

## LEAF ANATOMY OF HARPULLIA, MAJIDEA, AND CONCHOPETALUM (SAPINDACEAE)

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### SUMMARY

The leaf anatomical characters of *Harpullia* and the related genera *Majidea* and *Conchopetalum* are described in detail. *Harpullia* and *Majidea* both have stellate hair tufts together with solitary unicellular hairs, in *Conchopetalum* stellate hair tufts are absent.

A high variability below the species level is reported for several leaf epidermal characters. Other leaf anatomical characters such as the hypodermis, sclerification of the bundle sheath extensions, and the presence of secretory idioblasts and idioblastic sclereids also show a considerable variation. Characters with a higher diagnostic value within *Harpullia* are the type of stomata and in certain species the presence of idioblastic sclereids in the mesophyll.

Based on leaf anatomy the subgenus *Otonychium* within *Harpullia* can be distinguished by the cyclocytic stomatal type and absence of secretory idioblasts. The subgenus *Harpullia* is characterized by the paracytic stomatal type, which has not been recorded elsewhere within the Sapindaceae. A subdivision of the subgenus *Harpullia* cannot be made, because of an obvious lack of mutual correlation between the different leaf anatomical characters.

### INTRODUCTION

This leaf anatomical study was undertaken in order to obtain a more complete survey of the characters of the genus *Harpullia* Roxb. and to provide additional character sets, in addition to macromorphological and palynological characters, for future phylogenetic analysis. As already shown in the studies of Radlkofer (e.g., 1886, 1890), leaf anatomical characters may have phylogenetic significance. In the studies of the Sapindaceae genera *Guioa* (Van Welzen, 1989) and *Cupaniopsis* (Adema, 1991) most infrageneric groupings within these two genera are characterized by leaf anatomical apomorphies.

In addition to the genus *Harpullia*, the genera *Majidea* Kirk ex Oliv. and *Conchopetalum* Radlk. were investigated leaf anatomically. These related genera will be considered as outgroups in the phylogenetic analysis of *Harpullia*. According to Muller & Leenhouts (1976), *Conchopetalum* appears to be the most primitive genus of the tribe Harpullieae, and *Majidea* might be derived from this genus. *Harpullia* is quite comparable to *Majidea*; characters they have in common are among others stellate hair tufts and inflated, loculicidally dehiscent fruit lobes. Within *Harpullia* further specializations occur, such as reduction of the gynoecium, reduction in the number of stamens, and reduction of the number of ovules. The other genera of the heterogeneous tribe Harpullieae are difficult to relate to these three genera (Muller & Leenhouts, 1976) and therefore are not treated in this study.

The present study is an initial part of a larger project, i. e., a biogeographical study of the Malesian Archipelago. By means of the phylogenetic relationships within *Harpullia* and *Nephelium* (Sapindaceae), the historical biogeographical relations between the islands of the Malesian Archipelago will be analysed. After the reconstruction of the phylogeny of *Harpullia*, the West Malesian genus *Nephelium* L. will be analysed similarly. Both genera will be treated separately during all the analyses, because they are not closely related and occur in different parts of the Malesian Archipelago.

The genus *Harpullia* comprises 25 species, which are distributed mainly in East Malesia and the Pacific, with many endemic species in New Guinea. The genus was revised by Leenhouts & Vente (1982). *Harpullia* is divided into two subgenera: *Otonychium* Blume, with only two species, and *Harpullia* with the other 23 species. This subdivision was confirmed in the following studies by Leenhouts (1985) and Muller (1985). The first author made an attempt towards a natural system of *Harpullia*, while the latter described the pollen morphology of the genus with notes on the phylogeny. A further division of subgenus *Harpullia* was far less clear and was not translated into a formal taxonomy.

The genera *Majidea* and *Conchopetalum* both consist of two species. *Majidea* is distributed in Madagascar and tropical Africa, and *Conchopetalum* occurs only in Madagascar. The species of these two genera present in Madagascar were treated by Capuron (1969).

Leaf anatomical studies of the family Sapindaceae were carried out in the past by Radlkofer (e. g., 1886, 1890) and Solereder (1899, 1908). Radlkofer, the monographer of the family Sapindaceae, was also one of the pioneers in systematic plant anatomy. His anatomical notes can be found throughout his papers. An anatomical treatment of the whole family was given by Solereder, Radlkofer's pupil, in his survey of the systematic anatomy of the Dicotyledons (1899, 1908). Specific leaf anatomical characters mentioned for *Harpullia*, amongst other genera, include: paracytic stomata, parenchymatous hypoderm, stellate hair tufts, idioblastic sclereids, undulating anticlinal walls of epidermal cells, and cuticular pits in the loops of the undulations (see also Metcalfe & Chalk, 1950).

#### MATERIAL AND METHODS

The herbarium material used for the anatomical research of the genus *Harpullia* was obtained mainly from the Rijksherbarium at Leiden (L), unless stated otherwise (herbarium abbreviations as in Index Herbariorum). The herbarium material used for the anatomical research of the genera *Majidea* and *Conchopetalum* was obtained from Paris (P).

Of 24 species of *Harpullia* usually up to 5 specimens were examined of species with a rather limited distribution. In the case of *H. longipetala* 8 specimens were examined, because of variation in the presence of idioblastic sclereids in the mesophyll. More specimens were studied of widespread species, evenly distributed over their complete distribution area: 21 specimens of *H. arborea*, 16 of *H. cupanioides*, 8 of *H. petiolaris*, and 10 of *H. ramiflora*.

*Harpullia peekeliana* is the only species that could not be examined leaf anatomically because this species is only known from the rather extensive original descrip-

tion. The type was lost in the Berlin fire and no duplicates are known. The collection of *Hays 167* (LAE) is mentioned by Leenhouts & Vente (1982) as an interesting new species. However, it concerns only a single female specimen (male flowers and fruits unknown), and has not been formally described as a new species. The combination of 'primitive' character states, viz. 7 stamens and a 3-merous pistil, with the 'advanced' character state of 1 ovule per cell may well be due to abnormalities in an already described species. Until other collections are found with this specific combination of characters this single specimen has been omitted from further study.

Mature leaflets were rehydrated by boiling in water. Cuticular macerations were obtained after incubation of leaflet fragments (middle portion of the lamina, including midrib and leaf margin) overnight in a mixture of equal volumes of 30% hydrogen peroxide and glacial acetic acid; the macerations were then stained with Sudan IV.

Transverse sections of the middle portion of the lamina, including midrib and leaf margin, and the distal end of the petiolule were prepared on a sledge microtome. Paradermal free-hand sections were taken of the upper and lower surface of each leaflet. The free-hand sections and half of the transverse sections were bleached in household bleach and stained with a safranine-haematoxylin mixture (94:6). All sections were mounted in euparal.

Unstained leaf clearings of some of the specimens [marked (1) in the list of the specimens studied] were made by boiling the leaflets for 20 minutes in a 5% KOH solution. The leaflets were bleached in household bleach until they were translucent after cooling down and rinsing. The cuticular macerations and the unstained leaf clearings were mounted in glycerin jelly.

