

THE LEAF OF BAUHINIA

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Received December 15, 1951

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A. INTRODUCTION

In the genus *Bauhinia* three types of leaves occur, *a* simple, *b* butterfly-shaped with a deep incision at the top, *c* bifoliolate, (cf. fig. 1). In most species the leaves belong to type *b*, to which shape

some owe their Malay name "kupu-kupu" (butterflies). The resemblance with a butterfly is not confined to the shape, but extends to the way the "wings" are laid together at night.

I intend to treat the following species:

- Type *a*. *B. bidentata* Jack., *B. pyrrhaneura* Korth., *B. kockiana* Korth.,
B. assuruana Moric., *B. platycalyx* Benth., *B. cordifolia* Roxb.
 Type *b*. *B. flammifera* Ridl., *B. purpurea* L., *B. scandens* L., *B. tomentosa*
 L., *B. variegata* L., *B. monandra* Kurz and some others.
B. corymbosa stands close to type *c*.
 Type *c*. *B. binata* Blanco, (syn. *B. blancoi* Baker), *B. winitii* Craib.,
B. diptera Bl.

It seems possible to consider the three types as transformations of a single one. The data agree with this. There is a gradual transition between the types. In *B. scandens* L. type *a* and *b* can be found on the same plant, in *B. rubiginosa* Berg., type *b* and *c*. Leaves of all three

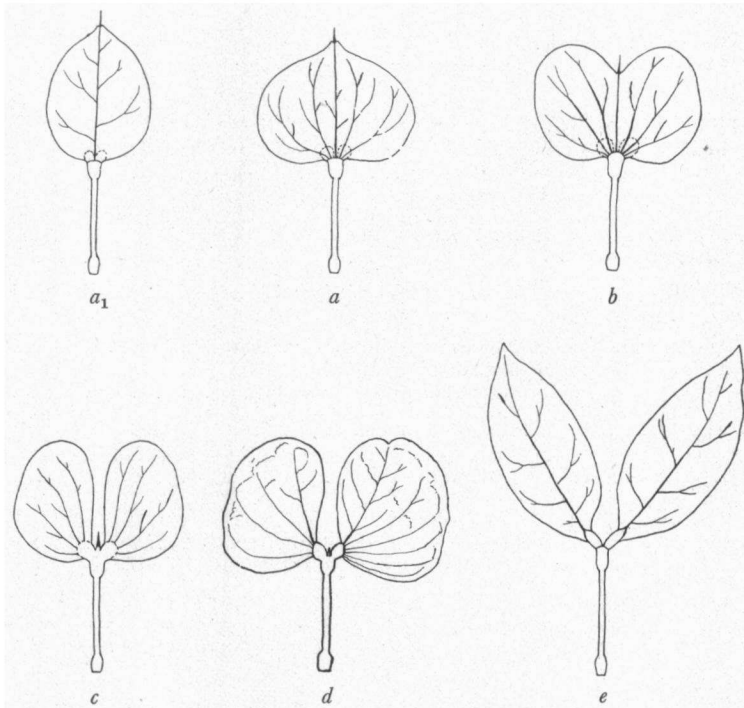


Fig. 1. Types of leaves in Bauhinieae and in Hardwickia;
*a*₁. *Bandeiraea tenuiflora*.
a. Simple-leaved type of *Cercis*, *Bauhinia bidentata* a.o.
b. Bilobate type of *B. purpurea* a.o.
c. *B. binata* a.o. bifoliolate types.
d. Monojugate compound leaf of *Hardwickia binata*. Different ways of venation combined into one leaf.
e. *Trachylobium verrucosum*, monojugate compound leaf.

types have the apical incision, though it is very shallow in those of type *a* (cf. fig. 1 and 4).

All three types show a petiole with a basal joint (primary pulvinus) and an apical joint near the lamina (secondary pulvinus). In comparison with other leguminous leaves, type *a* might be called unifoliolate and type *c* bifoliolate. The apical joint is undivided, even in bifoliolate leaves, where both "leaflets" are inserted on it. This joint has been overlooked by many botanists, probably because they used herbarium material, where the swelling is scarcely visible (cf. D, 2). A characteristic trait, common to all types, is the curious bristle (the German "Granne") at the bottom of the incision (in bifoliolate leaves therefore between the "leaflets" on top of the petiole).

Ecologically the three types also have much in common, viz. the tendency to fold up the lamina along the midrib. These nyctinastic movements are executed by means of special motile cushions (laminar joints) one at the base of each half of the lamina. They are distinct from the apical common joint but merge gradually into the rest of the leafblade.

Now the question arises which type is the original one. (The question may be put in the sense of phylogeny or of idealistic morphology).

Is it really true that the "simple" leaf of *B. bidentata* is the basic type from which types *b* and *c* have been derived, either by splitting (as a mere descriptive description may suggest) or by terminal inhibition of growth (pleuroplastic development), to use a more directly comprehensible terminology? An authority on morphology like TROLL has accepted the latter idea in his "Vergleichende Morphologie" (p. 1025 and 1591) and compares the *Bauhinia* leaf to the well known leaf forms of *Ipomoea pes-caprae*, and *Lourea vespertilionis*. BREMEKAMP (1) gave in a short note some arguments in favour of this idea.

Other morphologists like URBAN (10), VELENOVSKY (11), UITTEN (9) and FRIES (2) defended the opposite conception, according to which type *c* would have the original form out of which the simple leaf arose by fusion. WATARI (12) thinks the leaves of *Cercis* and *Bauhinia* can be classed as a case of palmately compound leaves with many leaflets. In two short notes in a popular journal VAN DER PIJL (6, 7) advanced some arguments in favour of fusion, but after the remarks of BREMEKAMP (1) the question must be treated in a more thorough and different manner. I feel justified in doing so now, because I had living material at my disposal, while most of the previous work was done in herbaria only.

It seems hazardous to plead for the possibility of fusion after it has come into discredit. TROLL has substituted it largely by the idea of non-disjunction (Nichttrennung). It is, however, not clear if in flower morphology he will also be able to avoid the term of fusion. We will include here under fusion cases where two primordia, usually separated, grow out together or where there is lack of complete differentiation. Seen in this way the term of "fusion" still

expresses the idea that the leaf of *Bauhinia* is homologous with two leaflets.

The main arguments against coalescence are:

1. The lack of the typical vein-point of leguminous leaves on the tips of the two leaf halves.
2. The presence of a palmate nervature in the leaf halves of types *b* and *c*, which also distinguishes them from ordinary leguminous leaflets.
3. The fact that the leaf halves are not folded in the embryonal state, as leguminous leaves are.

We will see that these points indeed, though not in contradiction of fusion in general, render a fusion between ordinary leaflets less probable at first sight. In the following all available data about the leaves are arranged systematically in relation to the possibilities of "splitting" and "fusion", or other explanations.

Cross references will not be given by page number, but by referring to the subdivisions given in the initial survey of the contents of this paper.

B. COMPARATIVE MORPHOLOGY

1. *The subfamily*

As a rule *Caesalpinioideae* have paripinnate leaves. For this reason one is at first sight inclined to consider the bifoliolate leaf of *Bauhinia* as the original form. Simple or unifoliolate leaves would be strange.

