

## SYSTEMATIC LEAF ANATOMY OF BACCAUREA, DISTICHIRHOPS, AND NOTHOBACCAUREA (EUPHORBIACEAE)

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### SUMMARY

The leaf anatomical diversity of the genera *Baccaurea* Lour. (43 species), *Distichirhops* Haegens (3 species) and *Nothobaccaurea* Haegens (2 species) (Euphorbiaceae) is described. Two species of *Aporosa* and three species of *Maesobotrya* were examined for comparison. The following characters are important for the delimitation of species: hair types, the position of the glandular areas on the leaf margin, the hairiness and size of the glandular areas, the number of epidermal layers, the presence of (mucilage) idioblasts in the epidermis, the presence of palisade parenchyma above the vascular bundles, and the birefringence of the spongy parenchyma cell walls. However, leaf anatomy did not yield characters for distinction between the five genera studied. Phenetic analysis resulted in a grouping based on leaf anatomical similarities that corresponds to a large extent with the phylogenetic position of species based on a cladistic analysis of largely macromorphological features (Haegens, 2000).

**Key words:** *Baccaurea*, *Distichirhops*, *Maesobotrya*, *Nothobaccaurea*, Euphorbiaceae, hairs, leaf anatomy, leaf glands, systematics.

### INTRODUCTION

Little is known about leaf anatomical diversity of *Baccaurea* Lour., the allied genera *Distichirhops* Haegens and *Nothobaccaurea* Haegens (Euphorbiaceae), and its use for genus and species delimitation and classification. The most important studies are: anatomy of leaf and petiole of Phyllanthoideae (Rothduscher, 1896); vascular bundles in Phyllanthoideae (Constantin, 1935); overall vegetative anatomy of Euphorbiaceae (Metcalf & Chalk, 1950); foliar stomata in Euphorbiaceae (Raju & Rao, 1977); the indumentum of Euphorbiaceae of New Guinea (Airy Shaw, 1980); and leaf morphology of Phyllanthoideae (Levin, 1986a). In these studies only a few species of *Baccaurea* are mentioned. However, a leaf anatomical study comprising the genera *Baccaurea*, *Distichirhops* and *Nothobaccaurea* had not yet been carried out. The present comprehensive study was carried out to support a phylogenetic and taxonomic revision of these taxa (Haegens, 2000), where many of the data presented here were incorporated in the overall analysis. The present paper presents the leaf anatomical range in much more detail.

## MATERIALS AND METHODS

*Character choice*

A pilot study was carried out to explore which characters might be of diagnostic value and/or be phylogenetically informative. Ten specimens of the following species were used: *Baccaurea angulata* Merr., *B. brevipes* Hook. f., *B. macrophylla* (Müll. Arg.) Müll. Arg., *B. motleyana* Müll. Arg. and *Nothobaccaurea pulvinata* (A.C. Sm.) Haegens. These species were chosen to represent the full phylogenetic and geographical range of this clade (Haegens, 2000). Macerations, stained paradermal sections of the upper and lower surface of the leaf, unstained and stained cross sections of the leaf margin, midrib and petiole were investigated. Leaf fragments (upper and lower surface) including the leaf margin with glandular areas, the lamina and the midrib were examined with SEM. On the basis of this pilot study and the literature a selection of characters was made that were of promising diagnostic and systematic value, and the sampling was extended to all species of the three genera, while at the same time the repertoire of microtechnical procedures was limited to observe the selected characters efficiently.

*Anatomy*

Characters that could be scored directly from herbarium material were examined with a stereomicroscope at fairly low magnification. For Light Microscopy (LM) and Scanning Electron Microscopy (SEM) mature leaves from herbarium specimens were rehydrated by boiling in water. Cross sections were made with a thickness of (20–) 30(–60)  $\mu\text{m}$ . The material for SEM was dried with a Balzers CPD 030 Critical Point Dryer and coated with gold using the Bal-tec SCD 005 Sputter Coater. The leaf surfaces were observed and photographed with a Jeol JSM-5300 SEM at 15 kV. The size of the glandular areas on the leaf margin was measured parallel to the margin in SEM photographs. The cell walls of the spongy parenchyma, the druses and fragmented crystals, and starch grains were all observed with polarised light. Strongly birefringent secondary walls of the spongy parenchyma are thick and appeared to be lignified (tested with Wiesner's reagent).

Finally, 10 species were examined for the contents of their idioblasts. For all examined species, half of the cross sections of the midrib were put in water and the other half in 96% alcohol. Samples in water preserve oil and in alcohol mucilage (Bakker, 1989). Sections collected in water were stained in a 1% aqueous solution of chrysoidin-acridin red for 3 mins for detection of oil (Richter, 1977). If oil is present, the contents of the idioblasts will stain orange to red. The sections collected in alcohol were stained in a 1% alcoholic alcian blue solution for 15 mins (Quintarelli et al., 1964). If mucilage is present, the contents of the idioblasts will stain blue.