The lower surface of some of the leaflets was also studied with a JEOL JSM-35 scanning electron microscope after critical-point drying of rehydrated herbarium material with dimethoxymethane and coating with gold, using a Polaron E 5100 series II sputter-coater.

The species and specimens studied are given below in alphabetical order; (1) = unstained leaf clearings; (2) = maceration only; (3) = transverse section only.

*Conchopetalum brachysepalum* Capuron: Madagascar, *Bosser 18566* (P); *SF (Mad) 803* (P), *23587* (P), *23614* (P). — *C. madagascariense* Radlk.: Madagascar, *SF (Mad) 18136* (P), *22111* (P).

*Harpullia alata* F. Muell.: Australia, *Bauerlen 123*; *Blake 12935* (NSW); *Johnson et al. 313* (NSW); *Moriarty 1676* (CANB); *L.S. Smith & L.J. Webb 3621* (CANB). — *H. arborea* Radlk.: China, *Yip 223*; India, *Raghavan 86283*; Ceylon, *Meijer 89*; Thailand, *van Beusekom et al. 4695*; *Geesink & Phengkhlai 6127*; Sumatra, *Meijer 5049*; Java, *Backer 30544*; Borneo, *S 33453*; *SAN 31606*; Philippines, *FB 20759*; *PNH 12482, 19855*; Celebes, *van Balgooy 3119* (2); *Whitmore & Sidiyasa 35294*; Moluccas, *van Balgooy 5053*; New Guinea, *Hoogland 5211*; *NGF 32285*; Australia, *Hyland 5968*; Solomon Islands, *BSIP 14669, 15866*; Tonga, *Buelow & Sykes 5*. — *H. austro-caledonica* Baillon: New Caledonia, *McKee 14648, 15547, 18736, 21998, 24002*. — *H. camptoneura* Radlk.: New Guinea, *Clemens 144* (1), *1283* (1); *LAE 66792* (1); *NGF 20904*. — *H. carrii* Leenh.: New Guinea, *Carr 12357, 12443, 12466*; *LAE 60224*. — *H. cauliflora* K. Schum. & Lauterb.: New Guinea, *Aet & Idjan 653*; *BW 13484*; *Jacobs 9311*; *LAE 52913*; *NGF 48337*. — *H. crustacea* Radlk.: New Guinea, *NGF 15646, 20954, 28057, 28767*; *Pullen 1798*. — *H. cupanioides* Roxb.: China, *Lei 826*; India, *Koelz 30893*; Burma, *Maxwell 75-280*; Thailand, *Maxwell 75-128*; Laos, *Kerr 20862*; Malay Peninsula, *FRI 21550*; Sumatra, *de Wilde & de Wilde-Duyffes 13955*; Java, *Wirawan 372*; Lesser Sunda

Islands, *Schmutz* 4285; Borneo, *Meijer* 487; *SAN* 31622; Philippines, *BS* 44075; Moluccas, *Jensen* 366; New Guinea, *NGF* 7518; *de Wilde* 1199; Australia, *Brown s.n.* (MEL). — *H. frutescens* F.M. Bailey: Australia, *Blake* 9598; *Briggs* 1952 (NSW); *Crome* 159 (CANB), 166 (CANB); *Hind* 342 (NSW). — *H. giganteacapsula* M. Vente: New Guinea, *Carr* 14504; *LAE* 62090; *NGF* 27614, 47662. — *H. hillii* F. Muell.: Australia, *Dietrich* 1104; *Jessup* 150; *L.S. Smith* 4121, 4408, 4409. — *H. hirsuta* Radlk.: New Guinea, *BW* 13622 (doubtful coll.); *von Römer* 980. — *H. largifolia* Radlk.: Solomon Islands, *BSIP* 3963, 5009, 7742, 13220. — *H. leptococca* Radlk.: New Guinea, *Darbyshire* 740; *Kara* 12; *LAE* 55357; *NGF* 12367, 30771. — *H. longipetala* Leenh.: New Guinea, *Carr* 11498 (2); *LAE* 73899; *NGF* 11693 (1), 22267, 25679 (1), 30337, 32909, 43596. — *H. myrmecophila* Merr. & Perry: New Guinea, *Brass* 13285, 13414. — *H. oococca* Radlk.: New Guinea, *Docters van Leeuwen* 10595 (2) (doubtful coll.); *Sayers s.n.* (2) (M). — *H. pendula* F. Muell.: Australia, *Dietrich* 1760; *Kanis* 2123; *Lazarides* 6890; *Smith* 4725; *Wrigley & Telford* *NQ* 579. — *H. petiolaris* Radlk. subsp. *moluccana* Leenh.: Borneo, *Kostermans* 4660; Moluccas, *de Vogel* 4495; var. *decidens* M. Vente: Moluccas, *de Vogel* 3077, 3267; var. *moluccana*: Moluccas, *de Vogel* 4102; subsp. *petiolaris*: New Guinea, *LAE* 73554; *NGF* 41023, 41755. — *H. ramiflora* Radlk.: Moluccas, *Anang* 649; Aru Islands, *Jensen* 257; New Guinea, *LAE* 74586 (doubtful coll.); *NGF* 35296, 35441; *Pullen* 7625; *van Royen & Sleumer* 7092; Australia, *Brass* 19121; *Forbes* 751 (MEL), 831 (MEL). — *H. rhachiptera* Radlk.: New Guinea, *LAE* 51779; *NGF* 31961. — *H. rhyticarpa* C.T. White & Francis: Australia, *van Balgooy* 1617; *Brass* 20172; *Hyland* 5977; *Irvine* 1434; *L.S. Smith* 3332. — *H. solomonensis* M. Vente: Solomon Islands, *BSIP* 13866; *Waterhouse* 645-B (3). — *H. vaga* Merr. & Perry: New Guinea, *NGF* 46042 (doubtful coll.); Solomon Islands, *BSIP* 15023, 16799; *Craven & Schodde* 42; *Kajewski* 2544.

*Majidea fosteri* Radlk.: Ivory Coast, *Aubréville* 149 (P); *Chevalier B* 22413 (P); Nigeria, *Brenan* 8821 (P); Cameroun, *Letouzey* 5307 (P); Gabon, *le Testu* 8232 (P). — *M. zanguearica* Kirk subsp. *madagascariensis* Capuron: Madagascar, *SF (Mad)* 3437 (P), 5416 (P), 7502 (P); subsp. *zanguearica*: Kenya, *Gillett & Kibuwa* 19874 (P); *Polhill & Paulo* 803 (P); Madagascar, *SF (Mad)* 16014 (P).

#### LEAF ANATOMICAL GENERIC DESCRIPTIONS

General leaf anatomical descriptions of the genera *Harpullia*, *Majidea*, and *Conchopetalum* are given below. For descriptive conventions and the terminology used for the various stomata types, see Wilkinson (1979). See Figures 1–14.