2. *Monojugate relatives*

Some *Caesalpinioideae* with monojugate bifoliolate leaves show a strong likeness to type *c*. Such instances, suggesting type *c* as the primitive one, are *Cynometra cauliflora* L., *Cassia bauhinioides* Gray, *Hymenaea* species, *Trachylobium verrucosum* Oliv., *Hardwickia binata* Roxb., and *Copaifera mopane* Kirk. Of these *Trachylobium* is especially important as it has just the same differentiation in three types of joints as *Bauhinia* (cf. fig. 1). Its primary leaves show a specially striking similarity with those of *Bauhinia* as the venation is the same and even the bristle between the halves is present. The compound (monojugate) leaves of *Hardwickia binata* cannot be distinguished from the leaves of *Bauhinia* type *c* (cf. fig. 1d). In monojugate leaves (even in those of *Hardwickia binata*) the sides of the leaflets that touch in the median line are in these plants often reduced. This suggests the possibility that in *Bauhinia* only the two outer halves may have been left and that the latter may have fused in some species.

An abnormal leaf of *Hymenaea courbaril* L. from Buitenzorg was highly suggestive in this direction. It was kindly sent by Mr C. VAN WOERDEN, curator of the Botanic Garden. The two leaflets had fused with the joints and the basal parts of the blades, giving a product strongly resembling a bilobate *Bauhinia* leaf. The two main

veins were united over a distance of 1—1.5 cm from the base. Originally I considered it as a weak point in this comparison that in real monojugate leaves the leaflets have only their own joints, while in *Bauhinia* the two leaflets or the two halves have their own leaf joints, but are both inserted on a common apical pulvinus. We will see however, that *Trachylobium* and *Hardwickia* form a link between these divergent structures (cf. C 1). In these relatives the monojugate condition can only be seen as a reduction of a pinnate leaf. It is not possible to consider their leaves as derived from a split *Bauhinia* type. It is to the contrary clear that *Bauhinia* is the more derivated type.

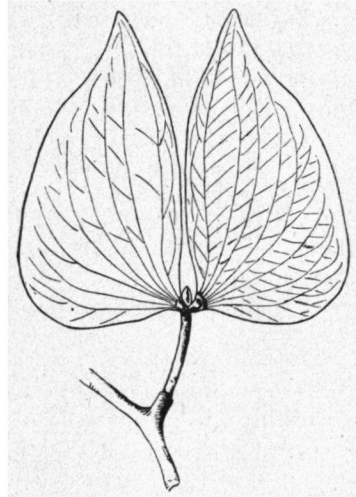


Fig. 2. *Copaifera mopane*, monojugate compound leaf. (after Hutchinson). In young plants I found no petioles.

3. *Imparipinnate relatives*

BREMEKAMP (1) pointed to *Caesalpinioideae* with imparipinnate, trifoliolate leaves, like *Krameria*. This makes type *a* and the "simple" leaves of the related genera of the *Bauhinieae* (*Cercis* and *Bandeiraea*) less exceptional and enigmatic. Speaking generally the group of the *Caesalpinioideae* is not so well defined that it is easy to say what genera are most closely allied to the *Bauhinieae*.

4. *Leaf or leaflet*

It is necessary to digress here on the morphology of leguminous leaves in general, because the value of the apparently simple leaves of type *a* and of the genus *Cercis* is not unequivocal. Most authors, especially URTIEN (9), call them simple, probably ignoring the apical joint. Is it, however, really necessary to consider this leaf type as a reduced form, as the apical leaflet of a pinnate leaf? For many leguminous genera, like *Desmodium*, this interpretation is generally accepted and it is favoured by the presence of stipellae on top of the rachis. It may be asked whether the presence of a double pulvinus can be considered sufficient proof for this interpretation. VELENOVSKY (11) (his fig. 185) already expressed doubt. Perhaps the petiole between lower and upper pulvinus is not simply homologous to the rachis of a compound leaf. It may sometimes be a growth zone intercalated between two parts of the single pulvinus of a real, simple leaf. The question whether *Bauhinia*, *Cercis* a.o. have a leaf or a leaflet may, however, be left aside so that we may return to the main point, splitting of an originally simple part or fusion between two originally separated ones.

5. *Cercis* and *Bandeiraea*

If we should finally conclude that in *Bauhinia* type *a* marks the end of the developmental range, this would have unexpected consequences for two nearly related genera of the *Bauhinieae*, viz. *Cercis* and *Bandeiraea* (*Griffonia*), resp. of types *a* and *a*₁. Their leaves are clearly homologous with those of *Bauhinia* type *a*. Without this comparison nobody would have suspected them of being compound structures. Yet their venation (mostly palmate) and the apical pulvinus mark them as something special in the family. The leaves of *B. flammifera* are exactly like those of *Cercis*. FRIES and UITTEN accepted this consequence and considered the leaves of *Cercis* as fusion products.

6. *Comparison of the leaf halves with stipules and stipels*

The peculiar structure and venation of the leaf halves suggests the possibility that they might be homologous with organs other than leaves, in the first place with stipules. The description given by TROLL (8) (p. 1281) of *Cassia basifolia* Vog., where two leaflike stipules are found one on each side of a bristle that represents the leaf, points to the same possibility. In *Bauhinia* a stipular nature of the leaf halves is out of question, as the leaves have two stipules at the base. These stipules too however, have very peculiar features, e.g. the occurrence of thorns in their axils (cf. URBAN (10) the inequality of the two partners in some cases etc. The trichomes in their axils, described by URBAN, are homologous to the colleters found in the axils of the sepals and of the cotyledons. The one that in American species is thornlike is, in those species I investigated, mostly represented by a nectar secreting thread. I first thought these threads might be identified with the prophylls of the axillary bud. In cross sections of growing-points of *B. purpurea* however, it is clear that they originate from the basal part of the stipules in their very early life. They imitate as it were the axillary buds of the leaves proper. In his "Die Pflanzenwelt" WARBURG says (p. 179) that in some American species these stipular threads do not develop into thorns, but into tendrils.

7. *Comparison with other organs*

It is not necessary to confine our discussion to a comparison with the leaves of other plant species but we may compare the foliage leaf of *Bauhinia* with other organs of the same plant. I refer to UITTEN's (9) attempts to find a parallel between leaf venation and inflorescence structure and even between primitivity of flower and leaf. He thinks that since the flowers of *Bauhinia* are primitive as compared with those of other *Bauhinieae*, its leaves too may be of a simpler type. It seems rather dangerous to apply this peculiar method to the flowers and leaves of the three *Bauhinia* groups. Of course it is justified to look for indications in favour of splitting or fusion in metamorphosed leaves as bracts and petals. It is curious that in none of these structures the least trace of a compound nature can be found. Never do bracts look double. The apical bristle, however, is always prominent. It is tempting but very speculative to compare the curious tendrils of some

Bauhinia species with their leaves. TROLL's figures on p. 850 show a double spiral with a rudimentary top between. Though this forms a striking analogy with the leaves there is no indication of homology. The homology of the tendrils and their bearers hides some riddles. They are compound just as the leaves possibly are. From URBAN's (10) study it is clear that not only the tendrils, but also the inflorescences are compound structures with a tendency to condensation into something apparently simple, with an arrested top rudiment and two flowers. In D 3c and D 4 comparisons even with cotyledons will present themselves.

