (e.g. *S. incana*), which also has its correspondence in *Myrica*. There may also occur a flattened, transversely extended column (this in *S. senegalensis* MERT. ex AND., Fig. 54 *q*), as there may at times be three stamens in a transverse row (FISHER, 1928, Fig. 6). In *Salix amygdalina* the middle-most of the three stamens is somewhat closer to the main axis and generally develops first at anthesis. Also in other cases it was observed (HEGELMAIER, 1880) that the stamens developed subsequently. While the stamens of most *Salix* species have a central position in the flower and are free from the bract, they are in some species, especially pronouncedly in *S. bracteosa*, carried up on the surface of the bract in a way that somewhat resembles the conditions in e.g. *Corylaceae* (Fig. 58 *b—c*, *e—f*, cf. also NAKAI, 1930, Tab. III and V). In *Populus* they spring from the central part of the obliquely developed disc (Fig. 54 c, 57 *A*), mainly from its larger, anterior part. As stated by HEGELMAIER (1880), the first stamen-primordia are developed in the centre and from there the development proceeds to the anterior part of the disc, to some smaller extent also to the posterior. The stamen-number may rise in *Populus* to about 60 or 70 (*P. laurifolia*); these high numbers, as well as the low numbers in *Salix*, must probably be due to secondary changes. Within the sections *Turanga* and *Leucoides* of *Populus* there occur connective-appendages at the tips of the anthers (Figs. 54 *d* and *f*); for instance in *P. lasiocarpa* (Fig. 54 *f*) they are as a rule emarginate, just as this also may be the case within *Juglandaceae*.

The carpels as a rule are 2 in number, in *Populus* sometimes 3 or 4. Their position, if they are two, has been somewhat differently interpreted. According to RAINIO (1926), who has examined Scandinavian *Salix* forms, even as regards their flower anatomy, the carpels in these are median, with the median placentas on their surface; VELENOVSKY