#### *Harpullia* Roxb.

*In surface view* — *Indumentum* consisting of stellate tufts of 2–12 unicellular hairs (Fig. 14), intermingled with solitary unicellular hairs, absent to abundantly present on both surfaces, often more densely so on the abaxial side, usually confined to the venation, on subglabrous leaflets usually a few hairs present on the midrib. *Papillae* absent. *Cuticle* smooth to striate on midrib and venation or on the entire surface; if anticlinal walls undulate then cuticle often thin in the loops of the undulations; cuticular flanges rather frequently pitted. *Unspecialized epidermal cells* polygonal, with straight to undulate anticlinal walls. *Epidermal cells above veins* square to rectangular, in rows parallel to the veins, showing the venation pattern of mainly midrib and major veins. *Stomata* predominantly paracytic to anomo-, tetra-, stauro-, or cyclocytic (Fig. 1 & 2), in *H. arborea* and *H. pendula* stomata predominantly cyclocytic to stauro- or tetracytic (Fig. 3), confined to abaxial side, small, up to 20 µm long, polar T-pieces of varying distinctiveness; subsidiary cells sometimes with radiating cuticu-

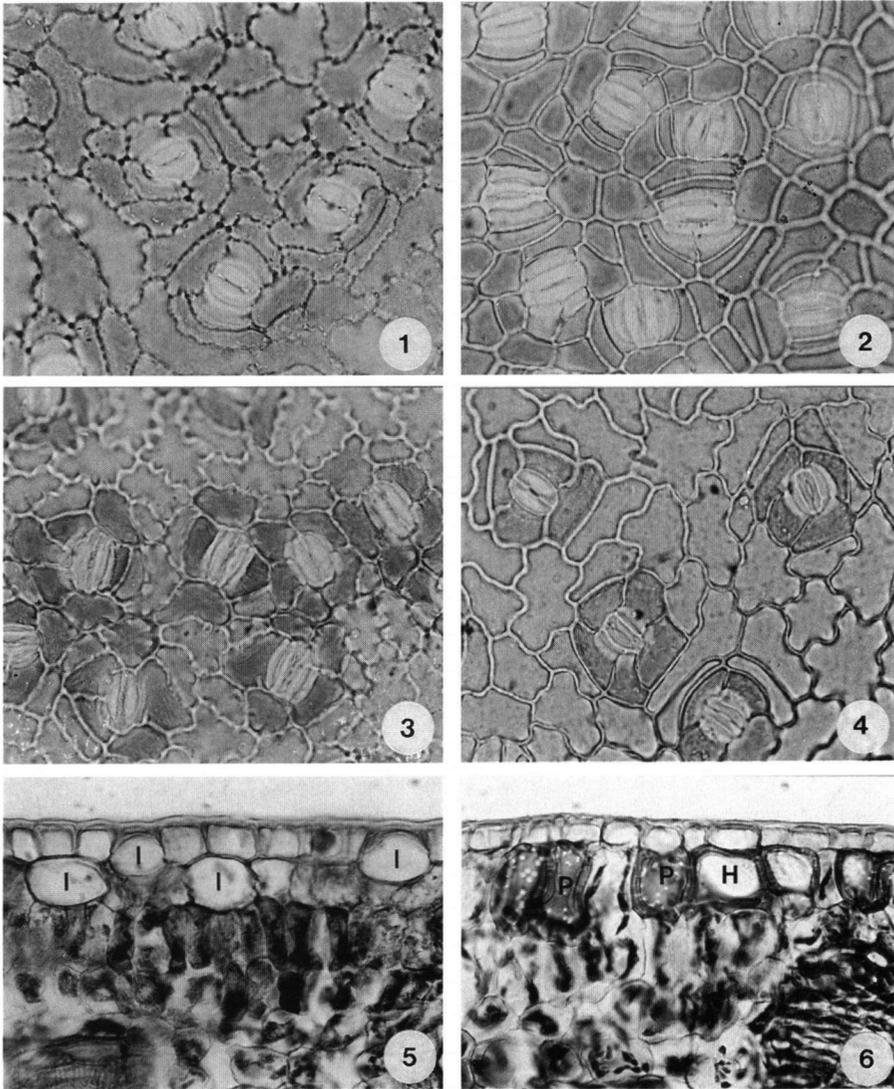


Fig. 1–6. — 1. *Harpullia austro-caledonica* (McKee 15547). Paracytic stomata, undulating anticlinal walls of epidermal cells pitted, and thin areas in the loops of the undulations; LM,  $\times 433$ . — 2. *Harpullia leptococca* (NGF 12367). Paracytic stomata, anticlinal walls of epidermal cells straight; LM,  $\times 433$ . — 3. *Harpullia pendula* (Wrigley & Telford NQ 579). Cyclocytic stomata; LM,  $\times 433$ . — 4. *Conchopetalum brachysepalum* (Bossler 18566). Cyclocytic stomata; LM,  $\times 433$ . — 5. *Harpullia camptoneura* (Clemens 144). Secretory idioblasts (I) in epidermis and palisade tissue; LM,  $\times 263$ . — 6. *Harpullia camptoneura* (LAE 66792). Discontinuous hypodermis with sclerified hypodermal cells (H) and sclerified palisade cells (P); LM,  $\times 263$ .