The zig-zag build of the young stem, with the leaves in alignment with the preceding part of the axis, suggests a sympodial structure of the stem. The situation of the leaves, however, is not in accordance with this idea. The axillary buds lie between the leaf and the continuation of the stem and there are no traces of arrested main axis ends.

C. PHYSIOLOGICAL AND ECOLOGICAL DATA

At night the whole leafblade of type *b* and both leaflets of type *c* together perform a movement vertically downward. Besides this the two halves perform inter se another upward movement resulting in a folding together. This folding happens also after too strong an illumination. As in all nyctinastic movements the ecological function of these changes of position is not clear, but the folding is a constant character. In *Bauhinia* it serves the two usual "purposes": the "sleep" at night and the avoiding of too bright light at noon. The latter function is usually considered as being the primary one, though in the most primitive plant with such leaf movements (the fern *Marsilea*) the two functions already go together.

1. Leaf movements and fusion

Fusionists explain the folding up as a consequence of the leaf's complex nature. According to them the two original leaflets have kept their independent way of moving in their own leaf joints. However strong this argument is, it does not explain why the complex product also has a common joint (our secondary pulvinus). It pleads against fusion that in binate leaves the two "leaflets" do not perform their downward movement independently—as is the rule in leaflets. This movement happens in the common joint. Since we know that *Trachylobium* leaves possess a common joint as well as separate leaf joints, this common movement of leaflets is no longer an objection. In *Trachylobium* the leaflets of young plants move just as the leaf halves of *Bauhinia* viz. with separate joints for folding up (the leaflet joints) and moving downwards (the common joint). I think the same happens in the monojugate leaves of *Hardwickia binata* and those of *Copaifera mopane* (*Colophospermum mopane* Kirk ex Leonard).

2. Leaf movements and splitting

"Splitters" have more trouble to explain the movements than fusionists. According to them the tendency to fold up must be some

new adaption to light factors, starting in the simple leaves, where it is not completely developed. In type *a* the folding at night is less apparent but can be seen for instance in young leaves of *B. flammifera*. These, however, still have an incision of 4 mm on a length of 95 mm.

In herbaria leaves of type *a* are found folded up more frequently than can be explained by youth only. In *B. platycalyx* Benth it is difficult to flatten the leaves entirely when preparing them for herbarium material. No actual folding up was seen in the living leaves of *B. Kockiana* and many other species with simple leaves. *Cercis* does not fold its leaves. Of course it has no explanatory value to kill the question by attributing the movement to a repetition of the unfolding movement in the sense of GOEBEL. The motile tissue at the base of the leaf halves is not an "unfolding joint" active in youth only, though an unfolding tissue may have been the starting point of the new development. According to "splitters" the incision and the final bipartition may be an expression of the tendency to facilitate the folding up. This agrees with what I saw in *B. scandens*, viz. that the deeply split leaves of young plants folded at night, but that the later ones, where the incision was not much deeper than $\frac{1}{4}$ of the total length, remained unfolded, even when dying, (cf. E 2). This expression of a tendency should be seen in the light of the "Gestaltungstypen" of TROLL, as expressed in his "Organisation und Gestalt im Bereich der Blüte". The ecological moment has become a morphological force. In the same sense nyctinastic movements and the dividing up of the leguminous leaf into leaflets are possibly related. And this "Gestaltungskraft" may tackle the big leaflet of the type of *Cercis*, repeating the process of leaf folding by dividing it first.

3. *Morphology and habitat*

Starting from the reasoning in C, 2 it is remarkable that indeed the leaves of type *c* show the most obvious play of the leaves. In a specimen of *B. winitii* I saw the two halves assume a profile position during the whole day, entirely covering the original upper side of the leaf. This side is entirely devoid of stomata. This relates to a plant from a shadowy place in Buitenzorg, brought to a less covered place in Bandung. After some weeks all the branches died. The newly formed branches at Bandung, however, orientated their leaflets horizontally. Obviously the plant is very sensitive to light. In *B. purpurea* both sides have stomata. It is impossible to find a correlation between leaf type and ecological factors in the milieu. Many species are lianas occurring in rain forests or in thickets. Types *a* and *b* are certainly represented among them, but I think type *c* is too. Other species occur as trees in savannahs or wet forests. The two bifoliolate species I know well (*B. winitii* and *B. blancoi*) seem to prefer very exposed places as plains and shores. These two species have small leaflets but in other bifoliolate species the leaflets are very large, up to 40 cm length, e.g. in the Bornese *B. diptera* Bl.

4. *The mechanism of the movements*

The nightly movements of the leafblade as a whole make bristle and "midrib" fold themselves back in such a way that their underside touches the petiole lengthwise. The bending happens in the apical common joint. This joint mostly allows no other movement. Only in very extreme cases (when leaves had to turn 180°) a torsion or bending to the left or the right occurred in it. This movement is no repetition of the movement of the young leaf when unfolding. The movement of the two halves occurs in a plane perpendicular to the former one. The bending is executed by means of the two laminar joints (see under D, 4). The orientation movements by which the blade places itself perpendicular to the light also take place in the laminar joints. One laminar joint then moves its leaf half downward and the other upward, — the blade as a whole remaining in one plane. This illustrates how these two laminar joints can behave independently and are not active in unfolding only. All joints together illustrate a tendency to differentiation of motility into two separate directions. At the same time *Bauhinia* shows a combination of the two types of nyctinastic movement in leguminous leaves, the one being downward, the other upward. The basal (primary) joint is able to execute movements in all directions.

D. ANATOMICAL DATA

1. *The bristle*

The apical bristle might in *Cercis* and many *Bauhinia* species simply be accepted as the veinpoint (mucro) of a leaflet or a leaf. On further consideration, however, the organ is too important to be accepted as such, as will also become evident in the study of its development (E, 3). The bristle is often very large and persistent, even in "simple" leaves, where the top region seems well developed and looks regular and acute.

In the simple leaved *B. assuruana* Moric. from Brazil the long bristle gives the leaf a fantastic appearance (fig. 3). In simple leaved species like *B. bidentata* the bristle has the same sharp kneecurve that the rhachis end of a compound leaf often shows. Even in the apparently simple leaved *Bandeiraea speciosa* Wills. the bristle is abnormally long for a mere vein point. That the bristle even in "simple leaves" with a very long and narrow tip (fig. 4) is situated at the bottom of an incision is very curious. This incision in type *a* can readily be accepted by fusionists as a remnant of the deeper incision in types *b* and *c*. To consider it as a beginning of the split in type *b* is far more artificial. This argument is decidedly against the interpretation of "splitters". In some simple leaved species there is not only a tendency to fold near the base (cf. C, 2) but also near the tip. It is then difficult to flatten the top region. This feature is difficult to be explained by "splitters".