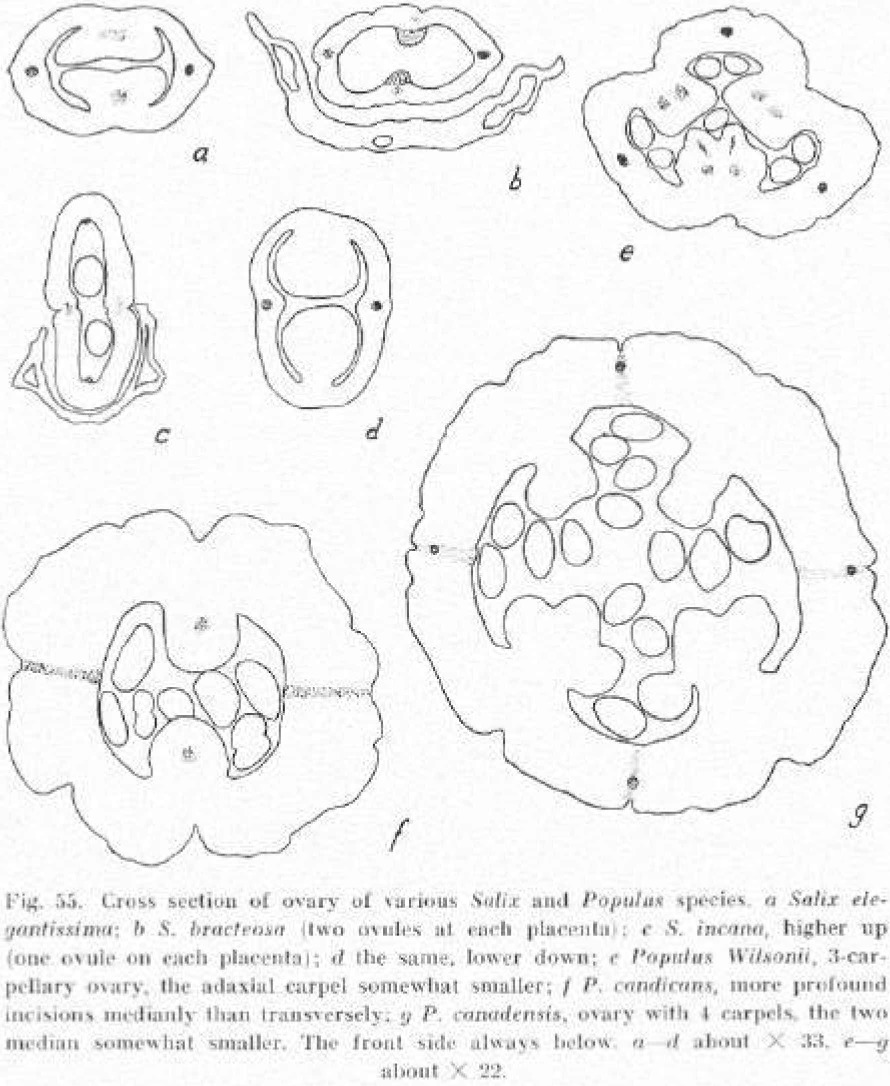

Fig. 55. Cross section of ovary of various *Salix* and *Populus* species. *a Salix elegantissima*; *b S. bracteosa* (two ovules at each placenta); *c S. incana*, higher up (one ovule on each placenta); *d* the same, lower down; *e Populus Wilsonii*, 3-carpellary ovary, the adaxial carpel somewhat smaller; *f P. candicans*, more profound incisions medianly than transversely; *g P. canadensis*, ovary with 4 carpels, the two median somewhat smaller. The front side always below. *a—d* about × 33, *e—g* about × 22.

(1904), Fisher (1928), and most other authors regard them as transverse both in *Salix* and *Populus*, the placentas thus being formed by their edges. From a cross section through the ovary of a more derived species (diandric or synandric) it may undoubtedly appear as though there were two median carpels, the ovary in for instance *Salix incana* being protracted in the median direction and showing deep transverse incisions (Fig. 55 *c*). A corresponding section of other, more original species (Fig. 55 *a—b*), or even lower down through the ovary of the same species (Fig. 55 *d*), shows other conditions, however: the transverse parts are here often thickened, with vigorous nerves, the ovary is frequently protracted in a transverse direction. In *Populus* the cavities are often deeper in the median direction or — if the carpels are more than two — above the placentas (Fig. 55 *e, f*). FISHER (l.c.) states that the median vascular bundles are sometimes split in *Salicaceae* into two, indicating that we here have two meeting carpel-edges, a splitting that also may be observed in for instance *Populus Wilsonii* (Fig. 55 *e*); in this species it is very obvious that the middle of the carpels is halfway between the placentas. Judging from these circumstances, the common interpretation that the carpels — if two — are transverse must be correct. For *Salix* this is also confirmed by the fact that sometimes (in *S. glandulosa* SEEM., NAKAI, 1930) two rudimentary carpels occupying a transverse position have been observed in the male flower.

When the carpels are three in number, which in *Salix* is only found in abnormal cases (observed in *S. fragilis* and *S. aurita* by v. SEEMEN, 1895) but in *Populus* is common in several species, the third carpel is generally median, adaxial, or also median, abaxial. It is often distinctly smaller than the other two (Fig. 55 *e*). As trimery is found in species of *Populus* that appear very original, as *P. pruinosa*, this might be supposed to be the primary and the dimery to have arisen by way of reduction. The theory of a reduction, however, is in conflict with the fact that the carpels are sometimes not only three, but four (even in the same specimen) and that this is found, for instance, in the hybridogeneous *P. canadensis*, thus no original form. In the trimerous and tetramerous gynoecia we probably have on this account instead an augmentation of the original dimerous number, in the same way as the number of the stamens increases in *Populus*.

As regards the stigmas, a development may be followed within *Salix* from carinal to commissural stigmas. In the pleiandric species they are transverse, thus carinal. Within *Diandrae* there are in for instance *S. silesiaca* (Fig. 56 *d, d'*) two transverse, rather horseshoe-shaped stigmas, the one well separated from the other. In *S. caprea* (Fig. 56 *e*) they are somewhat closer to each other, and in *S. daphnoides* they meet (Fig. 56 *f*). The next step is that the segments of the one stigma grow together with corresponding segments of the other stigma; this is sometimes the case in *S. viminalis* and is very beautifully found (Fig. 56 *g*) in the hybridous *S. stipularis* (concerning this see WIMMER, 1866, p. 184); two median, commissural stigmas are thus obtained. In their development the stigmas show great variation, especially perhaps in the pleiandric *Salix* species. Sometimes they are here short and broad, undivided, only with a fold at the middle (Fig. 56 *a* and *c*), sometimes they are extended, lobulate in the margin and united below (Fig. 56 *b*), reminiscent of *Populus*. Within the East-Asiatic series *Urbanianae* and *Chosenia*, on the other hand, they are deeply divided into narrow, round branches (Fig. 58 *a* and *d*).