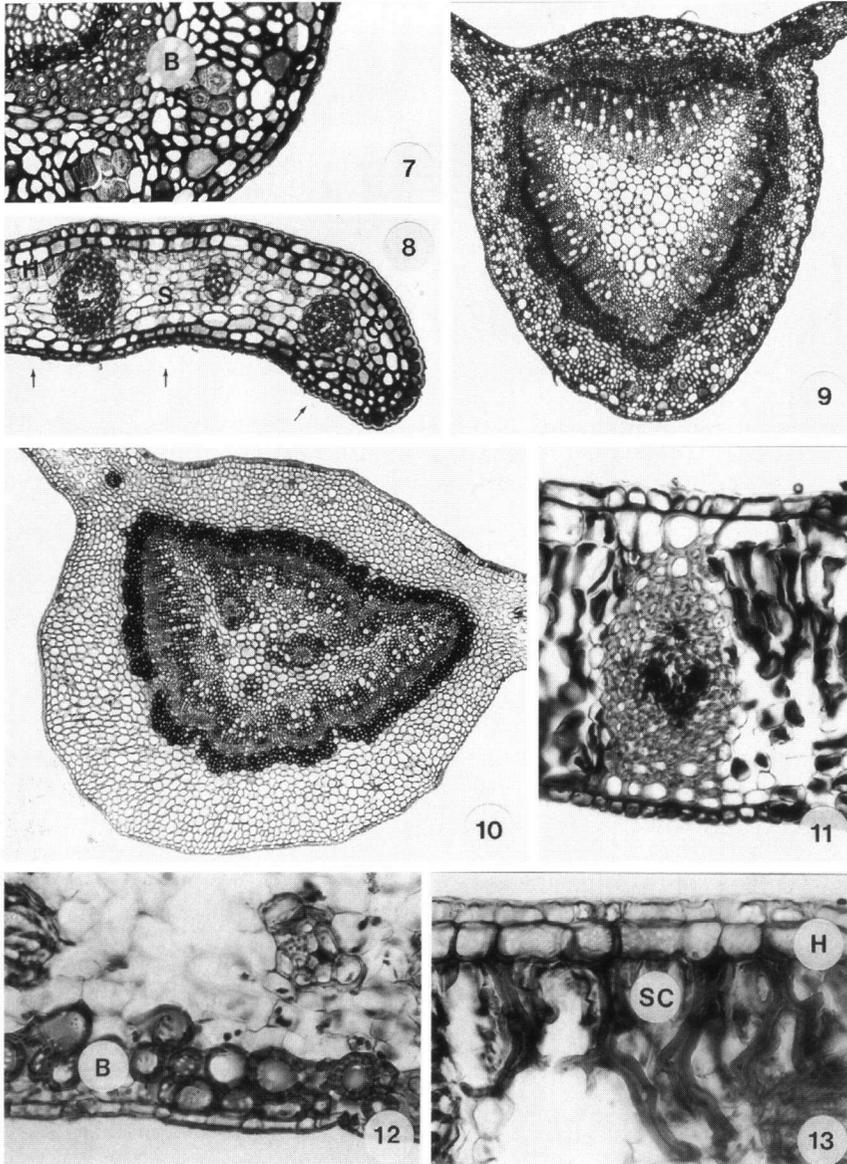


Fig. 7–13. — 7. *Harpullia solomonensis* (BSIP 13866). Brachysclereids (B) in ground tissue of petiole; LM,  $\times 107$ . — 8. *Harpullia* cf. *ramiflora* (LAE 74586). Leaflet margin with hypodermis (H) and collenchymatous tissue near edge (C) instead of spongy tissue (S); LM,  $\times 107$ . — 9. *Harpullia solomonensis* (BSIP 13866). Petiole with simple closed vascularisation; LM,  $\times 38$ . — 10. *Conchopetalum madagascariense* (SF (Mad) 18136). Petiole with complex closed vascularisation (two extra bundles in pith); LM,  $\times 42$ . — 11. *Harpullia leptococca* (LAE 55357). Bundle sheath extensions sclerified to both sides; LM,  $\times 263$ . — 12. *Harpullia camptoneura* (LAE 66792). Brachysclereids (B) in abaxial mesophyll; LM,  $\times 263$ . — 13. *Harpullia longipetala* (NGF 30337). Hypodermis (H) with sclerified cells and columnar to branched sclereids (SC) in mesophyll; LM,  $\times 263$ .

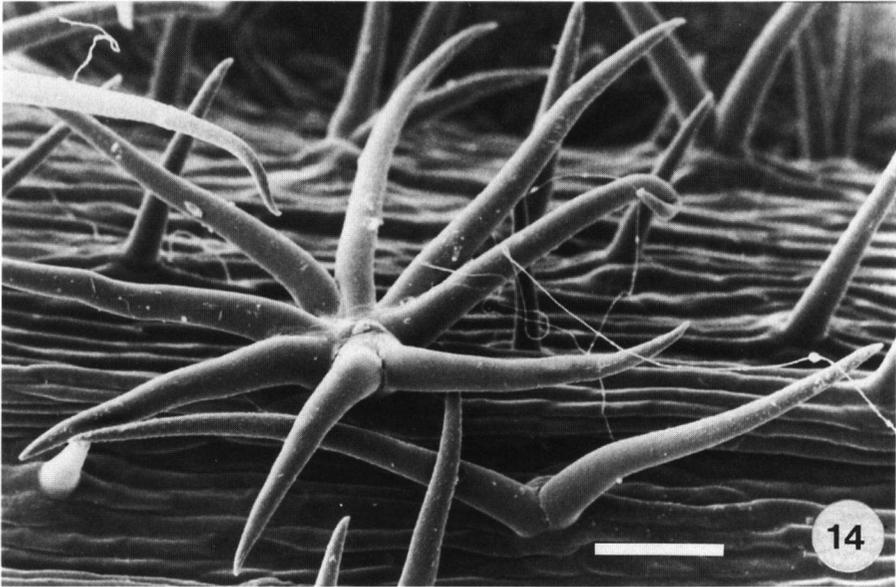


Fig. 14. *Harpullia crustacea* (Pullen 1798). Stellate hair, surface view; SEM, scale bar = 50  $\mu$ m.

lar striations; in *H. arborea*, *H. longipetala*, *H. pendula*, and occasionally in other species subsidiary cells staining more deeply with Sudan IV than the cuticle of unspecialized cells and guard cells; giant or water stomata often present on both surfaces, especially near the midrib. *Cork warts* rare to fairly frequent, probably always of traumatic origin.

*In transverse section* — *Lamina* dorsiventral. *Unspecialized epidermal cells* square to flat-rectangular, but usually erect over midrib and along margin of leaflet, adaxial cells larger than abaxial cells. *Hypodermis* locally developed over midrib and larger veins as a uniseriate continuation of the ground tissue of round, somewhat collenchymatous cells. In several species hypodermis adaxially developed as an interrupted or continuous layer of translucent, large, flat-rectangular to square cells with either thin walls or sclerified walls (in half of the samples of *H. camptoneura* hypodermis adaxially present as an interrupted layer of the formerly described cell type with sclerified walls, combined with sclerified palisade cells; Fig. 6). *Mesophyll*: palisade tissue composed of 1, 2, or 3 layers of square to long, erect cells; spongy tissue rather compact to rather loose. *Midrib* raised abaxially, flat to raised adaxially; ground tissue of round, somewhat collenchymatous cells; sclerenchyma sheath present around vascular system; the latter collateral, simple closed, with a flat to arc-shaped adaxial strand and a larger abaxial arc (Fig. 9). *Petioliule* with the vascular system at the distal end similar to that of midrib. *Larger veins* usually slightly raised, especially abaxially; bundles embedded in mesophyll or vertically transcurrent by poorly to distinctly differentiated bundle sheath extensions of ground-tissue-like parenchyma or of sclerenchyma to both sides (Fig. 11) or to abaxial side only; scler-

renchyma sheath present around the bundles. *Leaf margin* with marginal vein and supplied with collenchyma (Fig. 8). *Crystals* always present, varying from few to abundant, predominantly rhomboidal, sometimes druses; occurring around veins outside the sclerenchyma sheath, in the ground tissue of midrib and petiolule, usually also in pith and phloem, and sometimes subepidermally in parenchyma. *Secretory idioblasts* variously present, small to large, occurring in palisade tissue and very occasionally in the subepidermis, contents unknown, present in the adaxial and abaxial epidermis as mucilage cells, horizontal wall respectively always and often present separating the mucilage contents (Fig. 5). *Idioblastic sclereids* absent to abundantly present, solitary or clustered; brachysclereids often occurring in ground tissue and pith of midrib and petiolule (Fig. 7); brachysclereids present in mesophyll, especially abaxially, in *H. camptoneura* (Fig. 12), *H. cauliflora*, and *H. ramiflora* (in the last species in one of the samples only), in *H. longipetala* columnar to branched sclereids present in mesophyll (Fig. 13), on adaxial and abaxial side.

