

NOTES ON THE DILLENIACEAE AND THEIR ALLIES:
AUSTROBAILEYEAE SUBFAM. NOV.

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THE DISCOVERY of *Austrobaileya* was one of the gratifying results of the expedition undertaken by S. F. Kajewski in Northern Queensland in 1929. In describing the new genus and its type species, *A. scandens*, C. T. White quoted Diels to the effect (Contr. Arnold Arb. 4: 29. 1933) that *Austrobaileya* is a genus of the Magnoliaceae very closely related to *Drimys*, and expressed his own disappointment at the condition of the available material.

The type collection, indeed, is very poor, as shown by the isotype in the herbarium of the Arnold Arboretum. The single available flower on our sheet is too brittle for a satisfactory dissection and it is nearly impossible to interpret even its grossest morphology. Four years ago, fortunately, a second collection of *A. scandens* or of a closely related species was made by C. T. White himself on Mt. Spurgeon in N. E. Australia (White 10734, Sept. 1936), and this collection although far from complete is much better preserved than the original specimen secured by Kajewski. It consists of a section of an apical shoot, with six opposite leaves and three evolute flower-buds. There are certain discrepancies in leaf-venation, aspect of the blade and size of the floral parts between the Kajewski and the White numbers, but if these numbers do not absolutely represent the same species they are closely related forms and are certainly congeneric.

The data on the field label of the original Kajewski collection are given in full by White (op. cit., loc. cit.) and need not be repeated here. White himself describes the material gathered in 1936 as follows: "Large climber in rain forest. Perianth-segments pale green, outermost ones small, gradually larger towards the centre of the flower; innermost ones the largest. Stamens pale green, those of the outermost series the largest, marked with purple spots, few on the outer face, more on the inner. Stamens of the innermost series densely purple-spotted both inside and out. Carpels yellow, numerous, free." The determination, *A. scandens*, is by White.

The publication of the genus and of its type species are unsatisfactory as to description, which is not surprising considering how meager was

the material then available. The result of my own dissection (only one flower-bud about to unfold) closely agrees with the data on the field label of White 10734, showing that this plant, carefully dried, does not change much in color. I have found, however, that the inner segments of the perianth are smaller than the outer, which I believe to be due to the fact that my material has not yet reached the full stage of anthesis. The uncertainty whether the Kajewski and the White specimens are actually conspecific is a deterrent against presenting here a *descriptio emendata* in the technical sense of the word. The following, however, may be recorded in a description drawn from White 10734: Young flower (bud opened after maceration, but evidently about to unfold) about 3.5 cm. broad and 2 cm. long, its perianth consisting of three gradually merging yet sufficiently distinct whorls of appendages; the outermost of about 8 bracts becoming larger (largest about 0.5 cm. both ways) from the pedicel to the base of the perianth, of a firm texture, veined, brownish on back, pale yellowish green and subscarious on the margins; the central of 5 sepals (largest about 1.5 by 1 cm.), more or less cucullate so far as seen, colored like the largest bracts, but with the yellow hue at the margins tending to spread more diffusely towards the center of the sepal; the innermost of 5 petals somewhat smaller than the sepals and apparently more intensely green-colored; stamens in one series, apparently five, about 1 cm. long, 0.3 cm. broad, quite petaloid in aspect and carrying an anther without filament, sessile as an outgrowth from the midvein; anther introrse, 2-celled, longitudinally dehiscent, the slit sublateral; staminodes suggesting gradually sterilized anthers, i.e., in the present case stamens of petaloid habit with imperfectly evolute anthers; ovary of 8 nearly straight, free follicles on a slightly upraised torus, pale yellow, gibbous on the back, about 0.7 cm. long, the apparently epapillate, erect and introrse stigmas about half as long as the follicle; ovules borne marginally in (apparently) two collateral series of about 10–14 ovules altogether. The staminodes and the stamens reveal under the lens dark papillose regions, which might prove to be directly concerned with the emission of the “overpowering putrid smell” noticed by Kajewski. The floral pedicel is not manifestly articulate: it carries two minute triangular bracts at the base, is about 2 cm. long, quite slender, and emerges from a bud of apparently persisting scale-like cataphylls reminiscent of those of the bud of *Schizandra*.