*Phenetic analyses*

The following phenetic analyses were performed to check whether there is clustering: Ward's Method, Group-Average Method (Cole, 1969) and Principal Component Analysis (PCA) (Sneath & Sokal, 1973) using Statgraphics Plus 2.1 for Windows. Prior to the analyses the multistate character set was binarised. All the dendrograms were created using the Squared Euclidean distance metric (Cole, 1969).

### Collections

Collections used both for the pilot study and general study are indicated with (p), both for the contents of the idioblasts and general study with (i), for hairs only with (h). Collections with stellate scales are indicated with (s). Five collections of *Baccaurea tetrandra*, only examined for the presence of druses, fragmented crystals and starch grains in the idioblasts, are indicated with (t). Collections without a suffix were only used for the general study.

- Aporosa arborea*: Lainpi 859; Rahmat si Boeea (= Rahmat si Toroos) 5376 — *A. nitida*: Jacobs 5196; S 33729 (Othman Ismawi).
- Baccaurea angulata*: Endert 4800; SAN 153763 (Wood); SF 9310 (Sinclair & Kadimbin) (p) — *B. annamensis*: Harmand 1436; Poilane 1269 — *B. bracteata*: KEP/FRI 2527 (Kochummen) (h, s); PBU 416 (Sidyasa); Rahmat si Boeea (= Rahmat si Toroos) 5448; SF 34745 (Henderson) (h, s) — *B. brevipes*: KEP/FRI 8495 (Cockburn); Rahmat si Boeea (= Rahmat si Toroos) 5822 (i); Sangkhachand 1237 (p) — *B. carinata*: De Vriese Herb. Lugd. Bat. 994.355-118; Pullen 996 — *B. costulata*: S 41135 (Yii Puan Ching); Suzuki K 5554 — *B. courtallensis*: Ridsdale 67 (i); Ridsdale 622 — *B. deflexa*: Boschproefstation T3P380; Elmer 21118 (i) — *B. dolichobotrys*: S 41494 (Othman et al.); S 53328 (Bernard Lee Meng Hock) — *B. dulcis*: Dayar Arbain DA-476 (i); Dumas 1658 — *B. edulis*: De Jong 341; S 31991 (Paul Chai) — *B. javanica*: Rastini 217 (VIII.F.28) — *B. lanceolata*: De Wilde & De Wilde-Duyfjes 18860; S 2977 (Pickles) — *B. macrocarpa*: De Wilde & De Wilde-Duyfjes 15518; Elmer 21240 (i) — *B. macrophylla*: bb 25190; Forbes 2706 (p); SF 40743 (Sinclair & Kiah bin Salleh) — *B. maingayi*: KEP/FRI 10506 (Cockburn); S 41121 (Yii Puan Ching) (i) — *B. microcarpa*: Brass 27290 — *B. minor*: KEP/FRI 7108 (Cockburn); Kostermans & Anta 657 — *B. mollis*: S 38495 (Yeo & Jugah); S 3422 (Pickles) — *B. motleyana*: Chin See Chung 2776; De Wilde & De Wilde-Duyfjes 12781; Purselove 5446 (p) — *B. multiflora*: De Wilde & De Wilde-Duyfjes 20690; Rastini 61 — *B. nanihua*: Mogeia & Ramlanto 822; Prawiroatmodjo & Soewoko 1736 — *B. nesophila*: Brass 28298; LAE 70905 (Katik et al.) — *B. odoratissima*: S 22112 (Sibat ak Luang); S 26142 (Banyeng ak Nudong) — *B. papuana*: Brass 8157; Brass 23905 (i); BW 4526 (Lasschuit); Carr 14260; LAE 77101 (Gideon); Lam 875; NGF 29557 (Coode); NGF 31690 (Ridsdale); NGF 41905 (Henty & Lelean); NGF 47802 (Streimann) — *B. parviflora*: Burley et al. 1284; De Wilde & De Wilde-Duyfjes 12671; KEP/FRI 4008 (Whitmore); KEP/FRI 8166 (Cockburn); KEP/FRI 13515 (Loh Hoy Shing); KEP/FRI 32616 (Wong Khoon Meng & Khairuddin) (s); Maxwell 81-223; SAN 90925 (Termiji Arshid) — *B. philippinensis*: Sulit 6363; Wenzel 3007 — *B. polyneura*: KEP/FRI 17880 (Sohadi); SAN 89751 (Fedilis & Sumbing) — *B. ptychopyxis*: Parkinson 1612 — *B. pubera*: PBU 346 (Sidyasa); S 37783 (Paie) — *B. purpurea*: Carr 16270; NGF 41916 (Henty & Lelean) — *B. pyriformis*: De Wilde & De Wilde-Duyfjes 13887; McDonald & Ismail 3484 — *B. racemosa*: De Wilde & De Wilde-Duyfjes 14374; KEP/FRI 16923 (Chan) — *B. ramiflora*: MADw 24531 (Majumder & Islam) (i); Poilane 11696 — *B. reticulata*: Meijer 4613; S 40571 (Yii Puan Ching) — *B. sarawakensis*: Leighton 378; S 24597 (Sibat ak Luang); S 26272 (Sibat ak Luang & Jugah ak Kudi) — *B. seemanii*: Degener 15252; Smith 7413 (i) — *B. simalourensis*: Achmad 244; Achmad 728 — *B. sumatrana*: Meijer 4083; S 17010 (Paie) — *B. taiensis*: Spence 516; Whistler W682 (i) — *B. tetrandra*: BNB 4516; BS 34768 (Ramos & Pasgasio); Burley, Tukirin et al. 2378 (t); Celestino & Ramos 128 (t); Mabesa 2-26 (t), PNH 42094 (Mendoza); S 24262 (Paie) (t); SAN 4516 (Madani), SAN 32189 (Lajangah) (t) — *B. trigonocarpa*: Elmer 21608 (s); S 19761 (Chai) — *B. velutina*: KEP/FRI 17318 (Loh); KEP/FRI 104901B (Everett).
- Distichirhops megale*: NGF 28659 (Streimann & Katik) — *D. minor*: BW 4933 (Versteegh); SAN 99863 (Signin et al.) — *D. mitsemosik*: LAE 55701 (Stevens); Hartley TGH 12711.
- Maesobotrya barteri*: Bos 6824; Leeuwenberg 7975 — *M. pauciflora*: Zenker 2952 (s); Zenker 3321 (s) — *M. staudtii*: Zenker 1603 (s); Zenker 1748.
- Nothobaccaurea pulvinata*: Gillespie 2409; Greenwood 998; Qoro & Kuruvoli 13631 — *N. stylaris*: BSIP 8511 (Dennis); Tabualewa 15572.