***Majidea* Kirk ex Oliv.**

*In surface view* — *Indumentum* consisting of solitary unicellular hairs and stellate tufts of 2–8 unicellular hairs, absent to fairly abundantly present on both surfaces, often more densely so on the abaxial side, usually confined to the venation, on subglabrous leaflets usually a few hairs present on the midrib. *Papillae* absent. *Cuticle* smooth to striate on midrib and larger veins; cuticle faintly to conspicuously thin in the loops of the undulations; cuticular flanges sometimes pitted. *Unspecialized epidermal cells* polygonal, with undulate anticlinal walls. *Epidermal cells above veins* square to rectangular, in rows parallel to the veins, showing the venation pattern of midrib and major veins; minor veins prominent in the epidermal cell pattern of both surfaces. *Stomata* predominantly anomo- to staurocytic, confined to the abaxial side, small, up to 20 µm long, polar T-pieces often distinct; subsidiary cells occasionally with radiating cuticular striations, staining usually the same with Sudan IV and more deeply with saffranine-haematoxylin mixture than the cuticle of unspecialized cells and guard cells; giant or water stomata often present on both surfaces, especially near the midrib. *Cork warts* rare to fairly frequent, probably always of traumatic origin.

*In transverse section* — *Lamina* dorsiventral. *Unspecialized epidermal cells* square to flat-rectangular, but usually erect over midrib and along margin of leaflet, adaxial cells larger than abaxial cells. *Hypodermis* locally developed over midrib and larger veins as a uniseriate continuation of the ground tissue of round, somewhat collenchymatous cells. *Mesophyll*: palisade tissue composed of 1 or 2, sometimes up to 3 layers of long, erect cells; spongy tissue rather compact. *Midrib* raised abaxially, sometimes flat to usually raised adaxially; ground tissue of round, somewhat collenchymatous cells; sclerenchyma sheath present around vascular system; the latter collateral, simple closed, with a flat to arc-shaped adaxial strand and a larger abaxial arc. *Petiolule* with the vascular system at the distal end similar to that of midrib. *Larger veins* adaxially sunken or flat to slightly raised, abaxially flat to rather distinctly raised; veins embedded in mesophyll, larger veins sometimes vertically transcurrent by bundle sheath extensions of ground-tissue-like parenchyma; sclerenchyma sheath present around the bundles. *Leaf margin* with marginal vein and supplied with collenchyma. *Crystals* always present, varying from rare to fairly common, predomi-

nantly rhomboidal, sometimes druses; occurring around veins outside the sclerenchyma sheath, in the ground tissue of midrib and petiolule, often also in pith and phloem, and in *M. fosteri* sometimes small druses subepidermally in parenchyma. *Secretory idioblasts* and *idioblastic sclereids* absent.

### ***Conchopetalum* Radlk.**

*In surface view* — *Indumentum* absent (only present on axes of inflorescences, consisting of short solitary unicellular hairs). *Papillae* absent. *Cuticle* smooth; if anticlinal walls undulate then cuticle thin in the loops of the undulations, if anticlinal walls straight then cuticle thin in the corners; cuticular flanges sometimes pitted. *Unspecialized epidermal cells* polygonal, with straight to undulate anticlinal walls. *Epidermal cells above veins* square to rectangular on the abaxial side, and square to polygonal on the adaxial side, in rows parallel to the veins, showing the venation pattern of mainly midrib and major veins; minor veins not prominent in the epidermal cell pattern of both surfaces. *Stomata* cyclo-, stauro-, or anisocytic (Fig. 4), confined to the abaxial side, small, less than 20 µm long, polar T-pieces of varying distinctiveness; subsidiary cells occasionally with radiating cuticular striations, especially distinct around giant stomata; subsidiary cells staining more deeply with Sudan IV than the cuticle of unspecialized cells and guard cells; giant or water stomata present on the abaxial side on entire surface. *Cork warts* rare to fairly frequent, probably always of traumatic origin.

*In transverse section* — *Lamina* dorsiventral. *Unspecialized epidermal cells* square to flat rectangular, sometimes erect, but usually only erect over midrib and along margin of leaflet, adaxial cells larger than abaxial cells. *Hypodermis* locally developed over midrib and sometimes over larger veins on adaxial side as a uniseriate continuation of the ground tissue of round, somewhat collenchymatous cells. *Mesophyll*: palisade tissue composed of 2 (or 3) layers of short, round to long, erect cells; spongy tissue rather compact. *Midrib* raised abaxially, flat to raised adaxially; ground tissue of round, somewhat collenchymatous cells; sclerenchyma sheath present around vascular system; the latter collateral, simple closed in *C. brachysepalum*, with a flat to arc-shaped adaxial strand and a larger abaxial arc, in *C. madagascariense* complex closed, with an extra strand [*SF (Mad) 18136*] or central bundle [*SF (Mad) 22111*] above the adaxial strand. *Petiolule* in *C. brachysepalum* with the vascular system at the distal end similar to that of midrib; in *C. madagascariense* complex closed with two extra bundles in pith (Fig. 10). *Larger veins* usually slightly raised, especially abaxially, usually embedded in mesophyll or sometimes vertically transcurrent by bundle sheath extensions of ground-tissue-like parenchyma; sclerenchyma sheath present around the bundles. *Leaf margin* with marginal vein and supplied with collenchyma. *Crystals* always present, varying from few to fairly abundant, predominantly rhomboidal, sometimes druses; occurring around veins outside the sclerenchyma sheath, in the ground tissue of midrib and petiolule, often also in pith and phloem, and occasionally in mesophyll. *Secretory idioblasts* and *idioblastic sclereids* absent.

### LEAF ANATOMICAL CHARACTERS

Details about the characters of the different species are listed in Table 1 (next pages).

Table 1. Leaf anatomical characters of species of *Harpullia* and related genera.

