

ON THE SYSTEM OF THE SAPOTACEAE,
WITH SOME REMARKS ON TAXONOMICAL METHODS

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The Sapotaceae have of old a bad reputation among classifiers because of the extreme complexity in which the single features are distributed over its genera, species and individuals. It is, in particular, extremely difficult to find satisfactory generic delimitations and consequently, the family yields a rich field both for lumpers and for splitters. Both categories, and several intermediaries, have given their opinions, as has been recently recalled by Charles B a e h n i in his "Mémoires sur les Sapotacées I, Système de Classification" (Candollea VII, 1938, 394—508). It is my present purpose to deliver a few annotations with regard to this valuable publication, meant, not in the first place as criticism, but as contributions towards the extensive material which is needed for a well-founded insight into the structure of this prolific natural order.

In view of the often adverse opinions of earlier authors and of those investigators, like myself, who are intimately familiar with a part of the family only, without being sufficiently well acquainted with other parts, a new survey of the whole family by one man is highly desirable and we may look forward with vivid interest to B a e h n i's further papers. The one quoted above is, I presume, to be considered as a preliminary study and if I am well informed the next step will be a monograph of one of the most intriguing genera, *Pouteria*.

The backbone of "Mémoire" I is an extensive list of generic and sectional names, with short characteristics and with B a e h n i's preliminary ideas regarding their supposed place in the system. I do not know how many years the author has devoted himself to this work, but some points may make the impression of being insufficiently well-pondered, as will be discussed underneath. More surprising, however, is the fact that the paper concludes with a new system, which is apparently meant as the crystallization of the foregoing part; surprising, since a new system may usually be considered as

the final conclusion of a great number of detailed studies, rather than as preliminary to such studies. I know that by saying this, I make myself liable to the reproach of the pot calling the kettle black, as I have ventured to publish some tentative systems of the family myself, without being thoroughly known with all its genera. Both B a e h n i and I have apparently felt the urgent need of a revision and have been enticed to publish our opinions more or less prematurely. Therefore, since it may be a blind man trying to correct a deaf one, the following notes are most unobtrusively put before the reader.

As a matter of course, there are two purposes to be served in establishing a system of living creatures. The one is to procure a practical guide so as to find the proper name of a given plant; this is classification. The other is to strive for a scheme, reflecting as much as possible the supposed phylogenetic (or natural) development of the group. This is taxonomy as I see it. If, for a clear classification (an art or rather a skill, no science) a single or a few features suffice, the others may be safely neglected. But taxonomy (which is a science) requires as much evidence (morphological, anatomical, cytological, physiological, biochemical, geographical, palaeobotanical, etc.) as may be laid hands on so as to contribute to a possibly complete insight into the structure and the development of a natural group. One may get the impression that B a e h n i, in writing his "Mémoire", has not sufficiently discriminated between these two purposes. I do not think it is indisputable that "le but premier de la systématique est de permettre la détermination d'une plante et que son but second est de fournir une image des relations naturelles entre les membres d'un même groupe végétal" (l.c., p. 396). In my opinion, the two purposes are coordinated, as they serve different aims. And if there should be a subordination, the natural system should be put first, being the only scientific and the most fundamental one, just as pure science is basic to applied science.

Thus, B a e h n i's considerations leave us, at first sight, in uncertainty as to whether his system is to be considered as a practical classificatory scheme, as a natural system, or as a compromise between the two. In the text, B a e h n i repeatedly advocates a natural system, as may appear from the following quotations:

p. 408: „nous ne croyons pas qu'il soit légitime de séparer, les uns des autres, les membres d'une famille très unie, en se basant sur un caractère aussi fluctuant que la constitution de l'androcée. C'est un caractère commode, mais on se rend compte qu'il n'a pas de valeur intrinsèque quand on compare, par exemple, certains *Chrysophyllum* avec certains *Sideroxylon*". And

p. 411: „Nous nous sommes convaincu que c'est sur les caractères tirés de la position de la cicatrice qu'on peut fonder une classification naturelle”.

B a e h n i (l.c., p. 397—398) also states, that „une bonne classification doit être à la fois naturelle et pratique”.