In *Populus* the stigmas are always carinal. *P. alba* has deeply bifid stigmas, with two rather narrow segments (Fig. 56 *i*), in *P. tremuloides*, which belongs to the same section, the stigmas have a small middle-lobe between the two larger segments (Fig. 56 *k*), and in other sections they are extended, lobate and plicate, and many times larger (Fig. 56 *l*, *m*), which is doubtless connected with the wind-pollination.

A style may both be present and be lacking in *Salix*. Two free styles occur on the one hand in *S. bracteosa* and likewise in *S. Urbaniana* SEEM., in which two species, however, they are slightly united at the base (Fig. 58 *a* and *d*), and on the other hand in *S. glauca* (Fig. 56 *h*), belonging to quite a different group. Within *Populus* the stigmas are generally sessile on the ovary; in § *Leucoides* alone there is a quite short, branching style (Fig. 56 *l*). NAKAI (1930, with figures) has drawn attention to a peculiarity in *Salix bracteosa*, viz. that the stigmas are deciduous, the styles breaking off below the stigmas after anthesis; similar conditions are also found in ser. *Urbanianae* (cf. Fig. 58 *d*); and in *Populus*, too, the stigmas are early deciduous.

The intersexual flowers, with transitions between stamens and carpels, that are frequently found in *Salix* (for instance, regularly in *S. alba* × *babylonica*) have been thoroughly examined by RAINIO (1926). He shows among other things that there is not, as is often stated, a direct transformation of micro- into macro-sporangia or *vice versa*; pollen-sacs and ovules develop at different, definite parts of the sexual leaves, which have certain male and certain female parts. This is of interest with respect to the possibility thereby indicated that the sporophylls of the Angiosperms have developed from some lower type

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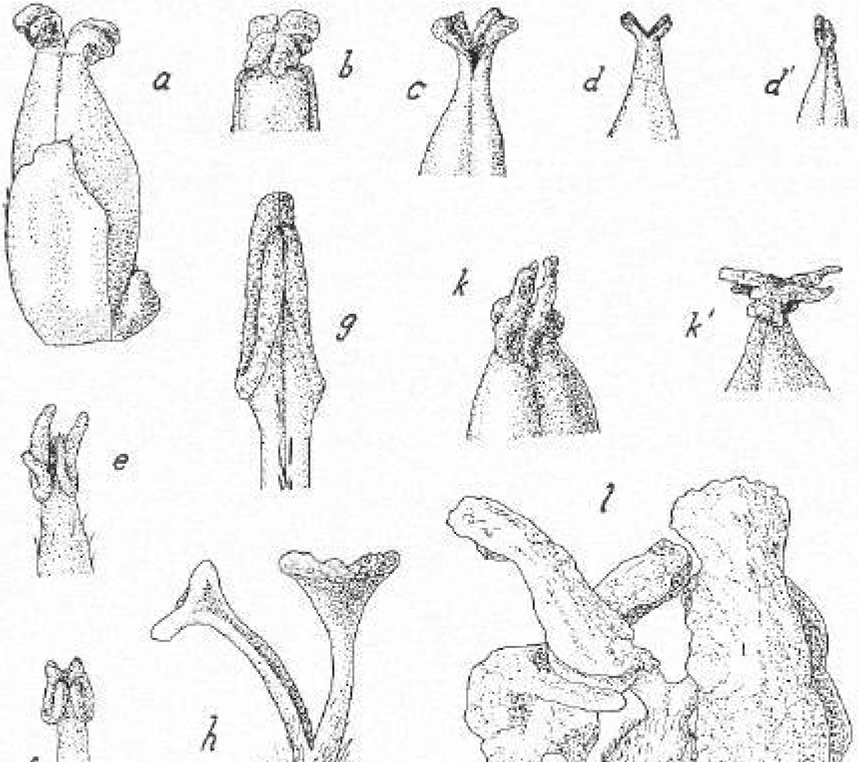
Fig. 56. Stigmas or female flowers of *Salix* and *Populus* (seen from in front or from the axis, except *d'* and *k'*, which are seen from the side). *a* female flower of *Salix Humboldtiana*; *b* stigmas of *Salix* sp. related to *S. Safsaf* from Senegal; *c* the same of *S. elegantissima*; *d*, *d'* of *S. silesiaca*, *e* of *S. caprea*, *f* of *S. daphnoides*, *g* of *S. stipularis*, *h* of *S. glauca*; *i* female flower of *Populus alba*; *k*, *k'* stigmas of *P. tremuloides*; *l* stigmas of bicarpellary pistil of *P. Wilsonii*; *m* stigmas of *P. Sargentii*. *a*—*k'* and *m* about × 15, *l* about × 10.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with microsporangia at a certain part, macrosporangia at another part of the sporophyll.

