ACTA SOCIETATIS
BOTANICORUM POLONIAE
vol. XL — nr 3
1971

Relationships of *Plumiereae* (*Apocynaceae*)

III. Based on floral vasculature

P.C. DATTA and R.K. MAITI

Department of Botany, Calcutta University, Calcutta 19, India

(Received: March 25, 1971.)

Abstract:

The study of the floral anatomy of some common Indian species of the tribe *Plumiereae* (*Apocynaceae*) supports the conclusions derived from the study of chromosomes and secondary xylem, which are: (1) *Holarrhena* are distinct from *Ervatamia* and should be placed in *Alostoniinae* (Schumann, 1895) and not under *Tabernaemontaninae* (Bentham and Hooker, 1876). (2) Different subtribes possess distinctive features; and, therefore, the classification into subtribes is justified. (3) *Tabernaemontaninae* are the most primitive subtirbe. from which the others can be derived. (4) *Alstoniinae* are heterogeneous and are composed of different evolutionary lines. (5) The genus *Plumeria* stands isolated in tribe *Plumiereae* and needs separation as a new taxon.

INTRODUCTION

The tribe *Plumiereae* of the *Apocynaceae* has been divided into four subtribes in the Englerian system of cassification (Schumann 1895). The genus *Plumeria* is under *Alstoniinae*, according to Schumann, as well as Bentham and Hooker (1876). The genus *Holarrhena* is under *Alstoniinae* in the Eglerian system, but under the *Tabernaemontaninae* of Bentham and Hooker. *Vinca* and *Lochnera* are distinct in the Englerian system (vide Torre and Harms, 1900–1907), but according to Bentham and Hooker, *Lochnera* are a section under *Vinca*. In order to find the phylogenetic relationships, cytology and wood anatomy of the common Indian species have been studied. These investigations have led to the conclusions that *Holarrhena* are distinct from *Ervatamia* and allied to *Alstoniinae*, that the classification of the tribe is natural, that the genus *Lochnera* is distinct from *Vinca*, that *Tabernaemontaninae* are the basic subtribe and that the genus *Plumeria* is distinct from all other genera of the tribe *Plumiereae*.

The present attempt is to obtain information regarding the vascular supplies in the flowers of the common species for verification of the previous conclusions.

MATERIALS AND METHODS

The species included in the investigation are:

Subtribe *Alstoniinae* — *Plumeria acutifolia* (Poir) Woodson, *Holarrhena antidysenterica* Wall., *Alstonia scholaris* R. Br., *Lochnera rosea* (Linn.) Reichb.;
Subtribe *Tabernaemontaninae* — *Ervatamia divaricata* (Linn.) Alston.;
Subtribe *Rauwolfiinae* — *Rauvolfia serpentina* Benth; *R. canescens* Linn.;
Subtribe *Cerberinae* — *Thevetia nerifolia* Juss.