RESULTS

*Survey of the leaf anatomical characters* (Table 1)

The leaf anatomical diversity of *Aporosa* p.p., *Baccaurea*, *Distichirhops*, *Maesobotrya* p.p. and *Nothobaccaurea* is summarised in Table 1 using binary coding. The range of variation of the most salient features is surveyed below.

*Lowermost pair of secondary nerves* (Fig. 1a)

The angle formed between the lowermost pair of secondary nerves and the midrib (consistent with the angles formed by the other lower secondaries, more acute, or more obtuse) was suggested to be a good character by Levin (1986a).

*Indumentum* (Plate 1a–c)

All the leaves of the studied species of *Aporosa*, *Baccaurea*, *Distichirhops*, *Maesobotrya* and *Nothobaccaurea* have unicellular solitary hairs, but several species have in addition tufted hairs. These tufted hairs are divided into 3 types: tufts consisting of

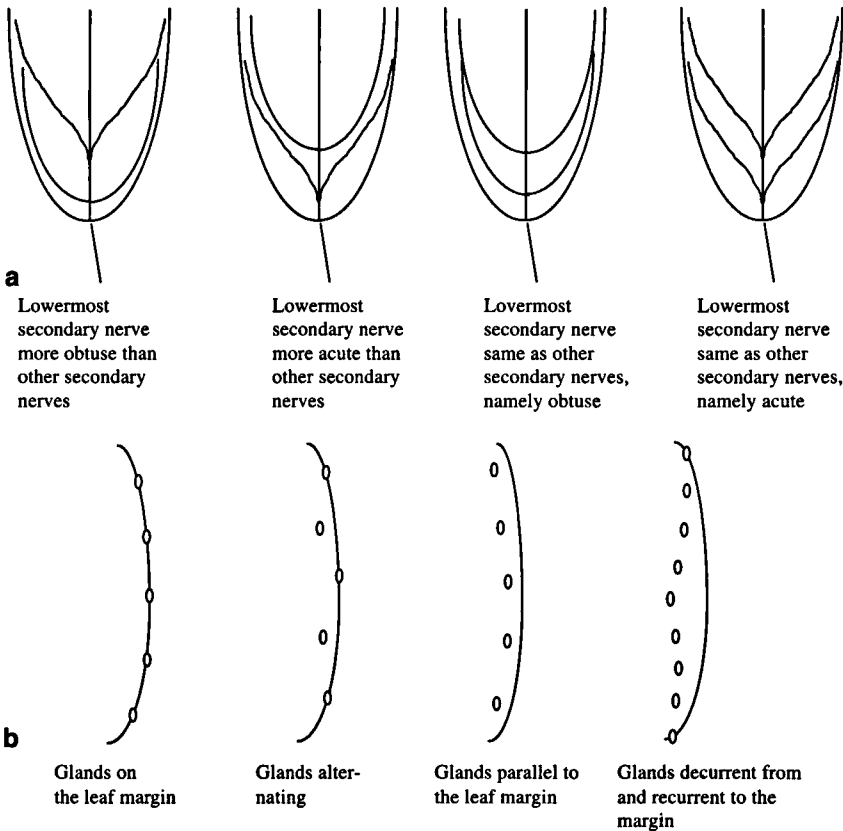
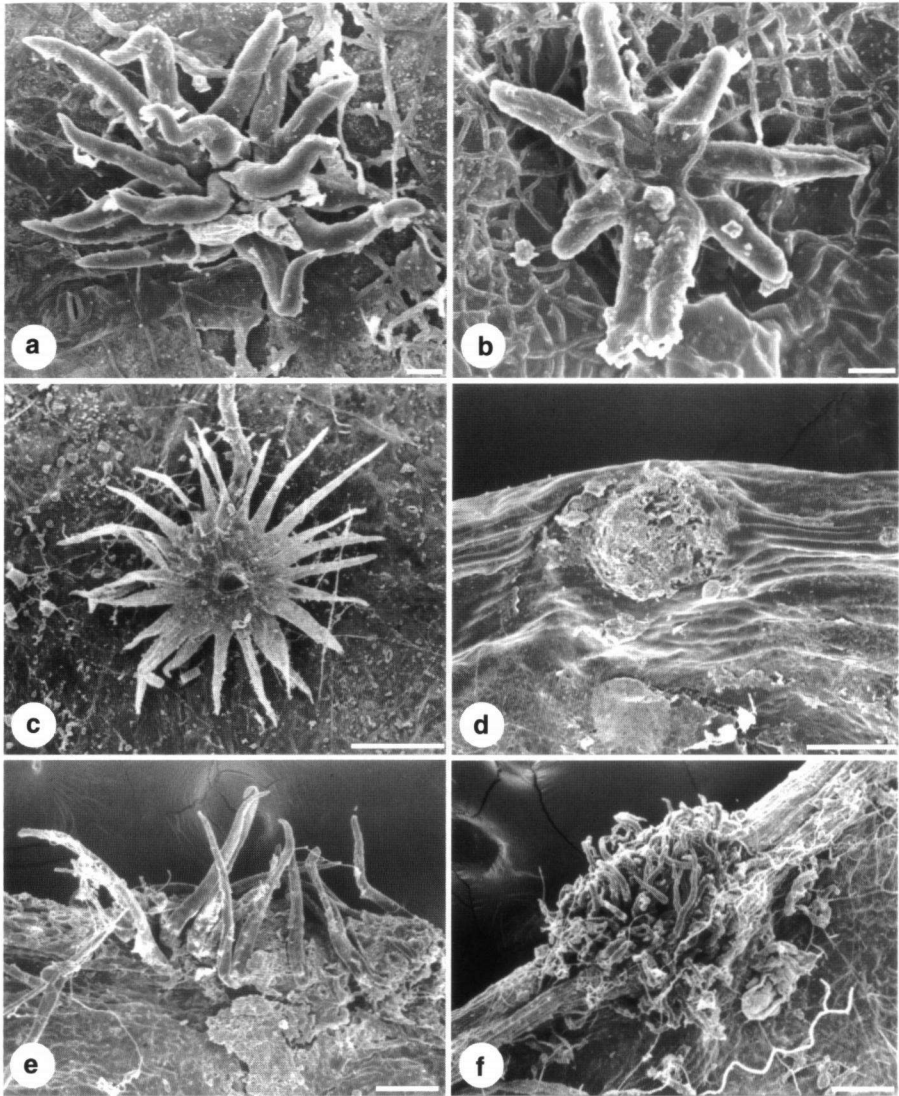
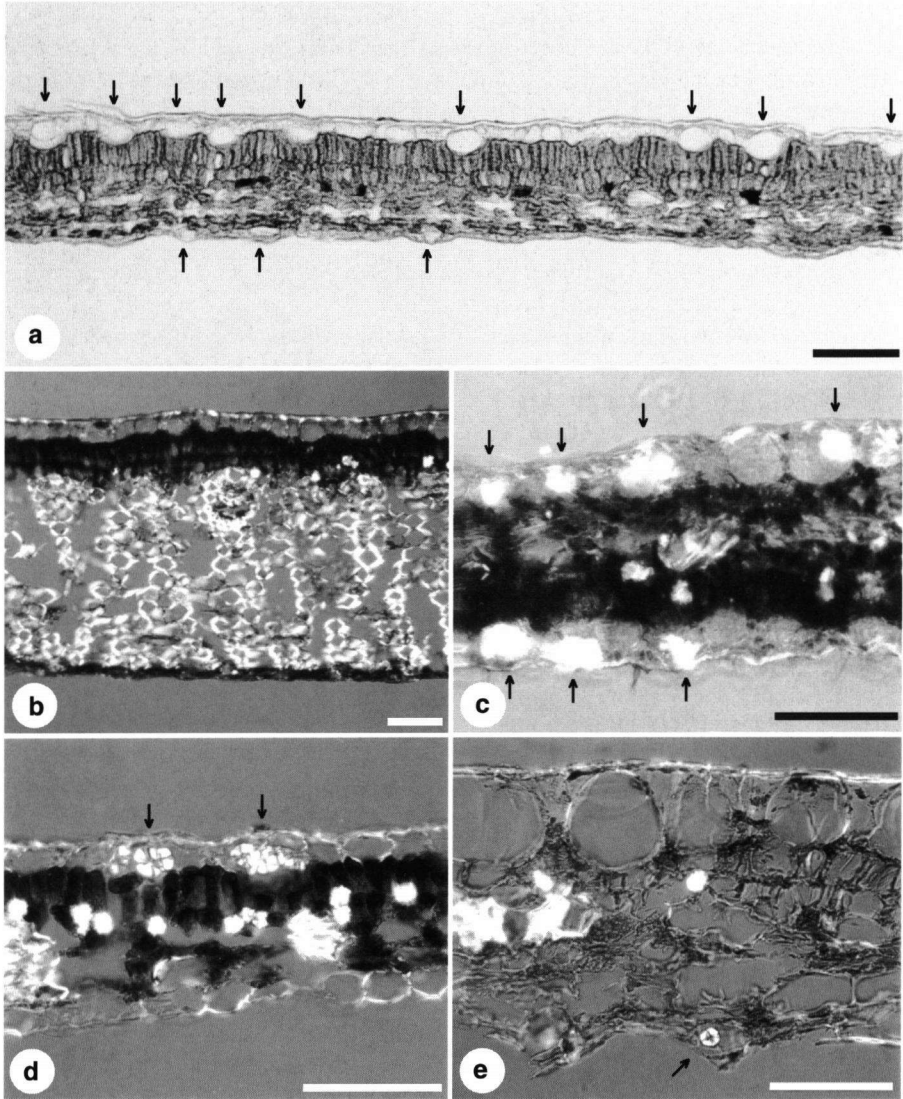