In the genus *Populus* there sometimes occur similar intersexual flowers, by the writer observed in a male individual of *P. tremula* var. *erecta* SYLV. (Fig. 57). They agree principally with corresponding flowers of *Salix*, but while the stamens here are always first united before they are transformed into carpels, in *Populus* individual, free stamens may be transformed, and at a more advanced stage there may be a union with some other stamen, with signs of a beginning transformation.

Regarding the origin of the flower it has already been pointed out that the small gland-like structures that sometimes occur around a particular stamen in the male flower of *Salix* suggest the correspondence of such a stamen to an original flower — that the present flower is thus a pseudanthium. The same thing may possibly also be indicated by the facts that the flower of *Salix* is sometimes furnished with a small joint at the limit to the pedicel (FISHER, 1928) and that the ovary is often raised on a stalk that may have similar small gland-structures to those which may occur at the stamens of the male flower (FISHER, l.c., Fig. 9). Also, the organization of the occasional bisexual flowers of *Populus* argues in favour of the pseudanthic nature of the flower. In the male flower of *P. tremula* one of the comparatively few (about 5—10) stamens is sometimes transformed into a carpel, viz. that one which is placed in the pocket-like depression in the disc, centrally in relation to the stamens emanating from the sides of the disc, mainly the anterior side (Fig. 57 *A*). Occasionally it now happens that another stamen in the vicinity is transformed into a carpel and then remains free from the first, so that two distinct pistils arise, with some stamens besides them (Fig. 57 *C*). This may surely be regarded as indicating that the stamens here correspond to small, dichasially arranged flowers, the central ones of which may sometimes develop into female flowers, i.e. that we have here a pseudanthium. The same thing may be confirmed by the fact that in *Salix*, according to LUNDSTRÖM (1875), there may exceptionally occur three pistils in the same female flower (observed in *S. glauca*).

The fruit in *Salicales* is of quite a different type from that in other *Amentiferae*: it is a capsule bursting at the middle of the carpels. It seems however possible to imagine a development from for instance the *Juglandaceae*, with which the *Salicales* also show some other resemblances. In *Juglandaceae* the fruit also opens — at germination —

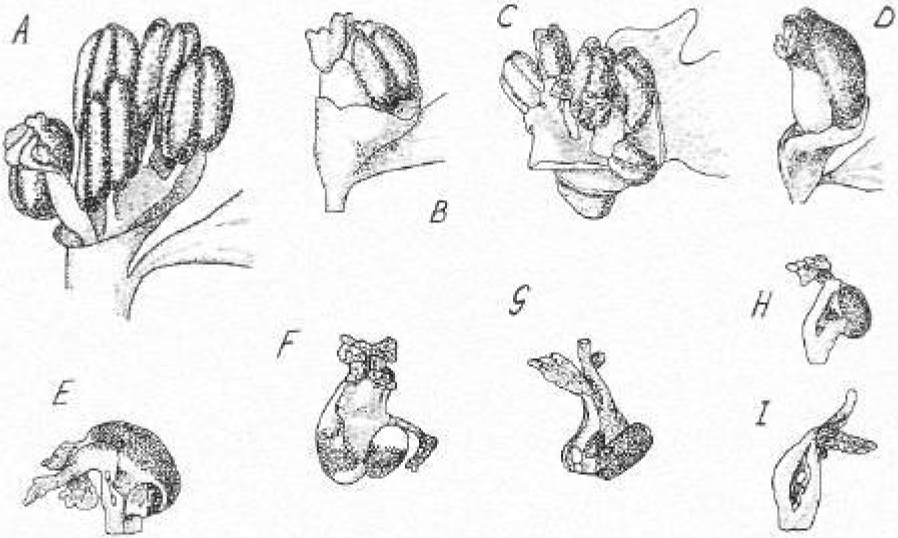

Fig. 57. *Populus tremula* var. *erecta*. *A—D* intersexual flowers from an otherwise for the most part male specimen. *A* flower with a carpel in the pocket-like cavity in the disc and 5 stamens; *B* flower with one pistil and one somewhat transformed stamen; *C* flower with two carpels, one larger and one smaller, and 5 stamens; *D* flower with coalescence between pistil and stamen; *E—I* various transitions between stamens and carpels. *A—D* about × 10, *E—I* about × 15.

at the middle of the carpels. It may be thought that this family, in view of its pronounced opening fissures and its highly probable development from a fruit with two or more seeds, derives its origin from a type with capsular fruit, to which the *Salicales* may also be traced back, and it is also possible that a development has taken place from the Juglandacean type in connection with an increase of the seed number.