On the other hand we have the first quotation given above (B a e h n i, l.c., p. 396) to prove that the first purpose of taxonomy is to yield the materials for identifying a plant (eventually by means of an artificial system). Moreover, B a e h n i declares (l.c., p. 397) not to need anatomical evidence, since „chez les Sapotacées les caractères morphologiques sont suffisants pour établir une classification naturelle et pratique”, a conclusion, by the way, which seems far from indisputable to me. It may mean that parts of the evidence may be neglected and therefore, that a possibly natural system is not striven for. In this connection it may be pointed out, that B a e h n i (l.c., p. 398) apparently follows those investigators like D i e l s and H o c h r e u t i n e r, who think that systematic units are no realities. I am personally of the adverse opinion and it may be important enough to recall this here, as this very fundamental principle of taxonomy cannot but influence one's insight into and considerations on taxonomical problems. The reader of the present paper will find, I think, that both B a e h n i's and my own results are largely influenced by our adverse opinions concerning this principle. As to this point, B a e h n i is apparently founding upon H o c h r e u t i n e r, whose considerations¹ are far from convincing to me. He is, apparently, at a loss in finding genera which combine features of different families. Nothing is more natural. No taxonomist would combine the Orchidaceae and the Asclepiadaceae because both have pollinia. “Homologous variations” of which I come to speak more in detail underneath, are an extremely frequent phenomenon, but they do not imply that natural limits are not existing. The ultimate consequence of H o c h r e u t i n e r's considerations is that the whole vegetable kingdom consists of individuals, whose characters are interwoven in such a way that any classification must necessarily be arbitrary and subjective. Why shouldn't we be still more consequent and include also the animals and all inanimate things? For him the ultimate unit is the individual, or eventually the cell. The latter may be true in Ecology, but not in Taxonomy; for both the individual and the cell are materializations of forces and processes of Life, and in the series cell — individual — systematic unit, there is an increasing influence of Time and a

¹ B. P. G. H o c h r e u t i n e r, La valeur relative des groupes systématiques — Boissiera II, 2, 1937, 1—7.

decreasing influence of environment. As I have circumstantially discussed elsewhere¹, for me the ultimate unit is, provisionally, the feature, or rather the gene, whatever the latter may be. It is, in my opinion, the combination of features, the type (typology), that characterizes a systematic unit. And typology means that also numerous minor features — and even intuitive impressions — which can hardly be expressed by words are involved in the conclusions. For me, the systematic units are “naturegegeben”, are natural discontinuities. Consequently, looking for generic limits is for me a scientific task and of much more importance than looking for more or less arbitrary characters which might be suitable for an artificial system. Yet, also an artificial system needs a basis and it should therefore keep contact with the natural one as closely as possible. It should, however, be always secondary, because only a perfect insight in the natural system is a safe-guard that no valuable characters have been overlooked.

In how far B a e h n i's system, as given at the end of his paper, is natural or artificial, will be discussed in detail underneath. On closer investigation, the reader gets the impression that B a e h n i has more or less unconsciously given a compromise. His conspectus in the form of a two-dimensional network (l.c., p. 507) is, in itself, a good concept with a natural bias, but it contains artificial elements which are not only due to its two-dimensionality; they also will be discussed below. Moreover, the fact that this conspectus has been established (l.c., p. 398) “pour résoudre les difficultés de la taxonomie des Sapotacées”, shows the intention to serve a practical purpose first of all.

Let us now discuss some points of B a e h n i's considerations. In his introductory notes (l.c., p. 396—398) he gives four principles, according to which he made his conclusions. Two of these are stating that proportions and numbers of flower parts of the same whorl should not be used for distinguishing genera. I cannot agree with this statement, since it is my opinion, that no single feature, however trifling it may seem, may principally be rejected; it is not the nature of a feature, but rather its constancy which makes it important and serviceable for classifying purposes, and in each case each separate character has to be carefully checked as to its classificatory value.

¹ H. J. L a m, Phylogenetic Symbols, past and present — *Acta Biotheor.* A, II, 3, 1936, 153—194.

—, Studies in Phylogeny I. On the relation of Taxonomy, Phylogeny and Biogeography — *Blumea* III, 1938, 114—125.

—, Over de eenheid der bijzondere plantkunde — *Vakblad voor Biologen* XIX, 11, 1938, 201—213.

In this respect classification and natural system are, in a way, adversaries, as the first one requires sharp discontinuities and the latter can be best studied and understood on the basis of variable characters.

In an earlier paper¹, I have more particularly discussed the nature of these variable features, which are to be considered as the materializations of genetically unstable gene-complexes that are in a period of "evolution". In the evolution, the development of single features² may be imagined as and represented by a series of subsequent phases and in several cases the direction of their development is fairly well known. A given feature may be in an active period or in a period of relative stability. In the latter case it is most suitable for classification purposes.

Let us now return to B a e h n i's work and consider some of his conclusions more in detail. His main subdivision of the Sapotaceae is based upon the placentation. Thus he created a subfamily *Basitraumae*, in which the ovules are basal and "erect"³ and the seeds have a circular and basal or subbasal scar (micropyle and hilum close together); and a subfamily *Pleurotraumae*⁴, the ovules of which are attached to the middle or the upper part of the cell, the scar of the seed being consequently long or large (micropyle and hilum far apart).

This is undoubtedly an important feature and it would certainly be still more important if we would know which is the more primitive condition, the basal or the apical affixion. It has been repeatedly recognized and used by earlier authors, e.g. by D u b a r d and later on by myself, but never as a sole principle. However, this feature is not as sharply discontinuous, as B a e h n i seems to suppose⁵. As I have shown in a recent paper on *Nesoluma*⁶, this genus, which I consider a very primitive one (perhaps the most primitive of the whole order), shows transitions, even within the same species from a fully basal to a fully lateral affixion (l.c., figs. 26, 58, 61). Furthermore *Sideroxylon tomentosum* R o x b. from British

¹ H. J. L a m, Ann. du Jard. Bot. de Buitenzorg, 42, 1932, 178—197.