A detailed microscopic investigation of the bristle is necessary, but one can understand that on the strength of the above mentioned facts fusionists already accept it as more than a leaf tip. FRIES (2)

ventured the speculation that it also contains the midrib-ends of the fused leaflets. The appearance in *Cassia basifolia* (cf. B 6) of a bristle representing the whole "Oberblatt" strengthens this opinion. For developmental data see E. One result may be discussed here before-

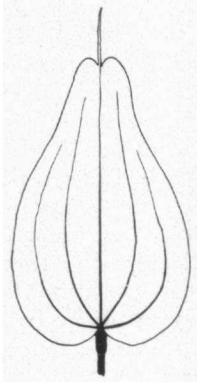


Fig. 3. Leaf of *Bauhinia assuruana*

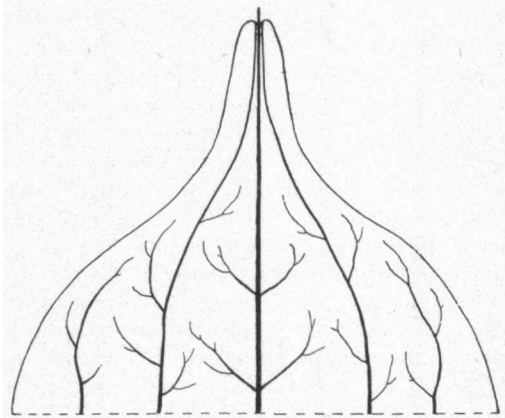


Fig. 4. *Bauhinia pyrrhaneura*.

hand. In the bifoliolate leaves of *B. binata* the bristle is in early youth externally equal to the two lateral protuberances that develop into the "leaflets". It is dorsiventral and concave as if folded and it encircles the edges of these "leaflets" like a roof (cf. fig. 7). This might be seen as proof of its nature as a leaflet. In other species too the bristle is more or less flat.

When comparing *Bauhinia* leaves with compound leaves one is struck by the resemblance of the bristle with the top of the rhachis that projects between the apical pair of leaflets of a pinnate leaf. In this relation it is indifferent if the top represents only the rhachis or the rhachis with the reduced terminal leaflet. The flat rhachis end of *Copaifera* (fig. 2, 8) finds its homologon in the flat bristle of *B. binata*.

"Splitters", however, can also accept the bristle as more than just a veinpoint. According to their views it may represent the arrested top portion of the leaf proper. That in all the species investigated the bristle is provided with a vascular strand agrees with both conceptions. Figures like the one in fig. 4, where the top region of the leaf has a number of parallel veins may lead to a comparison with *Acacia* phyllodes. The bristle on top of the phyllodes of some *Acacia* species, representing the lamina proper, has also much likeness to the bristle of *Bauhinia*.

Accepting for a moment the leaf of *Bauhinia* as a phyllode it should be compared to the alate rhachis of species like *Desmodium triquetrum*, broadened laterally, not medially like in *Acacia*. The bristle then would be the lamina.

The difference between pleuroplastic development of the basal

portion of a folded leaf and the broadening of the wings on both sides of a petiole is perhaps not so essential.

So many points, however, disagree with the nature of the *Bauhinia* leaf as a phyllode, that this idea should not be considered too seriously.

2. *The apical leaf joint*

The primary pulvinus has a normal structure and functions in the normal way. The apical pulvinus bends in only one plane, but is very active. As said before it is easily overlooked in herbarium material. TROLL (8) (p. 1025) ignored it. UTTIEN (9) (p. 406) even denied its existence.

Internally it has a very complicated structure. The vascular system induced FRIES (2) to consider the joint as a double structure, as the fusion product of two joints. On the one hand it is a fact that WATARI (12) and the many writers (BOUYGUES, COL, ACQUA, PETT) on the subject cited by him classify the apical joints of *Cercis*, *Bauhinia* and *Bandeiraea* as abnormal joints, deviating from all other leguminous leaves. The figures of FRIES contain many more details, but are in some points not very accurate. The differentiation between types with blunt and acute leaf halves is not tenable. Even the acute ones never have a real veinpoint. On the other hand he omits in his fig. 5 the really very conspicuous bristle of *B. bidentata*. In *Cercis* joints he figured the median vascular bundle, but not in *Bauhinia*.

Now fusion in joints of leguminous leaves cannot be ruled out. I found many instances, especially in *Clitoria ternatea*. In those cases the joint parenchyma was undivided but the vascular tissue was double (cf. *Hymenaea* in B 2). In the types *b* and *c* the double structure might find an explanation in a physiological necessity in relation to the folding up of the leaf halves, as the dividing of the two bundles must happen underneath the leaf halves. It is, however, possible to use as an argument in favour of FRIES that also in "simple" leaves of type *a* the vascular tissue is doubled, even in *Cercis*.

When speaking about the midrib (D 3d) we will also find the possibility of a physiological regulation as cause of its internal structure.

In *Bixa orellana*, a totally unrelated plant, where there is also a second leaf joint underneath the blade and where a compound nature is out of question, this apical leaf joint also shows an intricate vascular structure and the midrib arises from two of its strands. The same holds true for the many joints described by FUNKE (3). He does not differentiate between unfolding joints and joints with variation movements. The unfolding joint on top of the petiole of *Hibiscus similis* has almost the same structure as the one of *Bauhinia*. On the ventral side the stele splits, as a beginning of the flattening out into the lamina.

The internal structure of the *Bauhinia* apical joint therefore may also be physiologically determined. Its dorsiventrality certainly is in accordance with its function, movement in one plane only. Since we know that in *Trachylobium* there is a special common joint, as a new

formation under the pair of leaflets, the apical joint is no longer an argument contra fusion, but strongly pro.

In *Hardwickia binata* the monojugate compound leaf also has a distinct apical joint in the rhachis. Whether it is also present in *Copaifera mopane*, I dare not say. In the young plants I observed and in the herbarium material DR DE WIT furnished, there was only a short, undifferentiated, pulvinuslike rhachis. In fig. 2 (copied from HUTCHINSON) we see a leaf with a distinct rhachis above the basal pulvinus, without an apical pulvinus, but perhaps this has been overlooked.

3. *The venation*

a. The absence of a veinpoint in the leaf halves. The fact that the veins of the leaf half never reach the margin and never form a veinpoint, (even when both tips are acuminate) has been mentioned already. In forms like *B. winitii*, the leaf structure gives the impression of a fern leaf for this reason and also because of the round apex and the palmate venation. The two halves are therefore, up to present standards unacceptable as leguminous leaflets, least of all in type *c*, which should be the most primitive type according to fusionists.

b. The absence of a midrib in the leaf halves. In the introduction it was already pointed out, that the general lack of a midrib in the two leaf halves is not in accordance with their possible character as two leaflets. Sometimes (it is said) we find one thick vein in the halves of type *b*, but mostly and to my experience exclusively, a number of equal veins radiate from the laminar joint. We will refer to this as a palmate venation. When the condition of separated halves (in binate leaves) would be a primitive condition, we might expect that the original midrib would be visible, in some cases at least. Never, however, did I see a pinnate venation of the halves. Nor did DR H. C. D. DE WIT, who studied the taxonomy of the genus for the Flora Malesiana. Even the leaflets of *B. diptera*, which are rather narrow and have a length of 40 cm, are palmate.