Species	Column: 1	2	3	4	5	6	7	8	9	10	11
<i>Conchopetalum</i>											
<i>brachysepalum</i>	4	-	-	+	±/+	-	-/s	±/+	±/+	-	c
<i>madagascariensis</i>	2	-	-	+	±	-	s	-/+	-	-	c
<i>Harpullia</i>											
<i>alata</i>	5	-/v	v	±/+	-/±/+	-	-	-/±/+	+	-/+	p
<i>arborea</i>	21	v/e	v/e	±/+	-/±/+	-	-/s	+	+	-/+	c
<i>austro-caledonica</i>	5	v	v	-/±/+	±	-/v	-	-/±	±/+	-	p
<i>camptoneura</i>	4	v	v/e	±/+	-/±	-	-	±/+	±/+	-/+	p
<i>carrii</i>	4	-/v	v/e	±/+	-/±/+	-	-	+	-/+	-/+	p
<i>cauliflora</i>	5	v/e	v/e	±/+	-/±/+	-/e	-	+	+	+	p
<i>crustacea</i>	5	v/e	v/e	±/+	-/±	e	-/(s)	+	±/+	+	p
<i>cupanioides</i>	16	-/v	-/v/e	±/+	±/+	-/e	-	±/+	±/+	-/+	p
<i>frutescens</i>	5	-/v	v	-/±/+	-/±/+	-	-	±/+	+	-	p
<i>giganteacapsula</i>	4	v	v/e	-	-	-	-	-/±	-/±	-/+	p
<i>hillii</i>	5	-/v	-/v	-/±	-/±	-/v/e	-	-/±	-/±	-/+	p
<i>hirsuta</i>	2	e	e	±	-	-	-	±/+	-/±	-	p
<i>largifolia</i>	4	-/v	v	-/+	-/+	-	-	-/+	-/+	-/+	p
<i>leptococca</i>	5	-/v	v	-/±	-	-	-	-/±	-	+	p
<i>longipetala</i>	8	-/v	-/v	±/+	±/+	-	-	±/+	±/+	-/+	p
<i>myrmecophila</i>	2	e	e	±/+	-/±	-	-	±/+	±/+	+	p
<i>oococca</i>	2	v	v	±/+	±	-/e	-	-/+	-/+	-	p
<i>pendula</i>	5	-/v	-/v	±/+	±/+	-	s	±/+	+	+	c
<i>petiolaris</i>	8	-/v/e	v/e	-/±/+	-/±/+	-/e	-	-/±/+	±/+	-/+	p
<i>ramiflora</i>	9	-/v/e	v/e	±/+	-/±	-/e	-	±/+	-/±/+	-/+	p
<i>LAE 74586</i>	1	-	-	+	+	-	-	+	+	-	p
<i>rhachiptera</i>	2	v	v/e	±/+	-	-	-	+	-/±	-/+	p
<i>rhyticarpa</i>	5	-/v	v	±/+	-/±	-	-	±/+	-/+	-	p
<i>solomonensis</i>	2	v	v	+	±	-	-	+	±	+	p
<i>vaga</i>	5	v/e	v/e	±/+	±/+	-	-	±/+	±/+	-/+	p
<i>Majidea</i>											
<i>fosteri</i>	5	v	-/v	±/+	-/±/+	-/(v)	-/(s)	+	+	+	a-s
<i>zanguebarica</i>	6	-/v	-/v	±/+	±/+	-	-	±/+	±/+	-/+	a-s
Diagnostic value of characters		L	L	L	L	L	L	L	L	L	H

Legend: ( ) = sometimes present; / = or; ± = slightly present; + = present; - = absent; \* = present in one collection only out of 8 or more collections studied; ? = character state unknown. — Diagnostic value of characters: L = low, R = restricted, H = high.

#### Columns:

1. Number of samples.
2. Distribution of hairs on adaxial surface (e = over entire surface; v = on midrib and/or venation).
3. Distribution of hairs on abaxial surface (see legend of 2).
4. Adaxial cuticle with thin areas in the loops of the undulations.
5. Abaxial cuticle with thin areas in the loops of the undulations.
6. Adaxial cuticle striate (see legend of 2).
7. Abaxial cuticle striate [s = striae in a radiating pattern around (giant) stomata].
8. Anticlinal walls of adaxial epidermis undulating.
9. Anticlinal walls of abaxial epidermis undulating.
10. Stomata present in adaxial epidermis on midrib and/or larger veins.
11. Predominant type of stomata on abaxial epidermis (a = anomocytic; c = cyclocytic; p = paracytic; s = staurocytic).

(Table 1 continued)

Column:	12	13	14	15	16	17	18	19	20	21	22	23
Species												
<i>Conchopet</i>												
<i>brac</i>	e	-	-	+	-	-	-	-	-	-	-	-
<i>mada</i>	e	-	-	+	-	-	-	-	-	-	-	-
<i>Harpullia</i>												
<i>alat</i>	v	-	-	+	-	-	-/+	+	-	-	-	-
<i>arbo</i>	v	-/c*	-/t*	+	-	-	-	-	-	-/b	-/b	-
<i>aust</i>	v	-	-	+	-	-	+	+	-	-/b	-/b	-
<i>camp</i>	v	-/d	-/t/p	-	+	-	-/+	-/+	+	b	b	b
<i>carr</i>	-/v	-/d	-/t	+	(+)	-	-/+	-	-/+	-/b	b	-
<i>caul</i>	v/(e)	-/d	-/s	+	(+)	-	-/+	(+)	-	-/b	b	-/b
<i>crus</i>	v	-	-	-	-	+	+	+	-	-	b	-
<i>cupa</i>	v	-	-	+	-	+	+	+	-/+	-/b	-/b	-
<i>frut</i>	-/v	-	-	+	-	-	+	(+)	-	-	-	-
<i>giga</i>	v	-/d/c	-/t	-	+	+	+	+	-/(+)	-	-/b	-
<i>hill</i>	-/v	-	-	+	-	-	+	(+)	-/+	-	-/b	-
<i>hirs</i>	-/v	-	-	-	+	-	+	+	-/+	-/b	b	-
<i>larg</i>	-/v	-	-	+	-	-	-/+	+	-/+	-	-/b	-
<i>lept</i>	v	c	t	-	-	+	+	-	+	-/b	b	-
<i>long</i>	v	d*/c	t*/s	+	-	-	-	-	-	b	b	-*/c
<i>myrm</i>	v/e	-	-	+	-	-	+	+	+	-	b	-
<i>ooco</i>	v	?	?	?	?	?	?	?	?	?	?	?
<i>pend</i>	v/(e)	-	-	+	-	-	-	-	-	-	-	-
<i>peti</i>	v	-	-	+	(+)	+	+	+	-	-/b	b	-
<i>rami</i>	-/v	-	-	(+)	+	-	-*/+	-*/+	-/+	-/b	b	-/b*
<i>LAE 74586</i>	e	c	t	+	-	-	-	-	(+)	-	b	-
<i>rhac</i>	-/v	-	-	-	+	-	+	+	-	-	b	-
<i>rhyt</i>	-/v	-	-	+	-	-	+	+	-	-	-	-
<i>solo</i>	e	-	-	+	-	-	+	+	+	b	b	-
<i>vaga</i>	v	-	-	+	-	-	+	+	-/+	-	-/b	-
<i>Majidea</i>												
<i>fost</i>	v/e	-	-	+	-	-	-	-	-	-	-	-
<i>zang</i>	v	-	-	+	-	-	-	-	-	-	-	-
Value of characters	L	R	R	R	R	R	L/R	L/R	L/R	L/R	L/R	R/H

*Columns (continued):*

12. Giant stomata present in abaxial epidermis (see legend of 2).
13. Hypodermis on adaxial side (c = continuous; d = discontinuous).
14. Type of hypodermis cells (t = walls thin; s = walls sclerified; p = walls sclerified combined with sclerified palisade cells).
15. Large veins embedded in mesophyll to completely transcurrent, bundle sheath extensions not sclerified.
16. Large veins transcurrent to abaxial epidermis or completely transcurrent, bundle sheath extension(s) sclerified to abaxial epidermis only.
17. Large veins completely transcurrent, bundle sheath extensions sclerified to both sides.
18. Secretory idioblasts in adaxial epidermis.
19. Secretory idioblasts in abaxial epidermis.
20. Secretory idioblasts in palisade tissue.
21. Brachysclereids in midrib (b = brachysclereids present).
22. Brachysclereids in petiolule (see legend of 21).
23. Idioblastic sclereids in mesophyll (see legend of 21; c = columnar to branched sclereids present).