² —, Phylogeny of single features — Gard. Bull., Straits Settlements, 9, 1935, 98—112.

—, Blumea, Suppl. I, 1937, 97—106.

³ I suppose that "ascendant" is meant, for as far as I know, the ovules of the Sapotaceae are always anatropous and apotropous.

⁴ The Conspectus gives the orthography *Basi-* and *Pleurotraumae*.

⁵ It is not very practical either, as one has to dissect a flower to state the subfamily. The corresponding fruit characters are easier, however.

⁶ H. J. L a m, Monograph of the genus *Nesoluma*, etc. — Bern. P. Bish. Museum, Occas. Pap. XIV, 9, 1938, 127—165.

India shows the most ideal transition between the small, circular basal scar and the long and narrow lateral scar. These facts, however, need not prevent us from choosing the character in question as a basis for a subdivision, but on comparing it with other features (such as offered by the calyx whorls, the androecium, the albumen in the seed and even the venation of the leaves), I don't think it is justified to attribute to it so high a classificatory value and therefore personally I cannot enter upon B a e h n i's subfamilies, whose names are, for the rest, not in accordance with the International Rules of Botanical Nomenclature (Cambridge 1930, Art. 24).

The next character, accepted by B a e h n i, is whether the sepals are arranged in one or in more than one whorl; "La valeur du double calyce semble donc être fondamentale pour la classification des Sapotacées" (l.c., p. 403). It appears from the statement on p. 507 that the one whorl category includes the genera with spirally arranged sepals. Undoubtedly the character alternatives, defined in this way, form a good basis for a classification, but not for a natural system. The latter would require that the spirally arranged calyx and the whorled one be put into different categories. From my own phylogenetically coloured standpoint I would rather raise the calyx characters to the rank of subfamily indicators, as they show a distinct phase direction, in which the quincuncial phase is to be considered as the primitive one from which first of all the phase with two whorls of two sepals may be derived. It is, moreover, certainly a more practical character, than that of the placentation, as it may be studied both in flower (buds) and in fruit, and without dissecting. Also concerning this character, however, some transitional forms are known, even in the same plant: *Nesoluma polynesianum* (related to the *Pouteria-Planchonella* group), *Madhuca subquincuncialis*¹ (with quincuncial as well as biseriata 4-merous calyces) and *Aesandra dongnaiensis* (i.e. a *Madhuca* with albumen; the outer calyx whorl is 2- or 3-merous but, as far as I know, the calyx is never quincuncial).

In general, as far as I can see no single feature shows a sufficient and outstandingly serviceable discontinuity for a subdivision into subfamilies and under these conditions one is, I think, safer to base all subdivisions on combinations of features, which method, moreover, gives a better chance for approaching a natural system.

In addition, as far as my experience with the Sapotaceae goes, I would hold to the old principles of establishing a natural system, as far as possible, on the basis of "from the more primitive to the

¹ To be published in *Blumea* III, 2, 1939.

more secondary". I am, of course, well acquainted with the fact, that it is a syncopation to speak of a "primitive species" or a "primitive genus", as these terms concern cases in which primitive features are prevailing. We only know primitive phases of features or of tendencies and as these are often mutually independent, a plant may well comprise one character in a primitive and another in an advanced phase. The only method, I think, to find our way out of this labyrinth, lies in choosing and describing the right combinations of features (i.e. tendency phases). It is only natural that there will always remain specimens and even systematic units, about whose taxonomic place in the system we cannot be sure, for the simple reason that Nature itself has given them an intermediate position. We cannot pretend, for mere practical purposes, to encroach upon natural conditions in too rude a way; and if we would feel obliged to do so, we would have to do it in an apologetic way and never forget that we do an unnatural thing.

It is a well-known fact, that in many large families the same characters return in smaller systematic units such as species on the basis of characters of wider scope in larger systematic units, such as genera. This phenomenon has been called the "Law of homologous series in variation" by N. I. V a v i l o v¹. These "homologous variations" have been thoroughly examined in the Annonaceae by L. D i e l s² and it would be well worth while to do the same for the Sapotaceae. Although the method is probably less well applicable to that family, since no single tendency has thusfar been fully accomplished ("Richtung . . . zum Abschluss gekommen [ist] . . ."; D i e l s, l.c., p. 82), it may help to get a better insight into its natural structure. In the light of this phenomenon, some of B a e h n i's remarks are more or less naive, e.g. when he pretends that his two subfamilies are homogeneous and parallel (l.c., pp. 503—505), without apparently recognizing the fact that a perfectly similar subdivision into "homogeneous and parallel" groups may be established on the basis of calyx whorls as well as on that of petal appendages, of the number of androeceum whorls, the presence of stipules and of albumen, etc.