In the ovary there are parietal placentas at the coalescence lines of the carpels, generally each with several erect, anatropous ovules. In certain *Salix* species that also in other respects appear original, e.g. *S. heterochroma*, *S. bracteosa*, *S. Urbaniana*, there are only two ovules on each placenta, and this is also the case in a *Populus* species, *P. alba* (Graf, 1921). In these cases the ovules are placed basally in the ovary and are apotropous, thus a position similar to that in *Balanopsidales*. Regarding that in other *Amentiferae* this number is that usually occurring; it is here probably the original one, and the larger number that is found especially in *Populus* is a secondary phenomenon. In

Salix there is exceptionally a reduction to two ovules in the ovary (*S. incana*, cf. Fig. 55 *c*). According to GRAF (1921), there is in *Populus*, at least in certain species, an archesporium of several cells (though few-celled) and in this genus, in contrast to *Salix*, aporogamy, though not chalazogamy occurs. In some *Populus* species, further, a small inner integument was observed inside the outer one, whereas other species like *Salix* only had one integument. The inner integument was formed at the same time as the outer through differentiation of a swelling, at first unitary, and GRAF is not unfamiliar with the thought that we here have the formation of a new structure. The general opinion seems to be that the occurrence of two integuments is a more original state and that the ovules with one integument have arisen through coalescence of the integuments or reduction of one of them. Without doubt this is also the case in the family *Rosaceae*, as is shown by JUEL (1918), perhaps also in *Betulales*, whose unitegminous ovule may have arisen through reduction of the bitegminous one in *Fagales*, but the process need not for this reason have always followed the same course. The unitegminous ovule in *Juglandales* develops possibly in other groups into a bitegminous one, and such a development may also occur within *Salicales*.

As regards the hair-tuft that is found on the seeds of *Salicaceae* it has previously been mentioned that by some authors it has been considered to be homologous to the appendages that in *Juglandaceae* emanate from the placenta and surround the base of the ovule. This assumption seems to be well-founded, and is further corroborated by the fact that TAKEDA (1936) and KIMURA (1938) have shown that the seed-hairs in *Salicaceae* do not spring from the funicle, as is generally stated, but from the placenta, as the appendages in *Juglandaceae*.

Besides the two genera *Salix* and *Populus* that from of old have been referred to *Salicaceae* a third genus, *Chosenia*, has in later times been proposed and in general gained recognition. It includes only one species, *Ch. bracteosa*, and was proposed by NAKAI in 1920 (very good figures in NAKAI, 1930). It has been accepted by KOMAROV (1927, obviously with hesitation; in 1929 he refers it back to *Salix*), by WETTSTEIN (1935), REHDER (1940), and others, whereas by some authors (HULTÉN, 1928; FLODERUS, 1933) it is united with *Salix*. Without doubt it shows some very distinguishing features in its floral morphology, arguing for its generic value. This is especially true of the male flower, which deviates very much from the common conditions both in *Salix* and *Populus*. The two almost entirely free styles