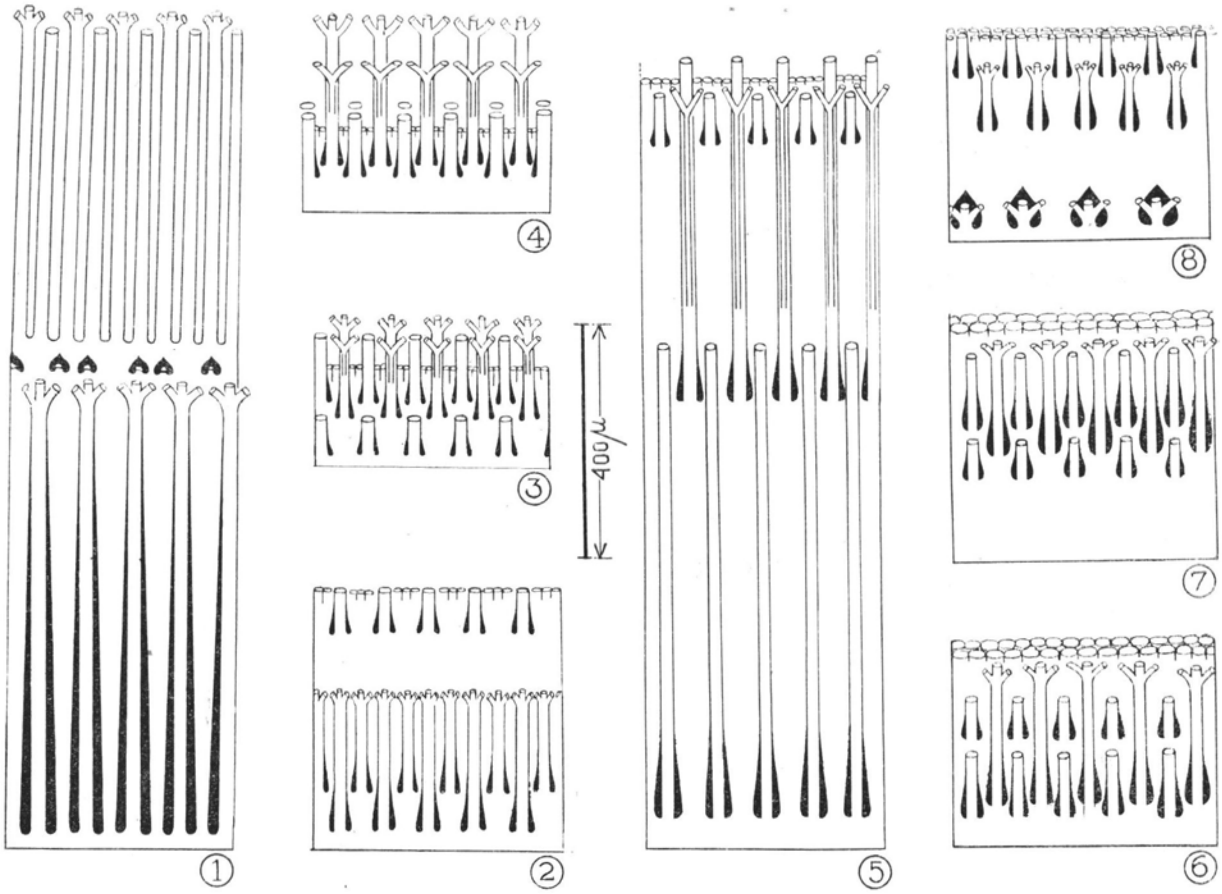
Flower buds at fully differentiated condition were fixed in formalin–propiono–alcohol (Johansen, 1940), washed, dehydrated, embedded in paraffin, microtomed at 14 μ (both transverse and longitudinal), dewaxed, stained with crystal violet and mounted by the usual procedures.

OBSERVATION

In *Plumeria* sp., five sepal traces originate directly from the stele and continue perpendicularly for a long distance before coming outwards (fig. 1). They branch in the receptacle. In *Thevetia nerifolia*, sepal traces come out almost horizontally from the stele, immediately producing some branches (fig. 8). Large number of branches form an anastomosis before the origin of successive vascular traces. *Holarrhena antidysenterica* shows an intermediate condition (fig. 2). In these three species the calyx is supplied by five sepal traces (figs. 11 and 12), while in the other species, sepal midrib traces and sepal margin commisural strands are formed. The commisural strands divide and supply the adjacent margins of two sepals. The commisural strands again come out from the common trace, which may be termed as sepal margin petal cord, supplying both sepal margins and petals. Additional sepal traces (as reported by Rao and Ganguli, 1963) have been noticed in a few buds of *Ervatamia divaricata*.