Fig. 1. a. The angle formed between the lowermost pair of secondary nerves and the midrib in comparison with other secondaries; b. the position of the glandular areas in the leaf margin.



**Plate 1.** a. *Baccaurea macrocarpa*, tuft consisting of free hairs; b. *B. nanihua*, stellate tuft; c. *B. parviflora*, stellate scale; d. *B. purpurea*, glandular area on the leaf margin glabrous; e. *Aporosa arborea*, glandular area on the leaf margin with intermediate hairiness; f. *B. deflexa*, glandular area on the leaf margin abundantly hairy. — Scale bars: a, b = 10  $\mu\text{m}$ ; c–f = 100  $\mu\text{m}$ .

free hairs, tufts of partly adnate hairs (less than 1/3 of their lengths adnate) and stellate tufts (more than 1/3 adnate). There is no evidence that they are fundamentally different since no basal cells were found for the adnate hairs. Yet these types are used for the phenetic analyses since they are easily recognisable in surface view, and the hairs with more than 1/3 of their parts adnate are always smaller. Five species



**Plate 2.** a. *Baccaurea pyriformis*, idioblasts (arrows) in both epidermal layers, in abaxial layer less than in adaxial layer; b. *B. multiflora*, birefringence of the spongy parenchyma; c. *B. nesophila*, numerous druses and fragmented druses (arrows) present in enlarged epidermal cells; d. *B. tetrandra*, numerous starch grains (arrows) present in enlarged epidermal cells; e. *B. odoratissima*, starch grains (arrow) infrequent in enlarged epidermal cells. — Scale bars: a–e = 100  $\mu$ m.

were found with stellate scales: *B. bracteata*, *B. parviflora*, *B. trigonocarpa*, *M. pauciflora* and *M. staudtii*. Since their presence was highly variable below the species level and only a few collections possessed them, this character was not used for further analysis.