## INFRA-SPECIFIC VARIATION

The infraspecific variability may be due to genetical variability or ecological factors, as mentioned by Baas (1975).

In the case of *Majidea zanguebarica* leaf anatomical characters do not vary between the two subspecies. In the case of *H. petiolaris* the two subspecies differ in the following leaf anatomical character: subsp. *petiolaris* is densely hairy over the entire surface on both sides of the leaflets, in subsp. *moluccana* the indumentum is confined to the venation only. Between *H. petiolaris* subsp. *moluccana* var. *moluccana* and var. *decidens* no differences in leaf anatomy could be found.

The characters used in the generic descriptions and given in Table 1 are not all of the same diagnostic and systematic value. The diagnostic value of the characters on the species level is indicated at the bottom of Table 1 (L = low; R = restricted; H = high). In the present study the diagnostic value of a character is defined as the degree in which the character states are constant at the species level. Some characters may be very variable below the species level and have therefore a low value, e.g., undulations of the epidermal anticlinal walls, thin areas of the cuticle in the loops of the undulations, and striation of the cuticle, as already mentioned by Van Staveren & Baas (1973), Den Hartog-van ter Tholen & Baas (1978), Van Welzen (1989), and others. Another problem, mentioned by Den Hartog-van ter Tholen & Baas (1978), are the difficulties in defining different states of gradually varying characters unambiguously. For this reason other leaf epidermal characters such as pitting of the cuticular flanges and distinctiveness of polar cuticular T-pieces, have been left out of Table 1.

Within a species the indumentum can vary in density and distribution of the hairs. The occurrence of hair types is constant within a genus (see 'Generic Delimitation', below).

The predominant stomatal type in a species is constant (see 'Interspecific Variation', below). Giant or water stomata can vary within a species from absent to present along the midrib and larger veins on both surfaces. On the abaxial side giant stomata can also vary in their distribution, they are either confined to the midrib and larger veins or they are also scattered in the areolae between normal stomata.

The lamina thickness can vary considerably within a species and has therefore been left out of Table 1.

The hypodermis can be absent or present within a species. In *H. carrii* the hypodermis varies from absent to an interrupted layer of thin-walled cells, and in *H. giganteacapsula* from absent to an interrupted or even continuous layer of thin-walled cells. In *H. longipetala* one sample (NGF 25679) has a discontinuous hypodermis consisting of thin-walled cells, the other 6 samples have a continuous hypodermis with sclerified cells. In two of the samples of *H. cauliflora* a hypodermis is present as a discontinuous layer of sclerified cells, in the three other samples a hypodermis is absent. In *H. camptoneura* the hypodermis is absent or present as a discontinuous layer of thin-walled cells or of sclerified cells combined with sclerified palisade cells. In *H. arborea* a hypodermis of thin-walled cells is present in one of the 21 samples only (van Balgooy 5053). In a doubtful collection of *H. ramiflora* (LAE 74586) a hypodermis is present as a continuous layer of thin-walled cells. In the 9 other sam-

ples of *H. ramiflora* a hypodermis is absent. Because it concerns a doubtful collection of *H. ramiflora* this collection is listed separately in Table 1.

The number of palisade layers can vary from 1 to 3, the cells can be square to long erect and the spongy tissue can be rather loose to rather compact within one species.

The veins can vary, usually dependent on their size, between embedded in the mesophyll (smaller veins) to vertically transcurrent (larger veins) within a species. Because of difficulties in defining discrete states in this gradually varying character, the above mentioned variation was combined in Table 1. The sclerification of the bundle sheath extensions varies between absent to sclerified in the abaxial part only in *H. carrii*, *H. cauliflora*, and *H. ramiflora*. In *H. giganteacapsula* the sclerification of the bundle sheath extensions varies between sclerified in the abaxial part only to sclerified in both parts. In *H. petiolaris* the bundle sheath extensions are sclerified to both sides or sometimes to the abaxial epidermis only, in one collection (*NGF 41023*) sclerification is absent. In *H. cupanioides* the bundle sheath extensions are not sclerified, except for one collection (*de Wilde 1199*) in which the extensions are sclerified on both sides.

Crystals are always present and vary mainly in frequency; therefore they have been left out of Table 1. Most infraspecific variation occurs subepidermally in the parenchyma; crystals can vary from absent to frequently present, the crystal type is less variable (see 'Interspecific Variation', below).

Within a species the frequency of secretory idioblasts varies usually from few to abundant, only in *H. carrii* and *H. cauliflora* secretory idioblasts vary between absent and fairly common. In some species secretory idioblasts are always absent (see 'Interspecific Variation', below).

Brachysclereids in the ground tissue and in the pith of midrib and petiole can vary within a species from absent to abundant. Columnar to branched sclereids in the mesophyll are restricted to *H. longipetala* in 6 collections; in one collection (*NGF 25679*) the sclereids are absent in the mesophyll. In this collection the hypodermis is also deviating. Brachysclereids in the mesophyll vary from absent to commonly present in *H. cauliflora* and are present in *H. ramiflora* in one collection only (*van Royen & Sleumer 7092*). In *H. camptoneura* brachysclereids in the mesophyll are always present.

In the present study the infraspecific variation could not be correlated with ecological data, as the information from the herbarium labels was insufficient for this purpose. Infraspecific variation of certain features, e.g., the hypodermis or the presence of idioblastic sclereids, might be due to a difference in exposure to light (sun or shade leaves), which cannot be checked in herbarium specimens.

It must be taken into account that the number of collections studied of a certain species might have influenced the infraspecific variation present in this study. It is notable that in all species studied more extensively, deviating character states occur (marked \* in Table 1). However, some less extensively studied species such as *H. camptoneura*, *H. carrii*, *H. giganteacapsula* (all 4 collections), and *H. cauliflora* (5 collections) also show considerable infraspecific variation.

In the widespread species a correlation between geographical distribution and infraspecific variation on leaf anatomical characters seems absent.

## INTERSPECIFIC VARIATION

This chapter gives a discussion of the leaf anatomical characters that are  $\pm$  constant within a species and have, therefore, a restricted to high diagnostic value on the species level, indicated at the bottom of Table 1, and a potential systematic value.