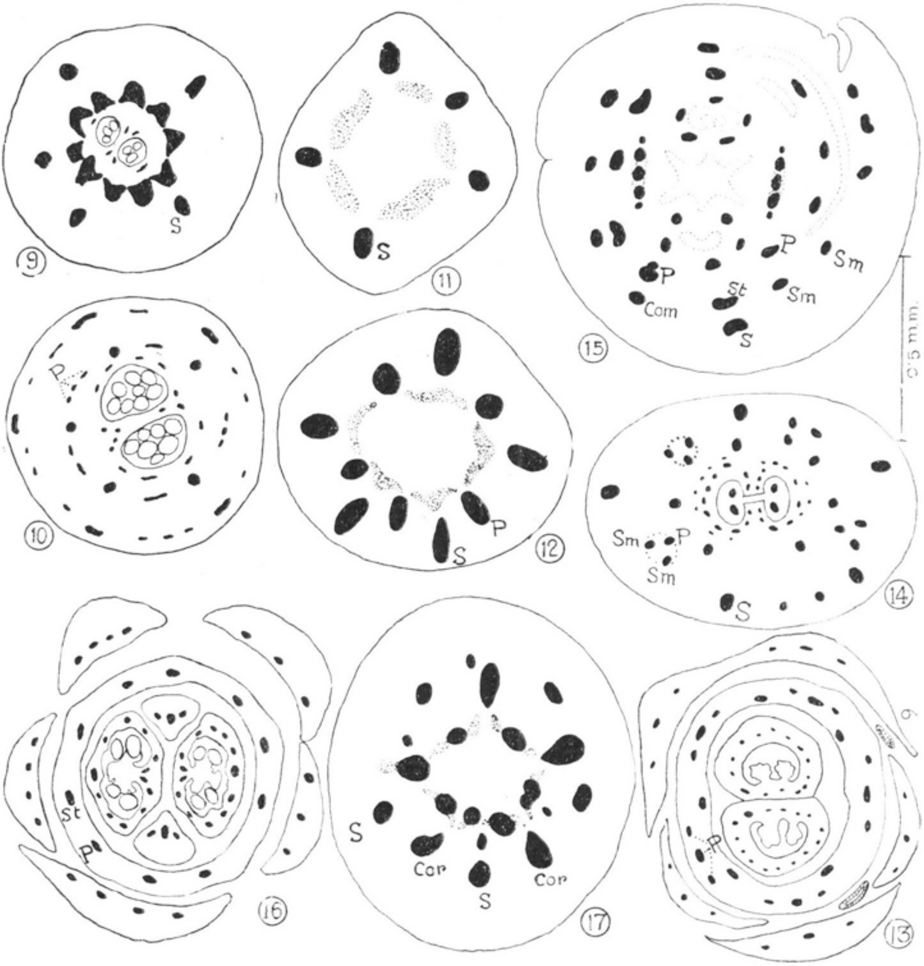
The distance between the successive levels of origin of sepal and petal traces is much pronounced in *Ervatamia divaricata* (fig. 5), *Thevetia nerifolia* (fig. 8) and *Plumeria acutifolia* (fig. 1). The last species differs from the former two by its sepal traces not coming out of the stele for a long distance after their origin. The longest distance is in *E. divaricata*.

The corolla tube is supplied by the median petal traces originated directly from the axial vascular cylinder of *Plumeria acutifolia*, *Holarrhena antidysenterica* and *Thevetia nerifolia* and joined with the sepal marginal traces (forming sepal-petal cords) in the other species (figs. 14, 15 and 18). Among the latter species, *Ervatamia divaricata*, *Lochnera rosea* and *Alstonia scholaris* can be distinguished from the species of *Rauvolfia* by the presence of prominent sepal-margin commisural strands, which are the longest in *E. divaricata* (fig. 5). *L. rosea* and *A. scholaris* (figs. 3 and 4), however, stand second and third in order of merit, and in *Rauvolfia* species they are indistinguishable, the sepal margin traces separating almost directly from the cord (figs. 6 and 7).