c. Palmate venation as a secondary regulation. If most points under *a* and *b* speak against the nature of the two halves as leaflets, it must be said that the palmate venation, especially in leaves of the simple type is just as little in accordance with the nature of the whole as one leguminous leaflet. Instances of leguminous plants with multi-nerved leaflets, like *Liparia sphaerica*, are very rare. *Cercis* always had an isolated position in this respect. The venation in leaves of type *a* is often the same as in *B. purpurea*, as may be seen in the palmate *B. bidentata*. Such leaves are almost identical with those of *Cercis*. The appearance of many collateral veins in the unquestionably true leaflets of *Copaifera mopane* Kirk (fig. 2) of a tribe very near to the *Bauhinieae* makes the situation more intricate. In this monojugate species the two leaflets have the same venation as the leaf halves of *B. purpurea* c.s. and the whole leaf is a close approach to the structure of *B. winitii*, and of *Trachylobium* seedlings which will be discussed

below. Even in a bifoliolate *Cassia* species, *C. basifolia* Vog. the same has happened. (cf. E 2). In other species of *Copaifera*, including some with monojugate leaves, the leaflets have a distinct midrib with side veins. The same holds true for a different monojugate *Cassia*, *C. bauhinioides* Gray.

In an Indian *Hardwickia* species (very close to *Copaifera*) the leaflets have also acquired a multinerved condition as a secondary phenomenon. *Hardwickia pinnata* Roxb. has pinnate leaves with alternating leaflets that are pinnatinerved. The two uppermost leaflets both show a tendency to assume a terminal condition. In *H. binata* Roxb. only this apical pair is left. It is curious that the leaflets have become multinerved as in *Copaifera mopane*. The primary leaves of seedlings already show this condition. The palmate venation in this plant is not yet complete. In many leaves the innermost vein still shows traces of being the primary midrib, by having stronger side veins and by reaching the margin in a shallow incision. The similarity between the leaves of *Bauhinia binata* and the pair of leaves of the nearly related *Copaifera mopane* and *Hardwickia binata* now becomes a strong argument in favour of fusion. Perhaps the multinerved condition is a prelude to fusion or non-disjunction of the two leaflets.

In some simple leaved *Bauhinia* and *Bandeiraea* species (types *a*) a predominant midrib is visible, but this too may be a secondary transformation. Often the midrib is accompanied by two strong nerves, originating from the base. This triplinerved leaf also does not make the impression of a primitive condition and is considered as proof of coalescence by fusionists. The most perfect examples of pinnate dicotyledonous venation are found in the simple leaves of other *Bauhinieae*, e.g. in *Bandeiraea tenuiflora* Benth (c.f. fig. 1, *a*₁). FRIES c.s. interpretes leaves of this type as the results of a convergent development after fusion.

As said before, venation may be regarded as more physiologically than morphologically determined. "Splitters" may use this to argue that the widening of the leaf to the type of *Cercis* (and *B. bidentata*) might have induced a pleuroplastic development of basal collateral veins, this in order to save the *Cercis* leaf as a primitive structure. Surely such an increase of veins may have happened in types *b* and *c*. The pleuroplastic development can be followed by the number of collateral veins in each half. It increases from the first to the later leaves of a seedling. In *B. purpurea* I made the following counts, in which $\frac{1}{2}$ means a vein that was visible as a thickening of the margin, but was still included in it: 1st. leaf (cataphyll) 1, $1\frac{1}{2}$ or 2; 2nd. leaf $1\frac{1}{2}$, 2 or 3; 3rd, 4th and 5th. leaf 3; 6th and 7th. 3 or 4, and the adult large leaves 5.

The venation of the leaf halves usually makes a primitive impression as if the lamina were not a well structured foliage leaf but a secondarily stretched outgrowth of some kind. Such a venation with a varying number of collateral veins can be expected in leaf sheaths, outgrown stipules and in leaves like those of *Plantago*, that have a more or less phyllodine character. We found, however, the same type of venation

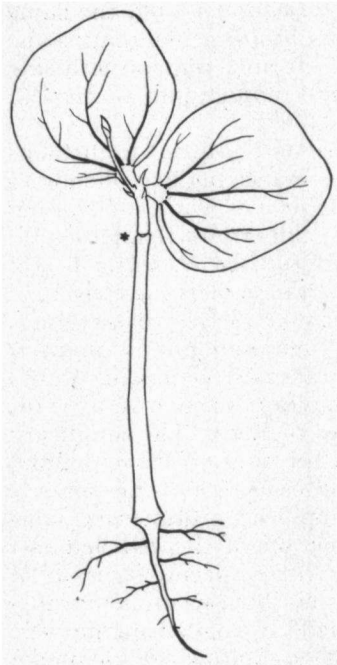


Fig. 5. *Trachylobium verrucosum*. Seedling with one primary leaf, complete with rhachis tip and stipulae. Scar of fallen cotyledones at the place of the asterisk.

in the *Cassia*, *Hardwickia* and *Copaifera* species, mentioned above, where the leaflets are not broader than in other species with pinnate venation.

I must remark that in many leguminous plants (e.g. *Sesbania*) where the ordinary leaflets have a pinnate venation and a vein point, the primary leaves have a more primitive venation with some collateral veins along the midrib and a median vein that does not run through to the margin and has no vein point. I even dare say the leaf halves of leaves of most *Bauhinia*'s look like regressions to cotyledons.

The process of cotylisation seems to occur especially in plants with binate leaves, e.g. *Copaifera*, *Hardwickia* and *Cassia* species. In some of them the process is extremely evident in the queer, giant primary leaves. In *Trachylobium verrucosum* the two primary leaflets imitate cotyledons in an amazing way (fig. 5). They are rather thick, round, without mucro and palmate in contrast to foliage leaves. LUBBOCK (5) gave a figure of the almost identical seedlings of *Hymenaea courbaril* L. (his fig. 305), also with binate leaves. The

text accompanying this figure speaks of two simple, opposite, primary leaves. On p. 398, however, he nearly gives the correct explanation: a sessile binate leaf with leaflets having the appearance of simple opposite leaves. Besides the cotyledonoid appearance of the leaflets the long lasting inhibition of growth of the stem above this leaf makes the epicotyl an exact repetition of the hypocotyl plus cotyledons. I do not know whether there is also a correlation between the monojugate and the multinerved condition in other families, e.g. *Simarubaceae* and *Zygophyllaceae*, but amongst *Leguminosae* the common *Lathyrus* is another instance of it.

The arguments under *a* and *b*, which first served against the interpretation of the leaf halves as leaflets, viz. lack of a veinpoint, lack of a midrib and presence of palmate venation, lose their value now that we found all three phenomena in real leaflets as components of one physiological syndrome. Probably it also includes nonfolding in the bud (cf. C, 1) and probably the opposite position of so many primary leaves is its first symptom.

