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AN ATTEMPT TOWARDS A NATURAL SYSTEM OF HARPULLIA (SAPINDACEAE)

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SUMMARY

Starting point of the present study on *Harpullia* was the taxonomic revision of that genus by Leenhouts & Vente (Blumea 28, 1982, 1–51). The system to which that revision led is primarily intuitive and accordingly subjective. The intention of the present paper is to give a more natural system based upon more objective criteria and with the use of more scientific methods.

The fundamentals of a systematic study are species and characters (see chapter 2). The species are those presented in the taxonomic revision; the characters used are tabulated in the form of a synoptic key (see chapter 2 B).

In chapter 3 a survey is given of two intuitive systems, the one by Leenhouts & Vente and the preceding one by Radlkofer (1933-34).

The first approach was towards a phenetic system (chapter 4). The method used is a kind of simplified numerical taxonomy with weighted characters. *Weighting of characters is based upon the supposition that a character which is constant in most of the taxa concerned is heavier than one that varies in several taxa.* The phenetic system to which this led is expressed in figure 1 and given at the end of chapter 4.

In chapter 5 a phylogenetic approach is given. Phylogenetic valuation of characters, primarily with the use of out-group analysis, secondary of correlation, is discussed (5 A). All species got a phylogenetic formula, giving the primitive or derived states of the characters used, and a phylogenetic value expressing the degree of primitiveness or derivative (5 B). The method used is a simplified Hennigian cladistics, resulting in a kind of Wagner tree (fig. 2).

In chapter 6A a comparison is made between the intuitive systems, mainly the one by Leenhouts & Vente, the phenetic and the phylogenetic system developed here, and the pollen morphological phylogenetic system given by J. Muller (Blumea 31, 1985, 161–218, this issue). As a whole there appears to be a good agreement in many points between the different systems. The main exceptions are *Harpullia cupanioides* and still more so *H. hillii* because of their variability, *H. longipetala* that is macromorphologically rather primitive but palynologically advanced, and *H. rhachiptera* with a very aberrant pollen type and an uncertain position in the phylogenetic system.

A translation of phylogenetic systematics into formal taxonomy has been tried in chapter 6 B. It appeared difficult to express the branching of the phylogenetic scheme in the hierarchy of taxonomy, mainly because taxa should be delimited by clear boundaries defined by good, preferably conspicuous characters. The subdivision of *Harpullia* into two subgenera, *Otonychium*, incl. *H. arborea* and *H. pendula*, and *Harpullia* with the further 24 species is indisputable. More hesitatingly, a further division of subg. *Harpullia* into two sections, *Harpulliastrum* with only *H. austro-caledonica* and *Harpullia* with the other species is accepted. For different reasons it appeared impossible or undesirable to split off some other at first sight well circumscribed groups, however.

1. INTRODUCTION

The present study has to be considered in connection with two other papers, viz. 'A taxonomic revision of *Harpullia* (Sapindaceae)' by P. W. Leenhouts & Magda Vente (Blumea 28, 1982, 1–51) and 'Pollen morphology and evolution of the genus *Harpullia* (Sapindaceae-Harpullieae)' by J. Muller (Blumea 31, 1985, 161–218, this issue). Its intention is threefold:

1. To provide a phenetic and a phylogenetic system of *Harpullia*, both more precise than the mainly intuitive and accordingly subjective system given by Leenhouts & Vente.
2. To compare mutually the intuitive systems of Radlkofer (in Engler, Pflanzenr. 98, 1933-34, 1433–1462) and of Leenhouts & Vente, the phenetic and phylogenetic systems mentioned above, and the pollen morphological system constructed by J. Muller.
3. To see what influence these different systems may have on the taxonomy of *Harpullia.*

2. SPECIES AND CHARACTERS

In this chapter the 26 species recognised in the revision by Leenhouts & Vente and the 13 main characters on which these are based are enumerated, these being the fundamentals for the different systems.