In my opinion, the Sapotaceae — and other families under similar evolutionary conditions — have to be dealt with in a somewhat particular way. I am not very much of a splitter myself, but also the most convinced lumpner is obliged to return on his lumping steps on dealing with this family.

¹ Journ. of Genetics 12, 1922, 47—89.

² Sitz. Ber. Preuss. Akad. d. Wiss., Phys. Math. Kl. 9, 1932, 77—85.

Splitting is the field of the geneticist and as this is not approachable by taxonomic methods, this is the point in which P i e r r e failed. His observations are admirably accurate, as everyone knows who had the privilege of making use of his annotations, but this very accuracy made him, I think, draw his generic demarcations too narrow. In my opinion, D u b a r d has, in general, found the most suitable compromise, thus far published. For one cannot continue splitting without coming upon individuals. And equally one cannot continue lumping, without obtaining monstrous genera with an immense range of character phases — and still with more or less vague limits — genera, which require a thorough sectional subdivision. It will always remain arbitrary and a matter of fancy whether or not such sections should be raised to the rank of genera. As far as the Sapotaceae are concerned, my knowledge of the Malaysian and of some Polynesian groups have given me the conviction that the generic rank is preferable in most intermediate cases, as large genera are hard to survey and particularly because geographical isolations of groups are apt to be overlooked in a large genus. This is a point, almost entirely neglected by B a e h n i. Yet it may yield valuable evidence, as the present geographic distribution of a group is intimately connected with its evolution¹.

It is also on account of typological considerations that I prefer to consider *Sarcosperma*² as the representative of a separate, monotypical family, although it is certainly related to *Sideroxylon* (*Mastichodendron*). My impression is that B a e h n i has combined too much on the one hand, being inconsequent on the other in keeping other genera separate. Discussing only such genera as are more or less known to me, I would probably agree with E y m a's concept of *Pouteria*, but I hesitate to include such genera as *Achrouteria*³ and *Micropholis* (nervation!) and particularly *Planchonella*, although there is no sharp demarcation between them, both on geographical and on morphological grounds. *Planchonella* is distinctly much more constant in the numbers of its floral parts, its fruits are small, its seeds are in most cases provided with albumen, and its area is East-Asia to West-Polynesia, whilst *Pouteria* sensu E y m a is unstable in its floral numbers, with large fruit, the seed usually without albumen and with a main distribution in America, with some species as far West as Malaya. An analogous case, as far as the albumen is concerned, is found in *Dipholis-Bumelia*, which I

¹ Cf. H. J. L a m, *Studies in Phylogeny* II, *Blumea* III, 1938, 126—157.

² Cf. *Blumea* III, 1938, 184—185.

³ *Achrouteria* Eyma is an American *Planchonella* with large globose fruits, and *Pouteria*-like corolla.

would therefore logically keep separate also, being homologous variations on the same theme. But *B a e h n i* seems inconsequent in not including in *Pouteria* the genera *Calocarpum*, *Krausella* H. J. L a m¹ (apparently overlooked by *B a e h n i*) and *Chelone-spermum* (?).

A still more embracing combination is made regarding *Madhuca*, which in the sense of *B a e h n i* not only comprises the genera *Payena*, *Ganua* and *Burckella*, but also *Isonandra* and even *Palaquium*. I daresay I am acquainted with almost all known species of these genera, and I would emphatically hold my opinion that they are probably better delimited (morphologically, but also geographically!) than, say *Sideroxylon* and *Nesoluma*, which are maintained by *B a e h n i* and undoubtedly better than *Northia*, which has not a sharp demarcation towards *Manilkara*². Some of my publications³ give, in addition to my statements of 1925⁴, an idea of the structure of what was then called the Eumadhuceae, taxonomically and geographically. It is, however, utterly ununderstandable to me why *B a e h n i* includes also *Isonandra* (with 4-merous flowers but isomerous calyx and corolla) and *Palaquium* (with 6-merous flowers and isomerous calyx and corolla), but not *Aulandra*, which is undoubtedly closely related to *Palaquium*. I do not know *Tropalante*, M o o r e's text and picture giving no particulars on the nervation of the leaves (an important feature in the "Eumadhuceae"), nor of the fruit. The 5 sepals are said to be biseriate. These data are, in my opinion, insufficient to justify a combination with *Madhuca*. At any rate, it seems illogical to include *Tropalante* and not *Diploknema*. Also the distribution of the former (New-Caledonia) is an indication to be sceptical. As to *Aesandra*, this monotypic genus might fit into *Madhuca* sensu D u b a r d, if its seeds were not provided with albumen. On account of this feature and of some minor ones (exceptionally large sepals, the outer whorl of which is often 3-merous) I would suggest to maintain this genus as a good one, which again yields an excellent example of a homologous variation (albumen). In this connection I would exclude *Baillonella* beforehand from *Madhuca* on geographical grounds. Furthermore I would point out a few inconsistencies regarding *Madhuca*; in the statement on p. 507 *B a e h n i* inserts the genus in the category with "calyce simple", whilst the

¹ Nova Guinea IV, Bot. 4, 1932, 566, Tab. 127—128.