### *Glandular areas on the leaf margin* (Fig. 1b, Plate 1d–f)

Glandular areas in the vicinity of the leaf margin are situated on the leaf margin itself, parallel to the leaf margin, alternating, or decurrent from and recurrent to the leaf margin (Fig. 1b). The glandular areas on the leaf margin are divided into 5 size classes (Table 1). The hairiness of the glandular areas is scored as (sub)glabrous, sparsely hairy, and densely hairy.

### *Epidermis* (Plate 2a, c–e)

The number of epidermal layers is divided into 3 states: one adaxial epidermal layer and one abaxial epidermal layer; two adaxial and one abaxial epidermal layer; two adaxial and two abaxial epidermal layers. In *Aporosa nitida* some epidermal cells are divided into two daughter cells giving the appearance of being two-layered. The presence of idioblasts in the epidermis is scored as: absent; present only in the adaxial epidermal layer; present in both epidermal layers with as many in the abaxial layer as in the adaxial layer; present in both epidermal layers with less in the abaxial layer. The idioblasts of seven species tested positive for mucilage, one species tested negative for both mucilage and oil, and 2 species had no idioblasts. The druses and fragmented crystals in enlarged epidermal cells are divided into 5 classes: druses and fragmented crystals absent; druses infrequent; druses numerous; fragmented crystals infrequent; and fragmented crystals numerous. The starch grains in the enlarged epidermal cells are divided into 3 classes: starch grains absent; starch grains infrequent; starch grains abundant. *Aporosa*, *Distichirhops*, *Maesobotrya* and *Nothobaccaurea* do not contain druses, fragmented crystals, or starch grains in enlarged epidermal cells, except for *Nothobaccaurea stylaris* which has some druses and fragmented crystals in enlarged epidermal cells. Crystals and similar inclusions occur in some plants in ordinary cells, in others in certain tissues only, and a third group only in special cells called crystal idioblasts (Clowes & Juniper, 1968). In the epidermis of *Baccaurea* and *Nothobaccaurea stylaris* the druses are situated in special enlarged epidermal cells.

### *Mesophyll* (Plate 2b)

The mesophyll of all species studied is of the common dorsiventral type. Palisade parenchyma is present or absent above the vascular bundles. The birefringence of the spongy parenchyma is absent to weak, or strong. Druses in ordinary cells found in the mesophyll are divided into 2 size classes (Table 1).

### *Summary of varying leaf anatomical characters in Baccaurea*

#### *Leaf surface*

The angle formed between the lowermost pair of secondary nerves and the midrib is more acute, or more obtuse than the angle between the other secondaries and the midrib, or the same (Fig. 1a). The indumentum consists of unicellular solitary hairs and in addition sometimes of tufted hairs (Plate 1a, b), and exceptionally of scales (Plate 1c). Glandular areas scattered on the lamina are sometimes present; they are usually situated on the leaf margin (Fig. 1b). Their diameter varies from 100–640  $\mu\text{m}$ , rarely bigger, and they are glabrous to densely hairy (Plate 1d–f).



### *Epidermis*

The epidermis usually consists of one adaxial and abaxial layer, rarely two adaxial and one abaxial, or two adaxial and two abaxial layers. Mucilaginous idioblasts usually occur only in the adaxial epidermis or in adaxial and abaxial epidermis, but then with fewer and smaller idioblasts in the abaxial layer than in the adaxial layer (Plate 2a). There rarely are as many idioblasts in both epidermal layers or rarely the idioblasts are absent. Druses, fragmented crystals, and starch grains are rarely present in enlarged epidermal cells (Plate 2c–e).

### *Mesophyll*

The palisade parenchyma is usually interrupted above the vascular bundles. Sometimes the cell walls of the spongy parenchyma are strongly birefringent (Plate 2b). The size of druses in the mesophyll varies from 12–50 µm.

The vascular system of the midrib and the petiole is of the simple closed type. Midrib and petiole hardly differ from each other in this respect and do not vary for the different species (as judged from the pilot study).

### *Phenetic analysis*

The results of the phenetic analysis based on Ward's Method is illustrated in Fig. 2. Some collections of one species are never clustered. These species are: *B. parviflora* (which splits up into 3 groups, with one group consisting of *B. parviflora* s. str. and the former species *B. scortechinii*), *B. tetrandra* (which always splits up according to *B. tetrandra* s. str. and the former species *B. stipulata*), *Distichirhops minor* and *D. mitseosik*.

In some cases the collections of different species are always put together: *Baccaurea dolichobotrys* and *B. maingayi* (and in most dendrograms also *B. polyneura*), *B. dulcis* and *B. lanceolata*, *B. odoratissima* and *B. parviflora* (one collection), *B. parviflora* (the group with *B. parviflora* s. str. and the former species *B. scortechinii*) and *B. ptychopyxis*, and *B. sumatrana* and *B. trigonocarpa*. These species pairs show no or little variation in leaf anatomical characters.