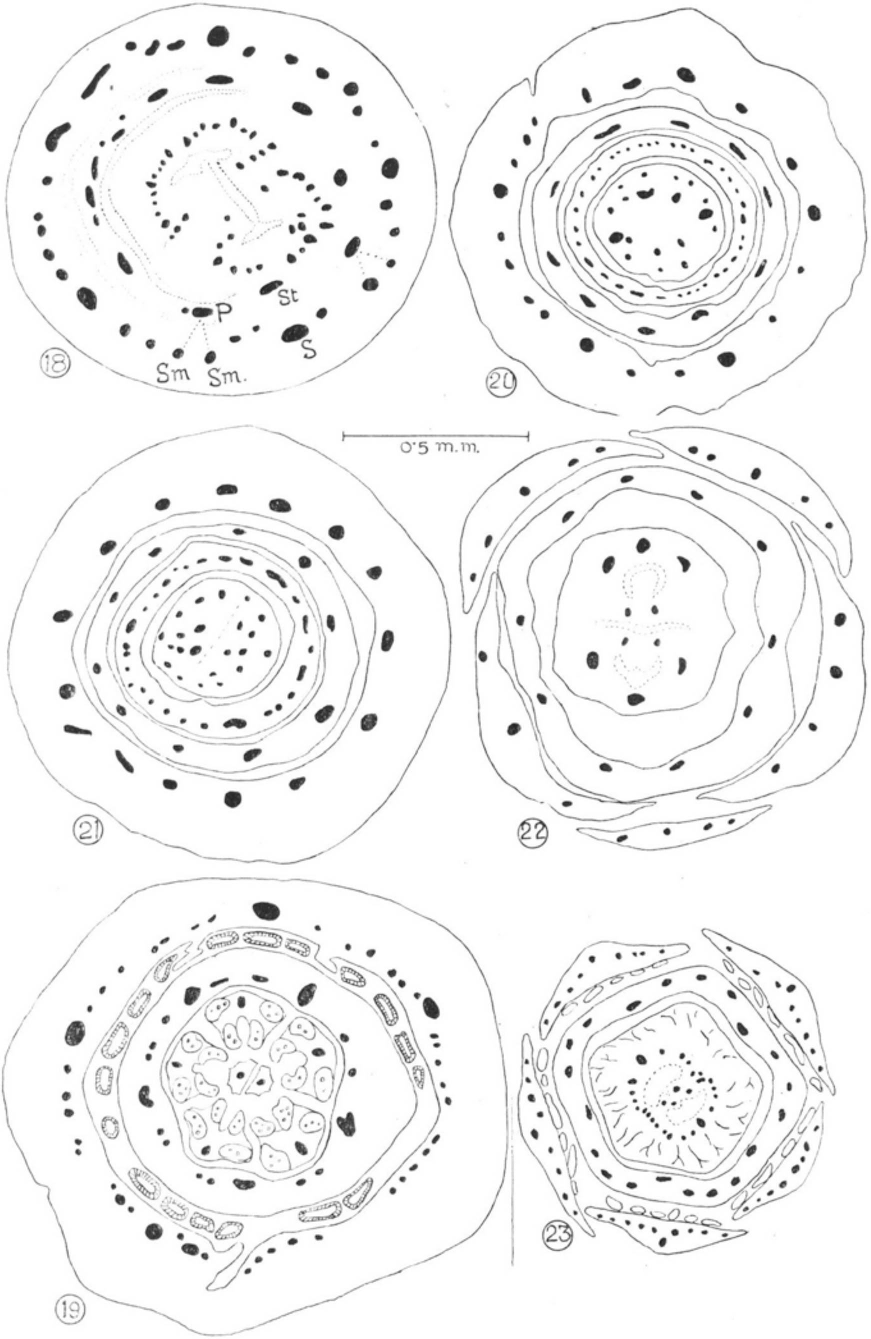
Figs. 1–8: Diagramatric representation of the axes of flowers of the species of *Plumiereae*, (as if split open at one side and spread, showing the levels of the origin of traces and the nature of branching). For convenience all traces of a particular se) have been drawn at the same average level, though they actually appear at different heights. 1, *Plumeria acutifolia* (Poir.) Woodson; 2, *Holarrhena antidysenterica* Wall.: 3, *Alstonia scholaris* R. Br.: 4 *Lochnera rosea* (L.) Reichb; 5 *Ervatamia divaricata* (L.) Alston; 6, *Rauvolfia serpentina* Benth; 7, *R. canescens* L.; 8, *Thevetia nerifolia* Juss.

Petal traces branch in the receptacle (much below the formation of corolla tube) of *P. acutifolia* (fig. 10), in receptacle just below the corolla tube of *E. divaricata*, immediately after the formation of corolla tube of *H. antidysenterica* (fig. 13), in the middle region of the corolla tube of *A. scholaris*, *L. rosea* and *T. nerifolia*, and at a considerably high level of *R. serpentina* and *R. canescens*.



Figs 9–17: Transverse sections of flower buds showing origin and branching of traces in *Plumiereae*. 9 & 10, *Plumeria acutifolia* (Poir) Woodson; 11 to 13, *Holarrhena antidysenterica* Wall; 14, *Alstonia scholaris* R. Br., 15 & 16, *Lochnera rose a* (L.) Reichb; 17, *Ervatamia divaricta* (L.) Alston. S = Sepal trace; = Petal trace; Sm = Sepal margin trace, Cor = Sepal-petal cord; Com = Commisural trace, St = Stamen trace.