The salient characters of *A. scandens vel aff.*, consequently, may be tabulated as follows:

- 1) — Leaves opposite (perhaps subopposite in some cases), estipulate,

glabrous like the whole plant and the flower, entire, with a camptodrome venation.

2) — Main vegetative axis abortive at the apex between, or slightly above a pair of leaves, with axillary buds as described. Bark of young shoots greenish, neither lenticelled nor dotted.

3) — Flowers single or paired from the axils of the leaves.

4) — Perianth of three gradually merging series.

5) — Stamens as "fertile petals," the polliniferous thecae outgrowing from the midvein of a petaloid structure, introrse, the slit sublateral.

6) — Staminodes as stamens left unfertile by the failure of the thecae to reach full physiological maturity.

7) — Gynoecium of apocarpous follicles, introrse, with a long stigma and two rows of ovules in a marginal position.

8) — Torus slightly upraised under the gynoecium.

A plant with this type of floral morphology may be suspected to belong to any one of several families, namely to the Magnoliaceae, Dilleniaceae, Annonaceae, Calycanthaceae, Monimiaceae, Lardizabalaceae, Menispermaceae. The characters of these families are difficult to interpret when full material is not available: it is to be understood, consequently, that the discussion below is essentially exploratory in nature.

The Menispermaceae and the Monimiaceae have 1- or at the most 2-seeded carpels by definition. This character does not agree with the many-seeded follicle of *Austrobaileya* and forbids considering this genus either as a Menispermaceae or as a Monimiaceae. It seems necessary not to overlook the fact, nevertheless, that in the Menispermaceae a climbing or scandent habit is dominant and that certain genera of this family (e.g., *Anamirta*, *Cissampelos*) have highly evolute stamens. The Monimiaceae have opposite leaves, which tends to bring them near to *Austrobaileya* at least in vegetative characters. The carpic structure of the Monimiaceae, however, is either in tendency or in fact an hypanthium, that is to say a receptacle with infolded margins that includes the carpels. Also an hypanthium is the carpic structure of the Calycanthaceae, which may be considered to be related in an almost even degree with the Monimiaceae and the Annonaceae. The Lardizabalaceae have many-seeded follicles, the ovules sometimes lining the whole of the carpellary cavity: their leaves are either palmately or pinnately compound so that their affinity with the Annonaceae is bespoken mainly by their having a basic ternate arrangement of the perianth-members. It may be suspected that the Menispermaceae and the Lardizabalaceae

represent groups which have evolved as dead-ends from an archetype which was ancestral to the magnolioid alliance. The Calycanthaceae appear to be a not very strong taxonomic offshoot of the Monimiaceae which last, together with the Annonaceae, may be regarded as two of the basic phyletic units of that alliance. Despite certain similarities with the Menispermaceae — as I have already noticed — *Austrobaileya* does not seem to agree with any of the families just mentioned. If more abundant material should prove that this genus is nevertheless to be treated as a Menispermaceae it is plain that the characters of this family will have to be amended, and even more that *Austrobaileya* will have a place entirely of its own in the classification of the Menispermaceae. It is a matter of regret that the condition of the ovules available at present is not such as to reveal whether the embryo is curved or straight.

The exclusion of the Calycanthaceae, Monimiaceae, Lardizabalaceae and Menispermaceae from the range of affinity of *Austrobaileya* leaves for immediate consideration only the Magnoliaceae, the Annonaceae and the Dilleniaceae (including the Actinidiaceae). Although the Dilleniaceae are commonly treated as close allies of the Guttiferae there can be no question that they are closely consanguineous with the Magnoliaceae and the Annonaceae.