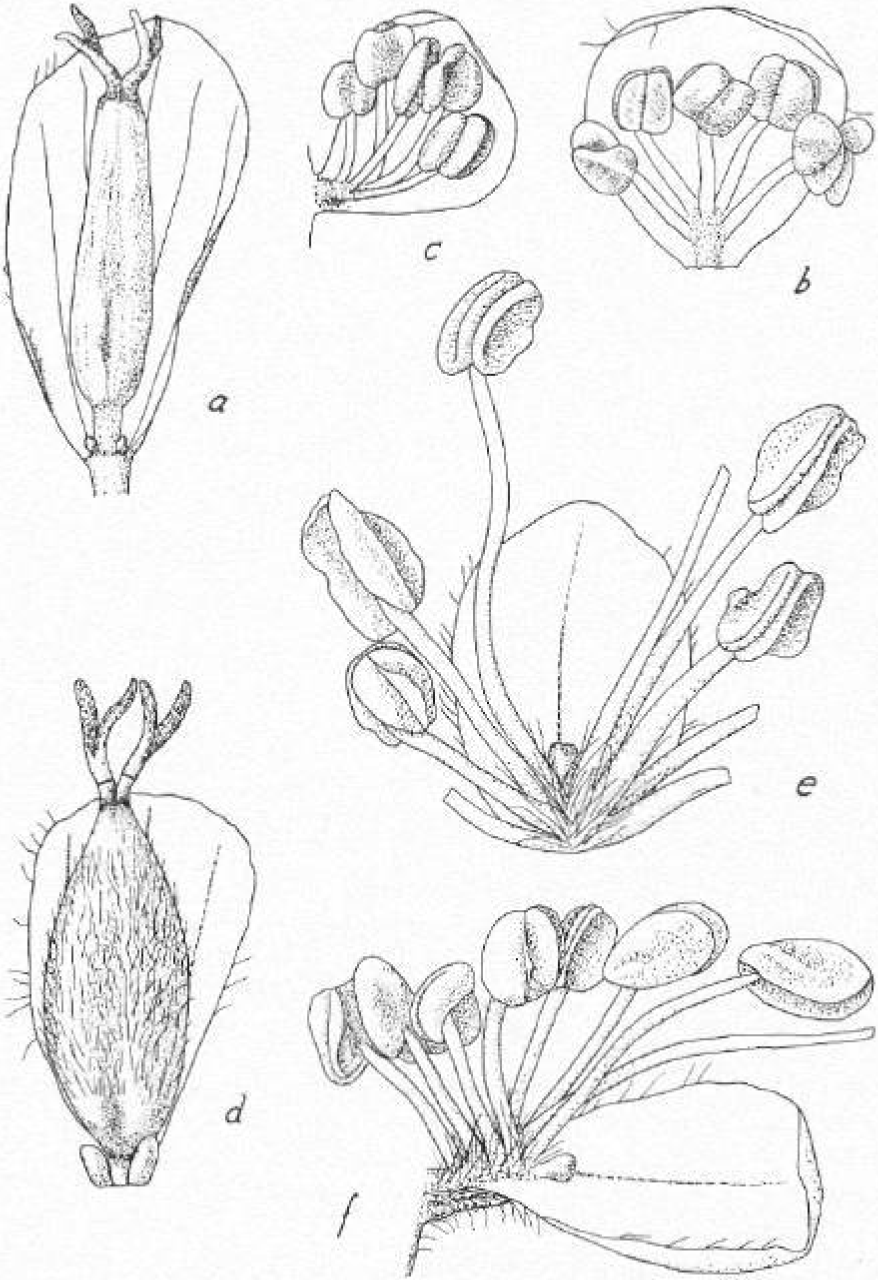

Fig. 58. *Salix bracteosa* (*a*—*c*) and *S. Urbaniana* (*d*—*f*). *a* and *d* female flowers (the glands in *a* occur only exceptionally, in *d* the breaking-places on the styles are indicated); *b* and *e* male flowers from above; *c* and *f* male flowers from the side. About × 15.

constitute another such feature, and their breaking below the stigmas after anthesis differs from most *Salix* species and shows some similarity to *Populus*, as well as the pendulous male catkin. A difference from both *Salix* and *Populus* is the fact that as a rule nectaries are wanting in the flowers. If there had not been any transitions between the *Salix*- and the *Chosenia*-type one might on this account have been inclined to regard *Chosenia* as a genus of its own. There is, however, a whole series of such transitions arguing for its inclusion in *Salix*. Firstly there occasionally occur in *Salix bracteosa*, as mentioned above, two lateral glands in the female flower, approaching a little to the axis. Further there are in ser. *Urbanianae* of *Salix* many resemblances to the *Chosenia*-type, especially in *S. Urbaniana*, which in several important characters shows a very strong approach to this type (Fig. 58 *d*—*f*): two lateral glands occur in the female flower, the styles are of the same type and break in a similar way, the ovary is of a similar structure, the stamens are to some extent carried up on the bract. A difference is that a small abaxial gland is present in the male flower; however, only an inconsiderable continuation of the development already begun in the flower is needed to give rise to the *Chosenia*-type.