² Cf. H. J. L a m, Bern. P. Bish. Mus. Bull. 141, 1936, 163.

³ H. J. L a m, Phylogeny of single features — Gard. Bull. Str. Settle. 9, 1935, 98—112.

⁴ H. J. L a m, Bull. Jard. bot. Buitenz. III, 7, 1925, II, 110—112.

calyx consists, with the exception of *M. subquincuncialis*, always of two whorls of two sepals, and not, as B a e h n i mentions on p. 460: "à quatre sépales connés à la base". If *Palaquium* is included in *Madhuca*, B a e h n i's characterization of the latter does not fit, that of *Palaquium*, however, being approximately correct.

In addition to the above, some scattered remarks may follow here on the basis of B a e h n i's paper, which are quite incidental and don't in the least pretend to be exhausting or complete.

M o r p h o l o g y.

It would be of prime importance to study all characters concerning their variability, tendencies and their phases and evolutionary directions with special reference, if possible, to primitive and advanced phases. In addition, the geographical distribution of characters or of certain combinations of characters may be useful for our insight into the natural system of the family.

Leaf. As B a e h n i has remarked, the venation yields important classificatory characters and has been repeatedly used for classifying purposes, e.g. by Engler, Pierre, Dubard and myself. As far as I am acquainted with Sapotaceous leaves there are four (B a e h n i only mentions two) main types of nervation, viz.

1. Tertiary nerves transverse (more or less perpendicular to the secondary ones, e.g. many species of *Palaquium* and *Madhuca*).

2. Tertiary nerves longitudinal, generally parallel with the secondary ones (e.g. *Payena*, species of *Planchonella*, *Chrysophyllum*, *Pouteria*, etc.).

3. Tertiary nerves hardly more prominent than the very minute and conspicuous areolate reticulation (e.g. *Nesoluma*; *Sideroxylon inerme* c.a.).

The types 1—3 are comprised in B a e h n i's first type.

4. All nerves parallel, very much crowded, the leaf striate (e.g. *Micropholis*, *Manilkara*). This is B a e h n i's second type.

The types 1 and 2 are united by many transition forms in the same genus (constant in the species) or even in the same species (e.g. *Palaquium Gutta*). It may be an important specific character (*Palaquium*, *Planchonella*) and in some cases (type 4) it has also generic importance (*Manilkara*, *Northia*, *Micropholis*). Particularly in the *Madhuceae* it is a character which is strongly correlated with others. It would be worth while to examine the American and the African Sapotaceae as to the usefulness of this feature. Type 3 is a special but very characteristic and geographically more or less significant modification of a combination of 1 and 2.

It may be also important to study fossil Sapotaceae leaves (as old as of Cretaceous age) concerning their venation.

Inflorescence. Nothing is said by B a e h n i about the inflorescences. It is well-known that these are usually fasciculate, the fascicles may be eventually reduced to one single flower. The original form may have been the raceme or the panicle. Therefore such racemose inflorescences as are found in *Sarcosperma*, in *Planchonella pedunculata*¹ and possibly also in *Pouteria lateriflora* (cf. B a e h n i, l.c., p. 488) are to be considered primitive conditions. The same is true for *Aulandra* which, moreover, shows a tendency towards cauliflory. In some species (e.g. *Planchonella nitida*) the fascicles are borne on leafless axillary shoots.

Flowers. Notice should be given to the tendency towards unisexuality. In *Nesoluma* and also in many species of the *Pouterieae*, the stamens are more or less abortive, which may give rise to female flowers.

Calyx. As I have mentioned above, B a e h n i has not given sufficient attention to the important characters of the calyx. His too brief considerations contain some errors (*Isonandra* and *Palaquium* with 5 sepals instead of 4 and 6 respectively; in *Isonandra* it is exceptionally 5 or 6, but the calyx is always biseriata) and, as far as I could see, he almost entirely neglects the spiral arrangement (except in the key on p. 506, n. 20), although S c h u l z e mentions it in his notice in the "Botanisches Zentralblatt"². I consider the calyx features of great importance, the spiral arrangement being the more primitive condition.

"*Staminodes*". I purposely put this word between quotation marks, as I am not sure that all organs, mentioned by this term are morphologically sterile stamens, as I have more circumstantially discussed in my *Nesoluma* monograph. Similar organs are also known in other families such as the Primulaceae. It would be worth while to investigate their morphological nature and also their eventual relation with the ventral (lateral) petal appendages of such genera as *Bumelia* and *Dipholis*.