The internode between the petalline and staminal traces is the longest in *Ervatamia divaricata* (fig. 5), considerably prominent in *Holarrhena antidysenterica* and *Thevetia nerifolia* (figs. 2 and 8), moderate in *Alstonia scholaris* and *Rauvolfia* species (figs. 3, 6 and 7), highly reduced in *Lochnera rosea* (fig. 4) and the origin of petal



Figs. 18–23: Transverse section of flower buds showing origin and branching of traces in *Plumiereae*. 17 & 19, *Ervatamia divaricaa* (L.) Alston; 20, *Rauvolfia serpentina* Benth; 21 & 22, *R. canescens* L.; 23, *Thevetia nerifolia* Juss.

and stamen traces simultaneous in *Plumeria acutifolia* (figs. 1 and 9) (as reported in *P. alba* by Rao and Ganguli, 1963). In all these species five stamen traces originate directly from the central stele, pass alternately with the petal traces in the corolla tube, then to the short filament near the corolla throat or slightly below it and ultimately into the connective and the two anther lobes. In *P. acutifolia* the filaments come out much below the corolla throat.

The ovarian and disc traces originate simultaneously or almost simultaneously. This level is below the origin of petal and stamen traces of *Plumeria acutifolia*, indicating a nearly inferior position of the ovary, while it is above the level of origin of the stamen traces in all other species. The distance between this level and the staminal traces level is longest in the two species of *Rauvolfia*, while it is moderately long in the other species.

No traces for the disc, gland or sterile ovaries could be recognized in *Plumeria acutifolia*, in which species above the basal part of the ovary, the receptacle (hypanthium) is found to continue without separation into the calyx and corolla-stamen tubes for a long distance. The disc is inconspicuous in *Holarrhena antidysenterica*, although a ring of traces is found to be formed at a basal region in the receptacle, which ultimately supplies the ovarian wall. In *Lochnera rosea* five traces alternating the two ovaries become gradually narrow and continue in two prolongations (figs. 15 and 16) may be interpreted as glands (Bailey, 1953) or sterile ovaries as in *Kopsia* (Rao and Ganguli, 1963). In *Ervatamia divaricata*, two groups of disc traces concentrate against the two ovaries and produce about 40 branches, some of which move inwardly and supply the ovaries. In *Thevetia nerifolia* the prominent disc is fused with the ovary wall (fig. 23). In *Alstonia scholaris*, the disc is semiannular; while, in *Rauvolfia* species, it is clearly annular (figs. 20 and 21). The ovarian vascular bundles in all the species studied fuse above the ovary into two bundles (one for each carpel) and proceed side by side along the style.

The ovary wall generally contains one large midrib trace, two prominent marginal vascular bundles, which divide and redivide at different levels to produce 6–7 branches in *P. acutifolia*, about 12–14 branches in *H. antidysenterica*, *A. scholaris*, *L. rosea* two in *Rauvolfia* sp. and *T. nerifolia*, and about 20 in *E. divaricata* (figs. 10, 13, 14 16, 19, 20, 21 and 23).

DISCUSSION

Characters of subtribes

Ervatamia divaricata (*Tabernaemontaninae*) can be distinguished by (1) possessing the most pronounced internodes between the gaps for successive traces, (2) having very long sepal-petal vascular cords and long commisural strands which are free from the petal traces, (3) the presence of additional sepal traces (Rao and Ganguli, 1963), (4) sepals which are generally supplied by 3 traces (formed by the two commisural strands and the sepal midrib traces), (5) the disc adherent to the ovarian wall, (6) and the branching of perianth traces at a low level. The two species of *Rauvolfia* (*Rauwolfiinae*) are characterised by (1) the moderate distances between successive whorls of gaps, (2) the absence of distinct commisural strands free from petal traces, (3) an annular disc, (4) branching of perianth traces at a high level, (5) and the sepals generally supplied by three traces, two derived from the petal-sepal cord and one from the midrib trace. *Thevetia nerifolia* (*Cerberinae*) may be distinguished by (1) the prominent distance between successive whorls of gaps, (2) the absence of sepal-petal cords and commisural strands, (3) a massive disc adherent to the ovary wall, with a highly branched large number of veins, (4) the branching of perianth traces at a very low level within the receptacle, (5) each sepal is supplied by 3 traces formed from the single trace which originates from one gap, (6) and an almost horizontal orientation of sepal traces after origin from the stele. The subtribe *Alstoniinae* presents a heterogeneity of vascular supplies in flowers. Of course, excepting *Plumeria acutifolia*, the other species investigated show some common characters: (1) the branching of petal traces near the middle region of the corolla tube, (2) the origin of stamen traces above the level of perianth traces, (3) and the presence of some residual stelar traces (after supplying the successive whorls) to supply the adnate or semi-annular disc, or some sterile parts. These characters are shared by *Alstonia scholaris*, *Holarrhena antidysenterica* and *Lochnera rosea*. Of these species, *Alstonia* sp. is distinguished by the presence of commisural strands and a semi-annular disc (not clearly annular like *Rauvolfia* sp.); *Holarrhena* sp.; by the absence of commisural strands, and the presence of a disc adnate to the ovary; and *Lochnera* sp.; by a combination of commisural strands and traces to sterile ovaries (according to the interpretation of Rao and Ganguli, 1963).