In the PCA (not shown) based on the data in Table 1, the first component only accounted for 11.3% of the total variance. This is probably due to the lack of information in the binarised characters. There is, however, an indication that the hair type is an important character. The results of the Group-Average Method and of the PCA were similar to the Ward's dendrogram with respect to the clustering of specimens and species.

## DISCUSSION

The results of this leaf anatomical study have to be interpreted with caution, since only 2 collections have been used for most species. For several species, however, up to 10 collections have been used to study the variation within one species. Generally there is very little infraspecific variation, but that does not mean that each species of *Baccaurea* shows a constant leaf anatomy.

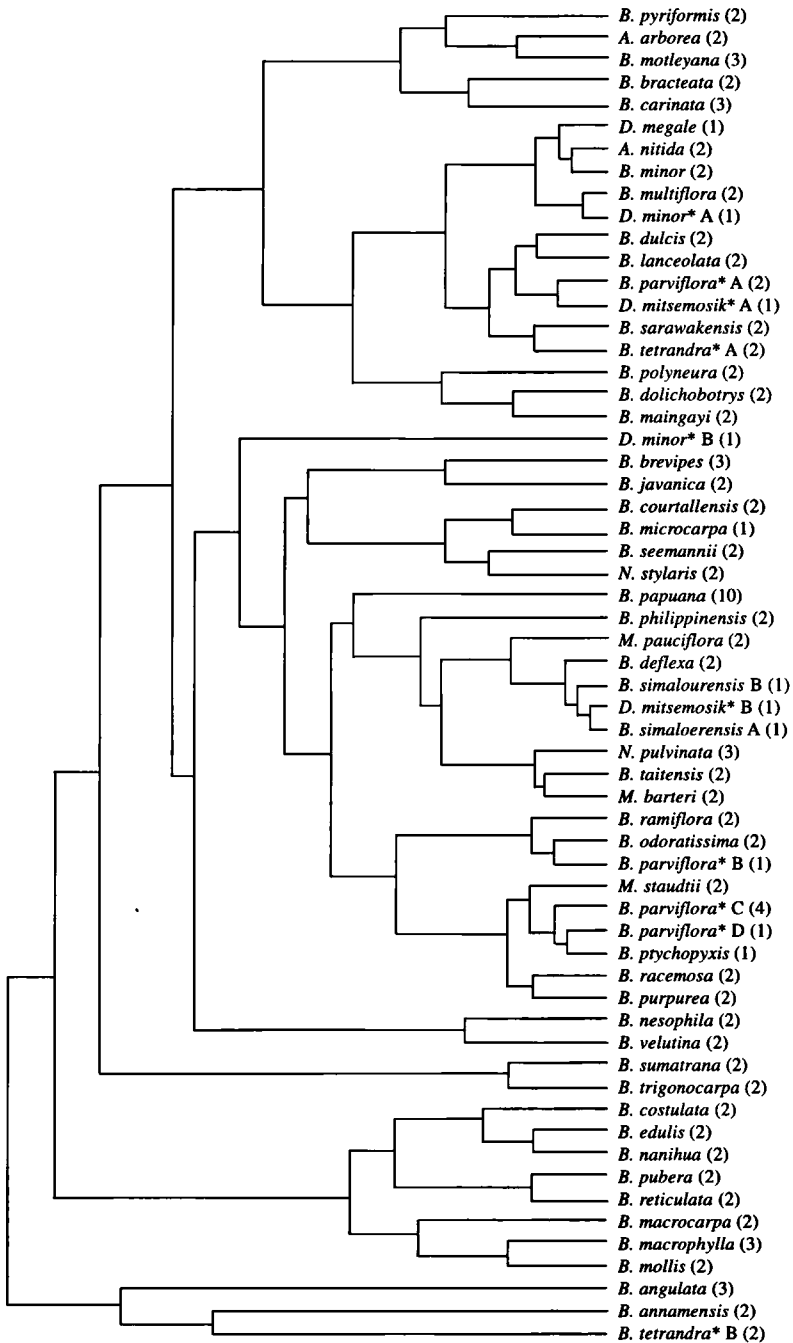


Fig. 2. The dendrogram obtained with Ward's Method, Squared Euclidean, shows grouping based on similarities between specimens, giving no indication about the extent of similarity between specimens within a group (\* = specimens of one species which do not group together).

*Characters with comments on their diagnostic significance*

The angle formed between the lowermost pair of secondary nerves and the midrib proved to be a very variable character, which makes the distinction of character states very difficult. For this reason it was decided to run all the phenetic (and in Haegens, 2000, also the phylogenetic) analyses without this character.

The type of hairs is the most diagnostic character for distinction of species according to the PCA. This distinctive character has been used for the first lead in the general key to the species of *Baccaurea* (Haegens, 2000).