The concept of typification is not suited to a discussion of systematic affinities because a family — at least as I understand it — is essentially an aggregate of forms which derive their origin from a common ancestral focus and follow therefrom a set line of evolution. It is quite possible to find coexisting in the same family carpic and floral structures which are not alike: *an homogeneous group may be so both on account of having the same morphology, or of having different types of morphology which have evolved from the same basic structures.* It is evident that very numerous families have sprung into being — as it were — on the same horizon of active taxonomic segregation, it being almost impossible, for instance, to say whether *Magnolia* is more primitive than *Buxus*, and *Cornus* than *Siparuna*. The truth of this statement is supported by Chalk's lists of primitive and derivative woods (Ann. Bot. n.s. **1**: 425–7. 1937) and is implicitly illustrated by the indifferent and conflicting results secured by Whitaker (Jour. Arnold Arb. **14**: 376–85. 1933) and by McLaughlin (Trop. Woods **34**: 3–38. 1933) in their study of the cytology and of the wood anatomy, respectively, of the Magnoliaceae. I fully agree with Anderson & Sax (Jour. Arnold Arb. **16**: 215. 1935) that the “webbing” of the phylogenetic tree may become so complex that one would scarcely use the word “tree” in describing it. Compared with the

type genus of the Magnoliaceae, of the Dilleniaceae and of the Annonaceae, *Austrobaileya* is seen to agree with none. It lacks the strobiliform arrangement of the gynoeceum and the 2-ovulate carpel of *Magnolia*; the numerous, incumbent multiovulate carpels of *Dillenia*; the syncarp and the prevailing extrorse stamens of *Annona*.

Drimys is the genus with which an affinity of *Austrobaileya* has been suggested. *Drimys* has, in fact, follicles with biseriate placentae borne in a marginal position on the carpel, as in *Austrobaileya*, and floral wrappers that very definitely tend to be 2-seriate. *Drimys*, however, has anthers which are not comparable with those of *Austrobaileya* and an inflorescence of a most interesting pattern which Parkin has defined (Jour. Linn. Soc. **42**: 556-7, fig. 9. 1914) as intercalary: in *Austrobaileya* the inflorescence is strictly axillary. The anther structure of *Galbulimima*¹ which Hutchinson has elected as the type of a distinct family, the Himantandraceae (Fam. Flow. Pl. **1**: 84, fig. 4. 1925), but which Sprague regards as a Magnoliacea (Hook. Ic. **31**: pl. 3001, 1-3. 1922), may be very close to that of *Austrobaileya*, if I am to judge from illustrations in the absence of actual material, but there is not the slightest affinity to be found between the carpel structures of these two genera. The free follicles of *Austrobaileya* are not matched by the syncarp of *Galbulimima* and by its carpels inclosed within a reticulum of fibro-vascular bundles and immersed into an abundant and aromatic parenchymatic tissue. The carpel structure of *Galbulimima* closely approaches that of *Zygogynum*, which genus to judge from the single dissection I have been able to make of the flower of *Z. Viellardii*, has crowded anthers arranged in a typically annonaceous manner.

I do not believe that *Tetracentron* can be seriously regarded as a true Magnoliacea. Its immediate affinities are with the Cercidiphyllaceae and the fact that *Tetracentron* and *Cercidiphyllum* have chromosomes like those of *Magnolia* both in number and structure (Whitaker, op. cit., 384) is not necessarily proof that these three genera are close phyletic allies as a systematicist may see them. Nor is *Schizandra* in any immediate way related to *Austrobaileya*. *Illicium*, of course, has carpel characters that are incompatible with those of White's genus, and so has *Liriodendron*. It is manifest that if *Austrobaileya* is to be

¹The nomenclatural issue: *Galbulimima* vs. *Himantandra* has been debated by Sprague (Jour. Bot. **60**: 137-8. 1922), who concludes for the validity of the former generic name in opposition to Diels. It seems well established that *Himantandra* was proposed *in advance* for a generic or subgeneric group *which might be recognized in the future*, hence is a "nomen provisorium" in the fullest sense of the Rules of Nomenclature. It may be noticed that fig. 11 of the illustration of *Galbulimima*, op. cit., loc. cit., shows a section of the fruit taken only at the upper end of the carpels, which last, consequently, are shown merely as slits in the surrounding parenchyma.

treated as a magnoliaceous plant it must be placed in a subfamily of its own, which in view of its gross morphology, habit and general characters is certainly not a desirable disposition.