Plumeria as a distinct group

Plumeria acutifolia is distinguished from all other species of the *Alstoniinae* by (1) the branching of petal traces in the hypanthium, (2) the origin of petal traces at the same level as the staminal traces, (3) the absence of residual stelar traces after supplying the perianth, stamens and regular carpels, (4) the perpendicular sepal traces growing for a long distance, (5) and a nearly inferior ovary. In all of these characters, *Plumeria* sp. stands isolated in the subtribe *Alstoniinae*. These characters of *Plumeria* are not only different from those of other species of the *Alstoniinae*, but also distinct from all the species of the tribe *Plumiereae*. These findings support the conclusions, derived from the study of the chromosomes and wood.

Position of *Holarrhena*

Holarrhena antidysenterica is different from *Ervatamia* sp. in (1) the comparatively short internodes between successive whorls of gaps, (2) the absence of commisural traces, (3) and the formation of petal-trace branches in the corolla tube. A comparison between the two species clearly shows that *E. divaricata* is primitive, while *H. antidysenterica* is a highly advanced species. Therefore, the present study does not approve the placing of *Holarrhena* under *Tabernaemontaninae*. Its position in the moderately advanced group, *Alstoniinae* can be justified.

Phylogeny of species

The conclusions arrived from the cytological and anatomical investigations in the previous parts are supported by the study of vascular traces of flowers. *Tabernaemontaninae* with prolonged internodes between successive whorls, long commisural strands and a disc adherent to the ovary seems to be the most primitive group. From this basic group, by shortening of internodes and traces, and by further annulation in the disc, *Rauwolfiinae* have probably evolved. The evolution of *Cerberinae* (as represented by *Thevetia nerifolia*) accompanies the change of position of the traces to the sepal margin (which, instead of joining with the patel traces become fused with sepal midrib traces), and the formation of a massive disc adnate to the ovarian wall. *Alstoniinae* may similarly be derived dfrom the same basic group; but, as has been seen during cytological and xylary investigations, there are different lines of specialization included in the *Alstoniinae*.

REFERENCES

Balley L. H., 1953, The Standard Cyclopedia of Horticulture, New York.

Bentham G. and Hooker J. D., 1873, Genera Plantarum, Reeve & Co. London, II: 681–728.

Johansen D. A., 1940, Plant Microtechnique, McGrew Hill Book Co. Inc., New York and London: 42.

Rao V. S. and Ganguli A., 1963, Studies in the floral anatomy of the Apocynaceae, Jour. Ind. Bot. Soc. 42: 419–435.

Schumann K., 1895, *Apocynąceae* [In:]Engler and Prantl: Die Naturlichen Pflanzen Familien VI (2): 109–189.

Torre C. G., and Harms H., 1900–1907, Genera *Siphonogamarum* Ad Systema Englerianum Conscripta, Lipsiae, Sumtibus Guilemi Engelmann: 404–410.

Pokrewieństwa w obrębie Plumiereae (Apocynaceae)

III. Badania nad unerwieniem kwiatów

Streszczenie

Przeprowadzone badania anatomii kwiatów niektórych pospolitych indyjskich gatunków z plemienia *Plumiereae* (*Apocanaceae*) popierają wnioski otrzymane na podstawie badań chromosomów i drewna wtórnego, a mianowicie:

1. *Holarrhena* różnią się od *Ervatamia* i powinny być umieszczone w *Alstoniinae* (Schumann, 1895), a nie w *Tabernaemontaninae* (Bentham i Hooker, 1876).
2. Różne podplemiona mają odrębne właściwości i wobec tego podział na podplemiona jest uzasadniony.
3. *Tabernaemontaninae* stanowią najpierwotniejsze podplemię, od którego wywodzą się wszystkie inne.
4. *Alstoniinae* są niejednolite i złożone z odrębnych linii ewolucyjnych.
5. Rodzaj *Plumeria* zajmuje w plemieniu *Plumiereae* pozycję izolowaną i powinien być wydzielony jako odrębny taxon.