The other species within *Urbanianae* form to some extent a transition between *Salix Urbaniana* and the rest of the *Salix*-genus. The close relationship of *S. bracteosa* to the whole group is shown by the fact that hybrids are observed between this species and both *S. Urbaniana* and another species of the group, *S. cardiophylla* (KIMURA, 1936, 1937). The series *Urbanianae* might then also be referred to the genus *Chosenia*; as a matter of fact, KIMURA (1928) has separated the series from *Salix*, though he referred it to a genus of its own, *Toisusu*, alongside *Chosenia*. As pointed out by NAKAI (1930), however, the characteristics distinguishing *Toisusu* are scarcely of sufficient importance to justify its being separated from *Salix*. The same must then also be said of *Chosenia*, owing to the continuous series of transitions that by way of *Urbanianae* unites it with other *Salix* groups. In agreement with FLODERUS (1933) I regard *Chosenia* only as a series of *Salix*, which is of interest by showing certain features reminiscent of *Populus*, although such features, as mentioned above, may also be found in other series.

With respect to the relationships between the two genera of *Salicaceae*, both GOMBOCZ (1924—1925) and FISHER (1928) arrive at the conclusion that *Populus* is a more primitive genus than *Salix*. Undoubtedly such a section as *Turanga* has also a primitive organization of the disc, and in the embryology of *Populus* there are some features that appear more primitive than in *Salix*. On the whole, however, it must be said that *Salix* has a more original floral organization. The variation is here considerably larger, this applying to the nectaries, the structure of the pistil (now carinal, now commissural stigmas of very different shape, with two styles, with one style, or entirely without style), the arrangement of the stamens (sometimes free, sometimes in columns) and their number, and also in the number of ovules there occurs a type that seems to be the original in several *Salix* species, whereas it appears to be very rare in *Populus*. In an anatomical respect also there is according to FISHER (1928) great variation in the *Salix* flower, whereas *Populus* shows very uniform conditions. On the whole it appears as if *Populus* were a type originating from the *Salix*-type — in its more primitive form — which was more uniform in the development of the disc and in other characters, and in which at the same time a certain increase in the number of stamens as well as of carpels and ovules had taken place, though certain primitive characters are also found. The wind-pollination occurring in *Populus* is also met with in *Salix bracteosa* (NAKAI, 1930) and perhaps (FISHER, 1928) also in some other *Salix* species, where the nectaries are petaloid.

In *Populus* the section *Turanga*, in its disc, shows some attachment to *Salix*; still stronger however do those attachments appear to be which occur in § *Leuce* in *P. alba*, a species that in the qualities of its stigmas and bracts approaches *Salix* and in the number of ovules agrees with some original *Salix* species. *Populus alba* and its allies should probably be regarded as the most primitive group of *Populus*, even though all other groups cannot be traced direct back to this, but a common origin may be presumed, from now extinct forms.

The order *Salicales* has to some extent an isolated position within *Amentiferae*. Without doubt it belongs to this group, but it is a somewhat divergent type, among other respects in its fruit and seed development. In these respects, however, it may, as previously mentioned, be a further development of the Juglandacean type, and its nectary- or disc-structure may also be a correspondence to the bracteoles occurring in *Myricaceae* and the perianth of *Juglandaceae*, *Leitneriales* in some degree forming the transition. The order is apparently a rather transformed type, which, however, has emanated from a primitive origin, probably most closely represented by the *Juglandales* type, though relationships apparently exist also in other directions within *Amentiferae*.

General conclusions on the Systematics of the Amentiferae.

From the foregoing account it is evident that there are great variations in the floral morphology of the *Amentiferae*. In spite of this, however, there are many common features of importance, indicating that the various orders are related to each other. This is already suggested by the »parallel» phenomena appearing in various orders, which without having any direct phylogenetic significance yet indicate similar dispositions. Within *Fagales* there occurs for instance in some forms a fruit-structure that shows striking resemblances to that of *Juglandaceae*, and in *Salicales* there is in *Salix*, ser. *Chosenia* a male flower of a type resembling that of *Corylaceae* in *Betulales*, while some *Salix* species in their male flower show great similarities to some *Myrica* species. Of greater importance than these parallel phenomena are apparently those essential agreements which are found in the structure and origin of the flower. As shown in the preceding pages, in all orders there are to be found either positive proofs or at least good probability reasons for the flower to be regarded as a pseudanthium that has arisen through union of a number of simply built flowers. Within *Juglandales* this development is very conspicuous in the family *Myricaceae* as regards both male and female flower, in *Balanopsidales* the same development may be observed as regards the male flower, while the female flower has probably arisen in the same way, and in *Fagales* the female flower has an organization that in some cases comes close to that of the most original *Myricaceae*, though the outer part-flowers in the pseudanthium only appear in abnormal cases, while the male flowers are more reminiscent of the male pseudanthia of *Balanopsidales*. The most original *Fagales* (*Lithocarpus*) and the most original *Juglandales* (*Myrica*) in this way come close to each other in important flower-morphological characters and apparently may be traced back to a common origin. Which of the two orders is the most original, is difficult to decide. The order *Juglandales* has here been placed first, this on the strength of the more original organization of the pseudanthium. On the other hand, the one-seeded ovary of *Juglandales* has undoubtedly, as mentioned above, arisen from an ovary with two placentas and at least 2, probably 4 ovules, and hence in this respect the order is more derived than *Fagales*. This, however, has probably not so great importance as the otherwise on the whole more primitive organization; still, it is better to confine oneself to the statement that both orders may obviously be traced back to a common origin. The order *Balanopsidales* is — as pointed out above — original in some characters, more derived in others, and is to be regarded as most likely a side line parallel to *Juglandales*; further data concerning this order, especially its embryology, are however highly desirable.