The position of the glandular areas on the leaf margin can be established directly from herbarium material. This character has two states which are common among the species studied, causing a segregation into two groups. The other two states are more uncommon and occur only in a few species. The glandular area on the leaf margin is very easy to measure when glabrous, but when densely hairy it becomes more complicated. In this study the glandular area with surrounding hairs was measured, probably overestimating the size in some species. However, the size and hairiness of the glandular area are reliable diagnostic characters, which provide information because of the large differences between individual species.

The number of epidermal layers has one common character state, the other two states occur less frequently. This character is not useful for segregation of the species into large groups, but can be used for the delimitation of some species. This character was one of the 20 phylogenetically most informative characters (out of 102 characters) (Haegens, 2000). The presence of idioblasts in the epidermis has two common character states, which cause a distinction into two groups. The other two character states are useful for the distinction between a few species. Druses and fragmented crystals in enlarged epidermal cells can sometimes be found, but tend to vary much within a single species. The type of starch grains can be an important character at family level (Czaja, 1978). Starch grains probably are only temporary food reserves in the higher plants (Clowes & Juniper, 1968). Since the amount might be dependent upon ecological variables, it cannot be regarded as a reliable diagnostic character.

The presence of palisade parenchyma above the vascular bundles and the birefringence of the spongy parenchyma each have one common character state, while the other state only characterises a few species. These characters are thus useful for recognition of these few species. There are two sizes of the druses in the mesophyll. The species under investigation always possess small druses, and in addition many species also contain bigger ones. Since there is a gradual increase of size, this is not considered to be a good diagnostic character.

*Phenetic analysis*

In some cases the specimens of different species are always put together, therefore leaf anatomy alone is not sufficient for distinction between these species.

*Baccaurea dolichobotrys* and *B. maingayi* have female inflorescences and fruits which are similar for the two species; and they are also very closely related according to a phylogenetic analysis based on macromorphological and leaf anatomical characters, but the leaves are very different. *Baccaurea dolichobotrys*, *B. maingayi* and *B. polyneura* form a clade based on 6 characters in phylogenetic analyses. The number of epidermal layers is one of the three most important characters (Haegens, 2000).

*Baccaurea dulcis* and *B. lanceolata* differ macromorphologically in many characters. Still, they are closely related according to a phylogenetic analysis based on macromorphological and leaf anatomical characters (Haegens, 2000).

*Baccaurea odoratissima* and *B. parviflora* look very similar vegetatively.

*Baccaurea sumatrana* and *B. trigonocarpa* are very closely related sister species, which have similar male inflorescences and fruits. The number of epidermal layers is an apomorphy for this clade in the phylogenetic analyses (Haegens, 2000).

The specimens of some species never occur side by side in the phenetic analyses.

*Baccaurea parviflora* is macromorphologically a variable species in fruit characters: *B. parviflora* s. str. has fruits without ridges, and the synonymised former *B. scortechinii* has ridged fruits. Further complication lies in the position of the male inflorescences as *B. ptychopyxis*, sister species of *B. parviflora*, which has ridged fruits, has axillary inflorescences, and *B. parviflora* is cauliflorous. The differences found in the leaf anatomical study do not split *B. parviflora* and *B. ptychopyxis* according to the macromorphological differences. So both macromorphological and leaf anatomical characters indicate a heterogeneous gene pool for *B. parviflora* and *B. ptychopyxis*.

*Baccaurea tetrandra* can be split leaf anatomically into two forms, namely *B. tetrandra* s. str. and former species *B. stipulata*, based on the presence of druses and fragmented crystals in enlarged epidermal cells, and the presence of starch in these cells. However, the four specimens examined were the extreme macromorphological forms: *B. tetrandra* s. str. occurs only in the Philippines and the leaves dry brown, and *B. stipulata* only occurs in Borneo and has a white wax on the dried leaves. Examining more specimens revealed intermediates for both macromorphological and leaf anatomical characters, indicating that a distinction will not be possible. Moreover, the two separating leaf anatomical characters are diagnostically not very reliable.

The genera examined in this study are very closely related (Haegens, 2000; Levin, 1986b; Webster, 1994) and belong to subtribe Scepinae of subfamily Phyllanthoideae. The few specimens studied of *Maesobotrya* and *Aporosa* are leaf anatomically not distinguishable from *Baccaurea*, *Distichirhops* and *Nothobaccaurea*. Thus leaf anatomy yields no characters to distinguish between genera in this subtribe. Metcalfe & Chalk (1950) encountered the same problem for tribes. However, some leaf anatomical characters can be used for the delimitation of species and are phylogenetically informative as demonstrated by Haegens (2000).

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