The Annonaceae, as previously noticed, are a vast and complex aggregate and their anthers may resemble those of *Austrobaileya* in structure. While it is imprudent to generalize about the anthers of the magnolioid phylum as the dehiscent slit of the theca is mostly lateral, but becomes variously modified, subapical, subintrorse or subextrorse by secondary adaptations, it seems necessary to remark that the anthers of the Annonaceae are extrorse with few exceptions (*Eupomatia* and *Mezzettia* for instance), while they are introrse in *Austrobaileya*. Any taxonomist familiar with the Annonaceae, moreover, will intuitively exclude a possible kinship between *Austrobaileya* and the genera of this family. It did not occur to Diels, nor did it occur to other botanists or to myself that *Austrobaileya* is annonaceous, the incompatibility being suggested at sight by a sum of intangibles as well as of immediately appreciable characters. If it is true that the texture of the leaf of *Austrobaileya* and its inflorescence recall the characters of *Eupomatia*, *Cyathocalyx* and *Mezzettia*, the fact remains that these similarities of habit may not be overestimated and can not be properly utilized to bring *Austrobaileya* under the Annonaceae.

My first impression upon seeing *Austrobaileya* was that this plant is dilleniaceous, although it obviously differs from the majority of the Dilleniaceae in having lateral, single or nearly single flowers. Upon dissection I learned that the theca of the anther has a structure not incompatible with that of the genera of this family, although the stamen as such can not be said to resemble that of *Austrobaileya*. As I have ultimately reached the conclusion that this genus — at least on the basis of the available material — had better be treated as the type of a new subfamily of the Dilleniaceae I believe it advisable to deal briefly with the basic characters of this family.

In the Dilleniaceae, with the exception of *Tetraceras*, there is a definite tendency towards the carpels becoming incumbent or accumbent upon a more or less evolute torus, which is homologous with the carpophore that supports the carpels of *Magnolia*, *Exochorda*, *Eucryphia*, etc., and originates from the axis of the flower. In *Dillenia indica* the carpels are quite ventrally incumbent upon a large, short torus, and carry numerous seeds; in *Hibbertia* the carpels are less manifestly incumbent than they are in *Dillenia*, but in *Hibbertia volubilis*, at least, the torus can be traced with ease. *Actinidia* differs from other Dilleniaceae in having its numerous carpels surrounded by a common epicarp, which causes the fruit ultimately to be a berry, and has induced some syste-

matists to consider this genus as the type of a distinct family. It is suggested by this brief analysis that the Dilleniaceae, *sensu lato*, are related to the Magnoliaceae as the same fundamental structures and tendencies can be traced in both families. I may, in fact, restate here the previously expressed opinion that the Dilleniaceae are rather Magnoliales than Guttiferales.