With reference to the modern distrust about the possibility of fusion of leaves, I should like to point to the well-known cases where the two cotyledons of *Leguminosae* have grown together. (*Astragalus* and

Hedysarum). Seeing this the fusion of two cotyledonoid leaves is not so improbable.

d. The midrib. According to the "splitters" the midrib when poorly developed may be seen as affected by the apical growth inhibition. It seems uncertain if this is a sufficient explanation for its internal reduction in bilobate species like *B. purpurea*. In other plants with pleuroplastic development, like *Cercis*, *Ipomoea pes-caprae* and *Lourea* the midrib is shortened indeed but it sends out many side veins and is still physiologically important. In *Bauhinia purpurea*, however, the midrib is, though seemingly thick, entirely unimportant. It has no side veins or almost none and contains but few and thin veins. VELENOVSKY already noted this. When a leaf is made to suck up a solution of methylene blue, the dye soon becomes visible in the nerves as a thick line extending to the top in the leaf halves, but in the midrib it shows as a thin line in the lower part only. These data have from a morphological point of view restricted value. The reduction may have no morphological background at all, but may be a physiological regulation as said under *c*. It may also be a necessary consequence of the mighty tendency toward folding up. The lack of side veins facilitates folding along the midrib. This in its turn makes lateral veins necessary as a compensation.

On the other hand the fact that in simple leaves (type *a*) the midrib is well developed is not necessarily a proof for the primitivity of this type either. This too may be a secondary regulation. As we saw venation is nowadays often considered as less important in morphological questions. Of course a peculiar type of venation to which no

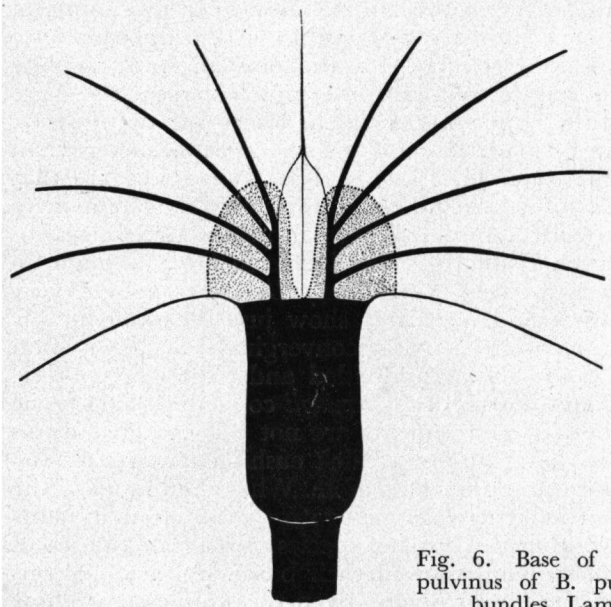


Fig. 6. Base of lamina and secondary pulvinus of *B. purpurea* with vascular bundles. Laminar joints dotted.

physiological significance can be assigned, will always remain a valuable indication for the morphologist.

For the time being we will have to admit that the origin of woody elements in the midrib of *B. purpurea* seems to point to a compound and derivative nature. The woodvessels are partly a continuation of a small unpaired median bundle from the apical joint that is not always easily detected. The main contribution comes from right and left as the end of the two bundles that branch into lateral nerves of the leaf halves (cf. fig. 6).

I may refer here to the detailed figures that WATARI (12) gave of the vascular strands in the petiole tips of *Bauhinia* and *Cercis* (his figures 13A and 15M). For *Cercis chinensis* he figures a midrib out of one single strand in the petiole. Fusionists might consider the contributing bundles from the right and the left as the remnants of the main veins of the fused leaflets. It is most interesting that in *Cercis siliquastrum* too the "midrib" in spite of its seeming simplicity arises in a complicated way out of three separate bundles in the apical joint. The median small bundle cannot be detected here. It is as yet uncertain whether any morphological deductions can be based on this fact. In the apical joint of *Bixa* the midrib also originates from bundles from left and right, as we described under D, 2. In the figures of WATARI we see that in many leguminous plants (e.g. *Trifolium*, *Lupinus*) the midrib of true leaflets also arises by the fusion of vessels from different vascular strands in the petiole.

4. *The laminar motor zones*

Cushions of motile parenchyma cover the converging bases of the digitate veins in both halves of the lamina base near the points of contact with the petiole. They are best visible on the upper side of the leaf. That these cushions, referred to as the laminar joints, regulate the motions of the leaf halves, follows from simple experiments where the cushion either on the upper side or on the lower side is cut away. In this way leaves can be made to close and open instantaneously. In his "Die Pflanzenwelt" (vol. II, 1921, p. 178) WARBURG says that none of the halves has joints and he uses this incorrect statement to deny their nature as leaflets. Simple leaves also show these cushions (cf. C, 2). They are even visible to some degree in *Cercis*, though no motions were ever observed by me. Many *Bauhinia* species (very clearly *B. picta*, *variegata* and *monandra*) show just the same motile tissue at the base of the cotyledons. The converging veins also remain separate inside this "joint". It is undivided and causes no folding, only a movement up and down. In *B. tonningii* cotyledons have some kind of a petiole. The daily movements are not executed by means of a motor zone at its base but by a thick cushion that covers the base of the lamina and the top of the petiole. When compared to the adult leaf this cushion looks as if homologous to the laminar joints and apical pulvinus combined. In many species of *Bauhinia* the sepals have the same kind of mobile tissues at their bases. By means of this they bend back when the flower opens. Even the stipules may show

the same phenomenon. According to "splitters" the laminar joints must be new formations, already present in *Cercis*, where they serve no purpose in the full grown leaf. Under C, 2 we already saw that the cushions in *Cercis* and the like might be considered as derived from "unfolding joints"—only there is no trace of such tissues in any young leguminous leaf. To fusionists the laminar joints are homologous with the leaflet joints or parts thereof. This sounds plausible, the more so as the common (apical) joint of the petiole can be recognised as already present in *Trachylobium* and *Hardwickia*.

When the leaf halves are phyllode-like outgrowths or stipels these joints are also new, though there is a parallel in stipular joints.

E. THE DEVELOPMENTAL HISTORY

1. *The vernation*

In the introduction the fact that leaves of type *a* and *b* are in youth folded, just like ordinary leguminous leaves, was mentioned already.

If the leaf halves were originally leaflets one could demand that they should be folded separately as most leguminous leaflets are. Even in the separate "leaflets" of type *c*, however, I saw no trace of this folding. The vernation of type *c* remains to be investigated more thoroughly. Perhaps this argument of the "splitters" looses much of its value when fusionists bring forward the argument that the leaf halves are possibly not complete, but are half leaflets. FRIES already inclines to this idea (see D, 1). The leaflets of the monojugate *Cynometra cauliflora* might here be used as a model. They are strongly asymmetrical by a reduction of the sides touching each other (cf. B, 2). In young leaves of adult plants the narrow inner half is bent somewhat, but is not folded against the outer half. In seedlings they are folded in the bud. It is important that the leaflets of *Copaifera mopane*, which have palmate venation like the leaf halves of most *Bauhinia*'s are also not folded in the bud (fig. 8). Neither are those of *Pithecolobium dulce* (also asymmetrical and monojugate): Those of adult plants of *Trachylobium*, *Hymenaea stilbocarpa* Hayne and *H. courbaril* L. are folded when young, but their primary leaves are not.