The stomatal type is the only one of the leaf epidermal characters constant within the species and therefore has a high diagnostic value. Two main stomatal types can be recognized in the genus *Harpullia*; predominantly cyclocytic (to stauro- or tetracytic) in *H. arborea* and *H. pendula* and predominantly paracytic (to anomo-, tetra-, stauro-, or cyclocytic) in all other species.

The hypodermis is always present in *H. leptococca* (5 samples) as a continuous layer of thin-walled cells. In other species of *Harpullia* the hypodermis always shows infraspecific variation, therefore the hypodermis is of restricted diagnostic value and possibly only of some systematic value.

In *H. camptoneura*, *H. hirsuta*, and *H. rhachiptera* the bundle sheath extensions are sclerified in the abaxial part only in all collections studied, in *H. crustacea* and *H. leptococca* the extensions are sclerified to both parts in all samples. As the sclerification of the bundle sheaths shows infraspecific variation in several other species, this character has a restricted diagnostic value.

In *H. leptococca* the sclerifications of the bundle sheath extensions, the presence of a hypodermis, and the straight to curved anticlinal walls of the unspecialized epidermal cells might be correlated with the preference for dry habitats; coastal forest, dry forest, and savanna-gallery forest (see Baas, 1975; Wilkinson, 1979). All other species of *Harpullia* (also) occur in more humid areas, such as primary or riverine forest. In these species an obvious correlation between the habitat and certain leaf anatomical characters could not be found.

The type of crystals subepidermally present in the parenchyma shows some interspecific variation of rather restricted value, either predominantly druses as in most collections of *H. arborea* and *H. petiolaris*, or exclusively rhomboidal as in *H. longipetala*.

Secretory idioblasts are always absent in all collections studied of *H. arborea*, *H. pendula*, *H. longipetala*, and the outgroups *Conchopetalum* and *Majidea*. Idioblastic sclereids are always absent (also in midrib and petiolule) in *H. alata*, *H. frutescens*, *H. pendula*, *H. rhyticarpa*, and the outgroups *Conchopetalum* and *Majidea*. In this context absence only means absent in the sections studied; secretory idioblasts and idioblastic sclereids may still be present in other parts of the leaflets of the same specimen. Therefore, the diagnostic and systematic value of the absence of leaf anatomical characters must be considered with some caution.

In *H. camptoneura* brachysclereids are present in the mesophyll in all four collections studied. Because other species show infraspecific variation for this character, the diagnostic value has some restrictions. Columnar to branched sclereids are autapomorphic for *H. longipetala*, therefore the systematic value is low, but the diagnostic value is high, despite absence in one collection.

## GENERIC DELIMITATION

The genus *Harpullia* is leaf anatomically fairly homogeneous; a dorsiventral mesophyll with a few layers of palisade parenchyma and a spongy tissue with round to flat rectangular cells, epidermal mucilage cells often present, a simple closed collateral vascular system, paracytic stomata present in most species, stellate hair tufts and solitary unicellular hairs usually present, glandular hairs and papillae absent. Characters which are variously present within *Harpullia* and are absent in the outgroups are secretory idioblasts, idioblastic sclereids, and a hypodermis.

According to Solereder (1899) and Metcalfe & Chalk (1950) paracytic stomata are a unique character for both genera *Harpullia* and *Conchopetalum*. However, in the present study paracytic stomata were found in subgenus *Harpullia* only. The other subgenus and genera have stomatal types generally found in the Sapindaceae. The stomatal type in *Conchopetalum* is not paracytic but cyclo-, stauro-, or anisocytic. Within *Harpullia* subgenus *Otonychium* has predominantly cyclocytic stomata, and the genus *Majidea* has anomo- to staurocytic stomata. In the recent literature on leaf anatomy of the Sapindaceae anomocytic stomata are recorded for *Sapindus* (Farooqui & Venkatasubramanian, 1986), anomo- and anisocytic stomata for *Serjania* (Valente et al., 1984), *Paullinia*, and *Thinouia* (Valente et al., 1984), and cyclocytic stomata for *Guioa* (Van Welzen, 1989), *Cupaniopsis* (Adema, 1991), *Cnesmocarpon*, *Jagera*, and *Trigonachras* (Adema & Van der Ham, 1993).

The indumentum of both *Harpullia* and *Majidea* consists of stellate tufts of unicellular hairs (Fig. 14) together with solitary unicellular hairs; in *Conchopetalum* stellate hair tufts are absent. The leaves of *Conchopetalum* are glabrous, only on the axes of the inflorescences an indumentum consisting of short solitary unicellular hairs is found. Glandular hairs and papillae, which are very common throughout the family, are absent in all three genera studied.

Next to numerous other characters Solereder (1899) and Metcalfe & Chalk (1950) mentioned a parenchymatous hypodermis and crystals particularly frequent in the epidermis for *Conchopetalum*; these were not observed in the specimens studied.

The differences between *Harpullia* and the outgroups *Majidea* and *Conchopetalum* are summarized in Table 2.

Table 2. Differences between *Harpullia* and outgroups.  
(See general legend of Table 1 for explanation of /, +, and -)

Genus	Column:	1	2	3	4	5
<i>Conchopetalum</i>		un*	c	-	-	-
<i>Harpullia</i>		un / st	p / c	-/+	-/+	-/+
<i>Majidea</i>		un / st	a to s	-	-	-

**Columns:**

1. Type of hairs (un = unicellular hairs; st = stellate hair tufts; \* = on axes of inflorescences only, leaves glabrous).
2. Predominant type of stomata (a = anomocytic; c = cyclocytic; p = paracytic; s = staurocytic).
3. Hypodermis present or absent.
4. Secretory idioblasts present or absent.
5. Idioblastic sclereids present or absent.

## GENERAL CONCLUSIONS

On the basis of leaf anatomy the subgenus *Otonychnium* within the genus *Harpullia*, comprising the species *H. arborea* and *H. pendula*, can be distinguished by a combination of the following character states: stomatal type predominantly cyclocytic and secretory idioblasts absent. The groups of closely related species within the other subgenus *Harpullia*, as mentioned by Leenhouts (1985), cannot be recognized, neither can new groups be defined because mutually correlating characters are lacking.

One of the aims of this leaf anatomical study is to obtain additional characters for future phylogenetic analysis in addition to macromorphology and pollen. Leaf anatomical characters that may have phylogenetic significance can be found among the characters with a restricted to high diagnostic value mentioned in 'Interspecific Variation'. These characters are: the stomatal type, presence or absence and type of hypodermis, sclerification of the bundle sheath extensions, presence or absence of secretory idioblasts in the epidermis and the palisade tissue, and presence or absence and type of idioblastic sclereids in the mesophyll. Only after a phylogenetic analysis the 'true' systematic value of the characters can be determined, characters with a high systematic value will appear as apomorphies for infrageneric groupings.

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