The three remaining orders, *Betulales*, *Leitneriales*, and *Salicales*, scarcely show any present transition from inflorescence to flower, but there are obvious signs of the pseudanthic nature of the flower; the reduction of the original inflorescence has here only advanced somewhat further. The order *Betulales* is most closely connected to *Fagales*, though it is apparently somewhat more derived and shows some attachments in other directions as well. On the other hand, the order *Leitneriales* is in a similar way connected with *Juglandales*. The order *Salicales* deviates in different respects rather much from other *Amentiferae* and is probably to be regarded as the most derived group, on one hand with strong reductions, on the other with different fruit-structure and increased number of ovules. Without doubt, however, the group has separated from the other *Amentiferae* at an early stage of development; in the first place it attaches to *Juglandales* and *Leitneriales*.

The circumstance that the flower of the *Amentiferae* is a pseudanthium that is formed by union of simply built part flowers need not in itself mean that the group has an original position. In for instance *Euphorbia* there are also such pseudanthia, and there the simple part flowers have undoubtedly developed by way of reduction from more highly organized flowers. In the *Amentiferae*, however, there are no signs of such a development. And to this may be added as a — in the writer's opinion — very important fact that in their embryology there is a series of peculiarities reminiscent of original types, of the Gymnosperms or of *Casuarina*, an undoubtedly primitive genus. Some of these peculiarities, as the several-celled archesporium of the ovule, the free integument of the ovule, and the vascular bundles of the integument, are characters that may be met with here and there in the system of the Angiosperms and on this account have by some authors (cf. above) been regarded as of minor importance. Their common occurrence in one group seems however noteworthy, even though they may occasionally appear more or less isolated in other groups. And the chalazogamy occurring in *Amentiferae* has apparently no true correspondence within other angiospermous groups, except in *Casuarinales*: the so-called chalazogamy that occurs in other groups seems, at least in some more closely examined cases, to be of a different nature (cf. SCHNARF, 1929, p. 295—297). The *caecum*-structures occurring in *Fagales* and *Betulales* are also a special phenomenon, which is reminiscent of *Casuarinales*, just as some morphological flower-characters in *Betulales* also recall this group. By some authors the order *Casuarinales* is united to the *Amentiferae* into a common group: RENDLE (1925) places them in this way side by side, while BURTT DAVY (1937) includes *Casuarinales* in his subclass *Amentiferae*. In my opinion, however, this order differs so much from the *Amentiferae* that it cannot be included in the group, although there must exist a certain relationship that confirms the original position of the *Amentiferae*.

Among other groups that may attach to the *Amentiferae* in the first place mention may be made of *Urticales*. Here there is a perianth of similar type, superposed stamens, some embryological agreements. That the flowers are often bisexual need not mean any contrast; we have seen that to all appearances the flowers of the *Amentiferae* have developed from pseudanthia with female flowers in the centre. The genus *Rhoiptelea*, discovered in recent times (HANDEL-MAZZETTI, 1932), may to some extent serve to form the transition from *Amentiferae* to *Urticales*; in its general flower-structure, the nature of its fruit, etc. it agrees most with *Urticales*, but there are also some similarities to *Juglandales*, among others in the anatomy of the stem (WITHNER, 1941). Another order that also seems to have some relationships to the *Amentiferae* is *Proteales*, though it is more distant from it. It agrees in certain flower-morphological features and embryologically also shows some similarity, in the first place with *Salicales* (WETTSTEIN, 1935).

Under all circumstances there seem, judging from the present study, to be very good reasons for placing the *Amentiferae* — in accordance with ENGLER, WETTSTEIN, RENDLE, and other authors — among the most original Angiosperms, constituting a primitive type of great morphological and systematical interest.

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