The follicle of *Austrobaileya* is inserted upon a slightly upraised torus, tapers off to a long style and — to judge from the available material — appears to be broadly connate with the torus. A carpel of this nature is obviously epedunculate and only secondary adaptations are required to make it as fully incumbent as the carpel of *Dillenia*. In suggesting that *Austrobaileya* bears some affinity to *Hibbertia scandens*, which last is a vine very common in second growth in S. E. Queensland and has flowers with “a strong foetid smell like excrement” (*fide* C. T. White, in note on field label of No. 8237, in herb. Arnold Arb.) I do not care to have it understood that I believe that *Hibbertia* and *Austrobaileya* are closely related. I merely wish to suggest that a greater sum of affinities connects *Austrobaileya* with *Hibbertia* than with any other plant so far known to me. It is my opinion, based upon the material at hand, that *Austrobaileya* is an aberrant Dilleniaceae. It may be objected against this opinion that the very fact that *Austrobaileya* is an aberrant Dilleniaceae and has no place in the remaining families of the dilleniaceous affinity, is a sufficient reason why it should be elected as the type of a monotypic family. Such objection carries considerable weight and may prove decisive indeed, if another genus or subgenus closely allied with *Austrobaileya* were later to be reported, showing that rather than an aberrant Dilleniaceae this genus or aggregate is either a connecting link between different families, or definitely a dead-end of evolution. Before burdening the systematic record with monotypic families, however, it is highly desirable to have complete material for study and knowledge enough to rearrange the phyletic lines of the entire group to which the new addition is being made. The magnolioid alliance is notorious for the presence of genera which, narrowly treated, may be granted the status of monotypic families. The systematic position of *Austrobaileya* is in every respect as baffling and as controversial as that of *Galbulimima* which is hardly a true Illicieae; as that of *Zygogynum* which has an annonaceous disposition of the anthers and suggests the Annonaceae, moreover, in its cupule, in its carnose perianth-lobes and in other intangibles; as that of *Schizandra* which is a climber that scarcely resembles *Magnolia* in its dioecious flowers and in its subextrorse stamens becoming connate in the androecium; as that of *Tetracentron*

which although a *Cercidiphyllacea* in most respects has a mode of inflorescence which is *sui generis*; as that of *Trochodendron* which is certainly ill assorted with *Euptelea*. The extraordinary difficulty of satisfactorily classifying this alliance must be recognized as a matter of fact. It may be worthy of notice that Whitaker (op. cit., 383) states that there is no cytological evidence that justifies McLaughlin's placing *Cercidiphyllum*, *Euptelea* and *Illicium* in the Hamamelidales. Without the thought of questioning Whitaker's cytological findings I wish to point out that at least *Cercidiphyllum* and *Euptelea* can hardly be accepted as Magnoliales under the systematist's approach to classification. *Euptelea* is very nearly related to *Eucommia* which in its turn is consanguineous with *Daphniphyllum* and *Cercidiphyllum*, forming with them an affinity that is definitely linked with the pittosporaceous phylum, that is to say with an aggregate that is neither magnoliaceous nor hamamelidaceous, but may be suspected to be nearer the latter than the former. The very great value of the data of cytology and wood anatomy in systematic work should not blind us to the essential fact that classification may not disregard the requirements of visual evidence and of broad phylogeny.

As the best solution available at present and in consideration of the fact that *Austrobaileya* can not be longer treated as a genus of Magnoliaceae I elect *Austrobaileya* as the type of the Austrobaileyaee, a new subfamily of the DILLENIACEAE, with the following description:

Austrobaileyeae subfam. nov., rebus sic stantibus ad Dilleniaceas adducenda: Scandens, foliis oppositis vel suboppositis, floribus subsingulis axillaribus. Perianthii seriebus 3, e bracteis in petala gradatim transeuntibus; antheris introrsis e theca pollinifera didyma e nervo medio petali orta efformatis; staminodiis, scilicet petalis antherigeris abortivis, plurimis; carpidiis in torulo insidentibus, longe stylosis, marginibus ovuligeris; ovulis ad (?) 14 in acie duplici instructis. Typus: *Austrobaileya scandens* (quoad C. T. White 10734, in herb. Arnold Arb.).

A careful study of the wood anatomy of this plant is desirable. In view of the fact that it is a large scandent shrub it is possible, however that its wood anatomy does not show its truest and nearest affinities. It may not be forgotten that the woody structures of vines present a very special problem (Houlbert, in Ann. Sc. Nat., sér. 7, 17: 172. 1893), and that it is thus probable that the ultimate disposition of *Austrobaileya* will remain in the hands of systematists.

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