Gynaeceum. B a e h n i says that "l'ovaire est très généralement hirsute ou, tout au moins, velu". As can be concluded from other parts of his memoir, he seems to be insufficiently acquainted with genera like *Ganua* and *Burckella*, almost all species of which have an entirely glabrous ovary, whilst in *Palaquium* and *Madhuca* this condition is by no means rare.

¹ Cf. Blumea III, 3, 1939.

² Bot. Zentralbl., N.F. 32 (Bd. 174), 1939, 170.

Genera.

In his introductory remarks (l.c., p. 414) *B a e h n i* says that he has omitted non-essential characters. It may be due to an imperfect knowledge of the importance of certain characters in individual genera, however, that he in some cases (*Achras*, *Aesandra*, *Calvaria*, *Madhuca*, *Palaquium*, *Payena*, *Sideroxylon*, etc.) omitted also essential characters, and that his choice is not always the most suitable one. While we may esteem that he evidences the maintenance of genera, we cannot approve that he has decided "pouvoir (se) dispenser de donner les motifs qui nous a fait abandonner tel autre", even if he has discussed his general arguments before.

As to the remarks given here, if no arguments are mentioned, these may be found in the text above.

Aesandra. To be maintained.

Baillonella. Probably not a *Madhuca* (distribution).

Beccarimnea. Omitted by *B a e h n i*. *B. laurifolia* Pierre = *Planchonella* spec., *B. rigida* Pierre = *Planchonella firma* (Miq.) Dub.

Burckella. To be maintained.

Butyrospermum. To be separated from *Achras* because of its 4-merous calyx whorls and its distribution.

Calvaria. As *B a e h n i* remarks, the type species of *Sideroxylon* (*S. inerme* L.) has to be put together with the species described as *Calvaria*. I therefore agree with *B a e h n i*, inasfar he states that these species have to be named *Sideroxylon*, and that the generic name of *Calvaria* has to be dropped. See further under *Sideroxylon*.

Croixia (*Beccariana* Pierre) = *Palaquium ferox* H. J. Lam.

Dipholis. Probably to be maintained (albumen).

Diploknema. To be united with *Madhuca*? (cf. *M.* species with quincuncial calyx).

Ganua. To be maintained.

Isonandra. To be maintained. The calyx has sometimes 3-merous whorls (type yet different from *Palaquium*!).

Krausella H. J. Lam (Nova Guinea XIV, 4, 1932, 566, Tab. 127—128). Omitted by *B a e h n i* — Trees, Leaves with transverse tertiary venation. Sepals 6—8, spirally arranged. Petals 6—8. Stamens 6—8; staminodes 6—8, subulate. Ovary borne on a solid gynophore with disk rim and 6—8 cells, ovules attached in the lower half of the cell. Fruit unknown. — 2 Species in New Guinea.

Mastichodendron, see under *Sideroxylon*.

Nesoluma. Name erroneously in italics.

Northiopsis = *Northia* (cf. H. J. Lam in Bern. P. Bish. Mus. Bull. 141, 1936, 163).

Palaquium. To be maintained.

Payena. To be maintained.

Planchonella. Probably to be maintained.

Sarcosperma. Separate family on account of typological considerations (subopposite leaves with eventual auricles and glandular pits; racemose or rather paniculate inflorescences; ovary 2—1-celled; testa thin-crustaceous, not shining). Although the differences towards *Sideroxylon* (sensu Dubard) are not great (*Sid. tomentosum* Roxb. from British India is one of the very few Sapotaceae — *Niemeyera* may be another — which has a testa like that of *Sarcosperma*; cf. also the subopposite leaves in some *Planchonella* species such as *Pl. Lauterbachiana* and *Pl. suboppositifolia*, and in some species of *Pouteria*; auricles seem to be extant also in *Delpyodora*), the type of *Sarcosperma* is so much different from anything known in the Sapotaceae, that I would hold to keep it separate in the family rank (cf. *Blumea* III, 1938, 184—185).

Siderocarpus. *S. Vrieseanus* Pierre = *Planchonella Vrieseana* (Pierre) Dub.; *S. Beccariana* Pierre and *S. borneensis* Pierre = *Palaquium ferox* H. J. Lam.

Sideroxylon. As the type species (*S. inerme* L.) belongs to another group of species ("Calvaria") than those which were put to *Sideroxylon* by Dubard and others, the latter have to receive a new generic name. The species thusfar comprised under *Calvaria* have therefore to be named *Sideroxylon*; for the others I would provisionally propose the oldest valid synonym, viz. *Mastichodendron* Jacq. in Hedw. Gen. (1806) — Trees. Tertiary venation of leaves more or less parallel to the secondary nerves. Inflorescences fasciculate in the leaf-axils. Sepals 5, spirally arranged. Corolla 5-lobed, lobes imbricate. Stamens and staminodes 5. Ovary 5-celled, ovules attached to the base of the cell. Seeds with small circular scar and provided with albumen.

As far as is known to me, only the following species undoubtedly belong to this genus.