2. *The leaves of the young plant*

VELENOVSKY already was astonished that in *Cercis*, the leaf of which he considered as a double thing, the young seedling does not show the least trace of the supposed double nature of the leaves. The same holds true for *Bauhinia* of which I studied the germination in a great number of species, kindly sent by the curators of the Singapore and Buitenzorg Botanic Gardens. Unfortunately seeds of types *a* and *c* were not available, but we already know from LUBBOCK (5) (p. 465) that in the binate *B. carronii* F. Muell. the primary leaves of seedlings are also bifoliolate. The only result of interest of my cultures was procured by the teratological deviations discussed under F. Mostly the first leaves are large and of the adult type. In some species (*B. violacea*, *rosea*, *purpurea*) they are preceded by small cataphylls, not

fundamentally different from the adult type. *B. scandens* L. var. *Horsfieldii* Miq. ex Prain (the well-known "monkey rope") has the leaves split deeply in young plants, whereas those of full grown lianas are sub-entire with the incision reaching not more than 5 mm on a total length of 70 mm. I will not venture to draw conclusions from this curious fact, but it is not favorable to simple splitting. In *B. flammifera* this difference is also present, though not as marked. The lack of deviating leaves on seedlings of *Bauhinia* and *Cercis* is the more impressive as in other *Caesalpinoideae* seedlings show leaves of a special type. The study of their homologies (D, 3c), however, shed no light on the *Bauhinia* problem and made it even more intricate. In one species of monojugate *Caesalpinoideae* with palmate leaflets (*Copaifera*) the first leaves were also palmate. In some monojugate species with pinnate adult leaves the first leaves were palmate (*Hymenaea*, *Trachylobium*). The palmate leaflets of *Cassia basiflora* figured by GOEBEL (4) (fig. 1357) and by GLUCK are also from primary leaves. In normal leaves the lamina has disappeared (cf. B, 6). The results of *Hymenaea* and *Trachylobium* should not be explained in the sense of the biogenic law, as proving that palmate venation is more primitive than pinnate venation. The first leaf is simply more cotyledonoid.

3. *The development of the leaf*

First I will consider the best known species, *B. purpurea*, of type *b*. "Splitters" should expect a more simple outline in proportion to the leaf being younger. Fusionists should expect a more pronounced double structure. Both expect a median point, either leaf tip or rhachis tip. The fact is, that in the first stages the bristle is in proportion astonishingly large and that the two halves are small, but well differentiated. (cf. fig. 7d, e). This might still be explained as a leaf tip with pleuroplastic development underneath, though the median bristle is improbably large for just a leaf tip at this stage. In the simple leaved *B. bidentata* (fig. 7c) the initial stages have the sideward wings less pronounced. The knee in the bristle is a striking feature, somewhat uncommon in a leaf tip. The whole reminds one strongly of the differentiation between leaf lamina-rest and the broadened petiole in *Acacia* species with phyllodes (cf. TROLL (8) (fig. 995). More illuminating is the leaf primordium in the double leaved *B. binata* (cf. fig. 7a, b). It cannot be distinguished from the primordium of a monojugate compound leaf e.g. of *Copaifera mopane*, where the top of the rhachis is a flat protuberance. It consists of three more or less equal segments and certainly does not give the impression of a simple leaf with terminal inhibition. The median segment, the bristle, looks more like a leaflet itself accompanied by other leaflets or stipels. Of course it may also be homologous to the flat rhachis top seen in *Copaifera* a.o. genera (For the bud position of halves cf. E 1).

Serial sections of growing points reveal the distribution of meristematic tissue in young leaf primordia of *Bauhinia* species. In a binate species like *B. binata* the common base and the central lobe (the bristle) were found to lose their meristematic character very early

(fig. 9). What later on develops as the "leaflets" arises as wings from meristematic tissue on both sides of the groove in the common base. In a bilobate species like *B. purpurea* the difference in cell diameter and protoplasm density between the common base (the later midrib)

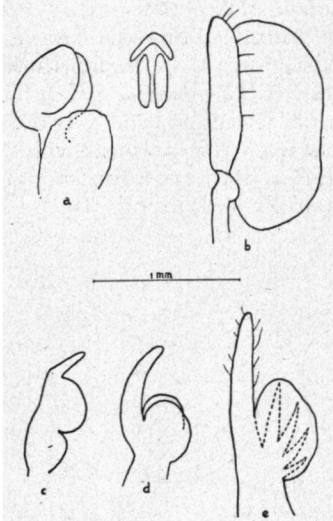


Fig. 7. Young leaves of different Bauhinia species, all at the same scale.
 a. *B. binata* very young with stipule.
 b. *B. binata* somewhat older, without the basal part. Cross section in between.
 c. *B. bidentata*.
 d. and e. *B. purpurea*.

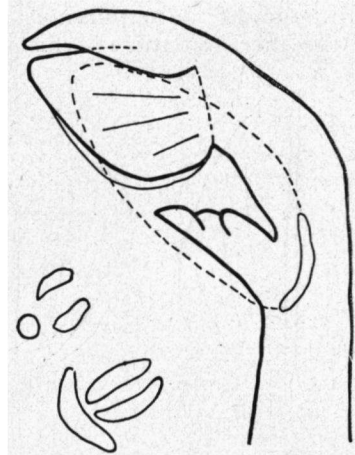


Fig. 8. *Copaifera mopane*. Growing point of young seedling, above the primary leaf. Stipule of oldest leaf cut away, scar and outline indicated. Cross sections through this leaf at different levels.

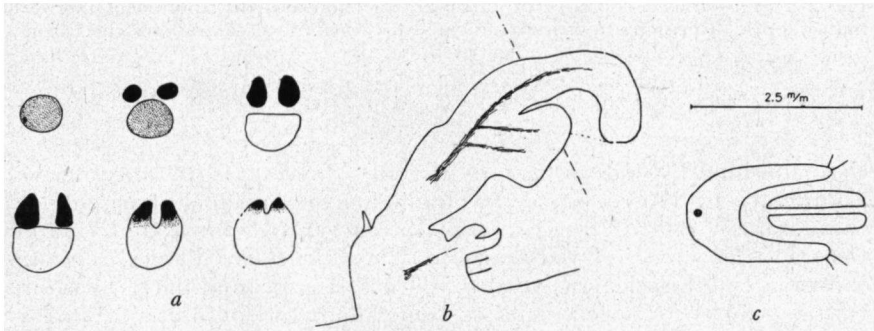


Fig. 9. Sections through young leaves of *B. binata*, all at the same scale.
 a. Very young. Cross sections at different levels from top (upper left) to base (lower right). The more a tissue is meristematic the darker it is tinged. Bristle not yet concave.
 b. Longitudinal section almost median, with axillar bud, axillar colleters and part of stipule.
 c. Slightly older. Cross section along the dotted line in b.

and the lateral outgrowths is less marked. In a simple leaved species like *B. kockiana* and *B. cordifolia* this common base remains entirely meristematic so that it is understood that it can stretch lengthwise together with the "wings" (cf. fig. 10).