1. **M. foetidissimum** (Jacq.) H. J. Lam, nov. comb. (cf. Dubard, Ann. Mus. Col. Mars. 20, 1912, 82), including *Sideroxylon portoricense* Urb., *S. jamaicense* Urb. and *S. domingense* Urb. — Antilles.

2. **M. Wightianum** (H. & A.) H. J. Lam, nov. comb. — Hong Kong, Tonkin, Cochinchina (cf. H. Lecomete, Fl. Gén. Indoch. III, 7, 1930, 887).

3. **M. racemosum** (H. Lec.) H. J. Lam, nov. comb. (cf. Lecomete, l.c., p. 888). — Tonkin.

4. Possibly also *Bumelia Picardae* Urb. (Haïti) and *Dipholis anomala* Urb. have to be inserted here.

I do not know *Sideroxylon tonkinense* Dubard from Tonkin and *S. oxyacanthum* Bail. from Abyssinia (cf. D u b a r d, l.c., p. 84). *S. tomentosum* Roxb. (= *Planchonella tomentosa* [Roxb.] Pierre) from British India is intermediate between *Mastichodendron* and *Planchonella* (seed scar); it is further deviating by a thin crustaceous testa. The other species of E. Asia, described by L e c o m t e and M e r r i l l, are mostly *Planchonellas*, although one or two *Mastichodendron* may be concealing amongst them. I am inclined to consider *Mastichodendron* in its proposed delimitation a regressive genus with a discontinuous relic area.

Treubella. Probably not Sapotaceous.

Tropalanthe. Insertion in *Madhuca* not certain.

Key to the Genera.

There are some mistakes in the key to the genera, e.g.

3. *Nesoluma* has staminode-like structures.
9. Is leading astray (discussion above).
14. According to the list of genera (l.c., p. 433), in *Delpydora* not the stamens but the anthers are connate.
18. *Northia* has often small staminodes (cf. also Bern. P. Bish. Mus. Bull. 141, 1936, 162—163).
23. *Aulandra*. The inflorescences are not cymose.

Conspectus of genera.

Some of the mistakes of the text and of the key are, of course, also returning in the conspectus:

Nesoluma, with eventual "staminodes".

Northia, ditto.

Sarcosperma, to be removed.

Madhuca. The insertion in the Pleurotraumae with "calyce simple" is not correct, the calyx being biseriata (except *M. subquincuncialis* and, eventually, *Diploknema*).

Ituridendron and *Tridesmostemon* are considered identical in the text (under the name of the latter).

Aulandra. The position of *Aulandra*, apart from *Madhuca* (f. *Baehni* comprising *Palaquium*), is unnatural.

The arrows connecting *Achras-Eberhardtia* and *Madhuca-Ituridendron* are ununderstandable to me both from a morphological and from a geographical standpoint.

It is, as a matter of course, impossible, to represent the complicated relations of a great number of genera in a sort of system of coordinates, but I suppose, that it has been merely *Baehni's* intention to obtain, first of all, a practical survey of the material.

In my opinion, however, very much detailed study remains to be done before we can venture to insert all genera in their proper place. First of all, a much more detailed study has to be made of the variability of single features and particularly of the leaf-nervation, the floral parts (calyx, "staminodes"; "dédoublement"; introrse and extrorse anthers) and the embryo (position, albumen). Eventually with the aid of statistical methods and at any rate with that of geographical data the generic limits have to be rechecked on the base of a fully known morphology. Few people would appreciate more vividly than I, if Dr. B a e h n i would be able to accomplish this task, with which we wish him every success.

I will end with a few suggestions towards the natural system of the Sapotaceae, as I see it on account of the considerations, laid down in the first part of this paper. A few months ago, and by a curious coincidence almost simultaneously with B a e h n i, I published a new tentative system of the family in my *Nesoluma*-monograph, quoted above (l.c., p. 137—141). This has only some pretention as to the main subdivision and to the groups I am more or less particularly acquainted with. However, the endings of some names of the groups are not in accordance with the International Rules of Botanical Nomenclature, Art. 24. I therefore avail myself of this opportunity to give here, once more, and in a concise form my present opinion on the system of the Sapotaceae. In choosing a name for a group, that of the oldest genus was taken as a basis. The following system is meant to be as close to a natural one as can be represented on a sheet of paper and in accordance with my provisional ideas of the phylogeny of the group. But I must stipulate that my knowledge in this field is still extremely scanty. As far as the American and the African genera are concerned, the scheme is very incomplete and likely to be due to alterations.

Subfamily I. SIDEROXYLOIDEAE, nova subfam. (= tribe *Sideroxylinae* Dub.) — Sepals spirally arranged. Calyx 5—8(—12)-merous or with two whorls of 2, 3 or 4 sepals (if 2, then the sepals sometimes unequal and not strictly opposite). Corolla isomerous or rarely pleiomerous (*Nesoluma*, *Chrysophyllum*); petals sometimes with ventral or lateral appendages (*Bumelia*, *Dipholis*), but never with dorsal appendages. Stamens epipetalous and often isomerous with petals, sometimes more (*Nesoluma*, *Achradotypinae*), in one whorl; alternipetalous staminodes often extant, more rarely none. Carpels usually isomerous with the calyx, rarely less, even more rarely more (*Pycnantra*). Circumtropic.

Tribe A. *Sideroxyleae* Dub. emend. H. J. Lam (= *Calvarieae* H. J. Lam, Bern. P. Bish. Mus. Occ. Pap. XIV, 1938, 139) — Seeds subglobose and albuminous, the scar circular or nearly so, basal or sublateral, large or small. Embryo oblique or more or less horizontal. Reticulation of leaves very minutely areolate. Staminodes, if any, usually large or petaloid. (*Nesoluma*, Pac. Islands; *Sideroxylon* [= *Calvaria* Comm.], Mascarenes, Madagascar, S. & E. Africa). Key cf. H. J. Lam, l.c.

Tribe B. *Bumelieae* Baill. emend. H. J. Lam (= *Eusideroxyleae* Dub., pro max. parte) — Seeds with small and basal circular scar. Embryo erect or slightly oblique, never horizontal. Reticulation of leaves not areolate.

Subtribe 1. *Mastichodendrinae*, novus subtribus — Petala estipulata. Semina albuminosa. — No appendages to the petals. Seeds albuminous. (*Mastichodendron*, *Argania*). Area disjunct.

Subtribe 2. *Bumeliinae*, novus subtribus. — Petala stipulata. — Appendages to the petals extant (*Dipholis* with albuminous, *Bumelia* with exalbuminous seeds). Tropical America and subtropical N. America.

Tribe C. *Pouterieae* H. J. Lam (= *Lucumeae* Baill. + *Chrysophyllinae* Engl.) — Seeds with or without albumen, the scar long and narrow or very large.

Subtribe 1. *Pouteriinae*, nom. nov. (= *Eulucumeae* H. J. Lam + *Chrysophylleae* H. J. Lam) — Stamens as many as petals or at most less than twice their number.

a. *Acyclicae* (= *Planchonellidae* H. J. Lam) — With spirally arranged sepals, or sepals rarely subbiseriate. (*Chrysophyllum*, *Planchonella*, *Krausella*, *Pouteria*, *Leptostylis*, *Sebertia*, *Micropholis*, *Achrouteria*, *Calocarpum*, *Bakeriella*, *Ecclinusa*, a.o.). Circumtropic.

b. *Cyclicae* (= *Achradidae* H. J. Lam) — Calyx biseriate, whorls 3—4-merous; stamens and staminodes isomerous with the calyx. (*Achras*, Trop. America; *Butyrospermum*, Trop. Africa).

Subtribe 2. *Achradotypinae* H. J. Lam (= *Achradotypeae* H. J. Lam) — Stamens 2 or more opposite each petal (*Achradotypus*, New Caledonia and New Guinea; *Omphalocarpum*, Trop. Africa; *Pycnandra*, New Caledonia).

Subfamily II. MIMUSOPOIDEAE, nova subfam. (= tribe Mi-

musopeae Hartog). Petals with dorsal appendages (rarely abortive). Calyx biseriate, isomerous with the corolla, the stamens and the staminodes (if any). Circumtropic.

Tribe A. *Mimusopeae* H. J. Lam (= *Eumimusopeae* Dub.) — Seeds with small, circular and basal scar. Flowers 8-merous (*Mimusops*, etc.).

Tribe B. *Manilkareae* Dub. — Seeds with long and narrow scar. Flowers 6-merous (*Manilkara*, *Northia*).

Subfamily III. MADHUCOIDEAE, nova subfam. (= tribe *Palauquinae* Dub.). Calyx with two fully cyclical whorls, rarely 5 spirally arranged sepals (*Diploknema*, *Tropalanthé*?, one species of *Madhuca*). Stamens twice as many as petals or more, rarely less, in two or more whorls; staminodes none (sterile stamens exceptionally extant). Petals without appendages. S. and E. Asia to Australia and Polynesia.

Tribe A. *Madhuceae* H. J. Lam (formerly a subtribe) — Petals and carpels more numerous than sepals, usually twice as many but not rarely more, carpels rarely less (*Burckella*, *Madhuca*-species). Sepals cyclically or spirally arranged, fully cyclical and 4-merous (biseriate) in *Burckella*, *Ganua* and *Payena*, mostly so in *Madhuca*, cyclical (?) and 5-merous in *Aesandra*, spirally arranged in *Diploknema* and *Tropalanthé* (?), and occasionally in one *Madhuca*-species.

Tribe B. *Palauquieae* Engl. (formerly a subtribe) — Calyx, corolla and gynaeceum normally isomerous. Calyx whorls fully cyclical (3-merous in *Palauquium* and *Aulandra*, usually 2-merous in *Isonandra*).

In so far this system is not fit for practical purposes, it would have to be augmented by a dichotomous key.