This is not just describing the difference between types *a*, *b*, *c* in other words. Combined with what we found about the shapes of very young leaves, with the idea of cotylisation in the leaf primordia (which makes them broader than is usual in *Leguminosae*), it offers a possibility to fusionists to explain the simple leaves of type *a* as double structures. Parts of the broad primordia with the palmate veins do not differentiate into pulvinus and lamina, but grow out together with the meristematic rhachis part, as indicated in fig. 10.

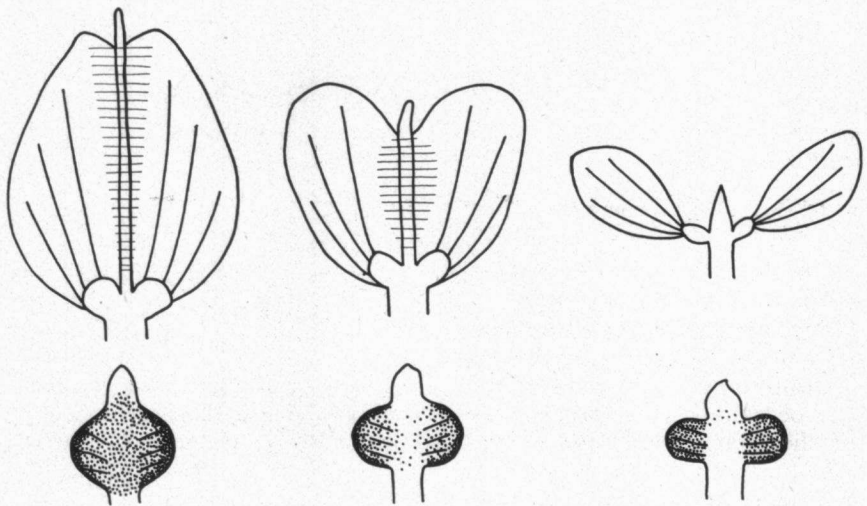


Fig. 10. Fusion as a consequence of broad insertion and distribution of meristematic zones. Meristematic tissue indicated by dots. Intercalary stretched zone indicated by stripes.

F. TERATOLOGICA

1. Foliar asymmetry

A considerable percentage of the first leaves of *B. variegata* are asymmetrical. This unequal development can lead to disharmony in the common midrib zone, so that the larger half forms bulges and becomes distorted. This disharmony shows the two halves as more independent than leaf halves usually are. In sprouts that arise from the axils of the cotyledons after removal of the plumula the foliar asymmetry is very frequent in other species too. In *B. acuminata* 75 % of the first two leaves are asymmetrical. In *B. picta* and some other species the asymmetry is still evident in later leaves. They sometimes tear up spontaneously. In *B. tonningii* (bilobate) I found the case of asymmetry figured in fig. 11. On one side lamina, petiole and stipule were well differentiated, on the other not at all. In other cases the

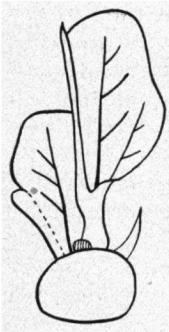


Fig. 11. Abnormal (assymmetrical) leaf of *B. tonningii*.—Axillar bud striped.

first named side was also so much larger that it occupied a terminal position with the midrib horizontally orientated. The absence of teratological and juvenile forms demonstrating the double character of the apparently simple leaf pleads against fusion. The absence of abnormalities where the bristle grows out into a lamina pleads against splitting or terminal inhibition as the cause of the peculiar shape.

2. *Abnormal position of the bristle*

Seedlings of *B. variegata* from the Buitenzorg Gardens showed the curious abnormality that the bristle was not terminal but placed halfway the length of the under surface of the leaf, like the stalk in a peltate leafbase. Out of five seedlings the peltate tip was found in 6 of the first and second leaves. This demonstrates that the leafblade is independent from the bristle and that the bristle is not just the leaf tip.

DISCUSSION

The author has no pretention of having solved completely the riddle of *Bauhinia*, one of the most difficult of botanical morphology. Many new arguments, however, have been discovered and many old ones have lost their value.

Combining all data pro and contra fusion or splitting the following can be said. (All data not outspokenly positive in one direction of another have been omitted, also as neutralising each other).

Definitely against splitting are the points: B, 1; B, 2; B, 3c.

In a negative way are not against splitting: B 3, B 7, E 2.

More or less pro fusion are: B, 1; B, 2; D, 1; D, 3c; D, 4.

In this way we reach, in a democratic though not exactly scientific way, a vote of: Fusion 8, splitting 3. The points B, 2 and B, 3c should get extra-value, augmenting the majority of the fusion-concept.

For the phyllode, or stipellae concept but superficial support could be found.

Though the patient detective work gave much satisfaction, the results obtained are of course not entirely satisfactory. Perhaps new methods will give a more unanimous decision. Botanists here feel the lack of the support given to zoologists by the study of embryology.

Some more general considerations can perhaps strengthen the majority vote.

Is it possible to judge about fusion or splitting independently from the details and considering them as a whole? Is it, speaking generally, more plausible to accept the sequence *a, b, c* than the sequence *c, b, a*? (No other series are considered possible).

What might be the developmental tendencies, ecological moments or structural relations behind both sequences?

What is most likely to have happened, knowing the family?

The sequence of fig. 1, viz. a_1 , a, b, c, d, e represents the splitting concept. In terms it might be described as follows: Terminal leaflet or simple leaf obtaining a secund pulvinus, cotylisation (rounding off near the tip, broadening, appearance of collateral veins), reduction of the midrib, tendency to fold as in the bud (facilitated by the palmate venation and the disappearance of sideveins from the midrib), deepening of the apical incision by inhibition of topgrowth, finally leading to the bifoliolate condition.

What is improbable here? The beginning and the end!

The appearance of an apical incision, of laminar motor zones and a long bristle in the beginning of the range (a_1) is strange.

In a way this sequence is a consequence of the tendency amongst *Leguminosae* to split up the leaf or of repeating itself. Only it is a somewhat strange detour to obtain by this convergence a condition already present in closely related genera and obtained there in a simple and usual way.

According to this concept the absence of a midrib in the free leaf halves would mean that the end of the development into two separate leaflets has not yet been attained. The difference with the leaflets of *Trachylobium* should be essential, although the plants are in other respects closely related.

Now let us consider the opposite sequence, d, e, c, b, a, a_1 . In terms this might be described as: a monojugate compound leaf (nothing special in the subfamily), with an extra joint in the top of the rhachis, both leaflets with multiplication of the veins and with a broader insertion, which leads to the unification of their primordia or common stretching of parts thereof, which finally gives one lamina. Ultimately this lamina changes its parallel venation back into the normal dicotyl venation and loses most traces of its origin.

What is improbable here? At first sight it seemed strange, that no species of type c has the original midrib of the leaflet, but assuming that cotylisation occurred before the fusion this objection loses its value.

That type a_1 is a convergence to the normal shape of a leaflet is strange, but is acceptable as it agrees with some peculiar features, that now prove to be relics.

The above considerations strengthen the conception of fusion in *Bauhinia*.

Special thanks are due to Prof. Dr C. E. B. BREMEKAMP and Dr H. C. D. DE WIT for their valuable criticism.

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