A. The species

The following tabulation gives in the first column the specific epithets of the 26 species recognised by Leenhouts & Vente, alphabetically arranged. Bold-typed are the three-letter abbreviations used in keys and schemes throughout this paper. The incompletely known species are marked with an asterisk. In the second and third column the phylogenetic formula and phylogenetic value respectively are given (for explanation, see chapter 5 B).

alata	A. b. c. D. e. f. G.	3
arborea	a. b-B. c-C. d-D. e-E. F. g.	1–5
austro-caledonica	a. b-B. c. d. e. f. G.	1–2
*camptoneura	a. b. C. D. E. f. G.	4
carrii	a. b. C. d-D. E. F. G.	4–5
*cauliflora	a. B. C. D. E. f. G.	5
crustacea	a. b. C. D. E. f. G.	4
cupanioides	a. b. C. d-D. (E)-E. f. G.	2½–4
frutescens	A. b. c. D. e. f. G.	3
*giganteacapsula	a. b. c. D. e. f. G.	2
hillii	a. b. C. d-D. e-E. f-F. G.	2–5
*hirsuta	a. b. C. D. E.	3 + ??
largifolia	a. B. C. D. E. f. G.	5

leptococca	a. b. c-C. D. (E)-E. F. G.	3½–5
longipetala	a. B. c. D. e-(E). f. G.	3–3½
myrmecophila	a. B. C. D. E. f. G.	5
*oococca	a. D. E. F. G.	4 + ??
*peekeliana	a. B. C.	2 + ????
pendula	a. b. c. d-D. (E)-E. f-F. g.	½–3
petiolaris	a. B. C. D. E. f. G.	5
ramiflora	a. B. C. D. E. f. G.	5
rhachiptera	A. b. C. D. E. f. G.	5
rhyticarpa	A. b-B. C. D. e. f-F. G.	4–6
*solomonensis	a. B. C. D. E. f. G.	5
*species nova	a. b. c. d. E.	1 + ??
*vaga	a. b. C. D. (E). f. G.	3½

B. The characters

The phenetic system of chapter 4 is based upon 12 characters, the phylogenetic one of chapter 5 on 7, all but one of which overlapping. For the sake of surveyability, the distribution of the different states of these 13 characters over the species has been given in a synoptic key. Under each lead, those species in which the character concerned is constant are printed in bold type, if the character varies the species is printed in meagre type. A name in brackets indicates that the character state concerned is exceptional for that taxon; a question mark indicates that the character is unknown.

1a. Vegetative parts more or less hairy: **ala. arb. aus. cam. car.** cau. **cru.** cup. **fru. gig.** hil. **hir. lar. lep. myr. ooc. pen. pet.** ram. **rha. rhy. spn. vag.**
  b. Vegetative parts glabrous or nearly so but for the buds: cau. cup. hil. **lon. pee.** ram. **sol.**
2a. Leaf rachis (and mostly also petiole) winged: **ala. fru. rha. rhy.**
  b. Leaf rachis and petiole not winged: **arb. aus. cam. car. cau. cru. cup. gig. hil. hir. lar. lep. lon. myr. ooc. pee. pen. pet. ram. sol. spn. vag.**
3a. Margin of leaflets undulate, dentate, or lobed: **ala.**
  b. Margin of leaflets entire: **arb. aus. cam. car. cau. cru. cup. fru. gig. hil. hir. lar. lep. lon. myr. ooc. pee. pen. pet. ram. rha. rhy. sol. spn. vag.**
4a. Inflorescences axillary to terminal: **ala.** arb. aus. **cam. car. cru. cup. fru. gig. hil. hir. lep.** ooc ?. **pen. rha.** rhy. **spn. vag.**
  b. Inflorescences at least finally rami- or cauliflorous: arb. aus. **cau. lar. lon. myr.** ooc ?. **pee. pet. ram.** (rhy). sol.
5a. Sepals in fruit at least partly deciduous: **arb.** gig. hir ?. **lar.** pee ?. **pen.** pet. spn ?.
  b. Sepals in fruit all persistent: **ala. aus. cam. car. cau. cru. cup. fru.** gig. **hil.** hir ?. **lep. lon. myr. ooc.** pee ?. pet. **ram. rha. rhy. sol.** spn ?. **vag.**
6a. Petals: claw and auricles present: **arb.** gig ?. ooc ?. **pen.** sol ?.
  b. Petals: claw and auricles absent: **ala. aus. cam. car. cau. cru. cup. fru.** gig ?. **hil. hir. lar. lep. lon. myr.** ooc ?. **pee. pet. ram. rha. rhy.** sol ?. **spn. vag.**

7 a. Disk glabrous: aus. **fru. pen.** rhy.
  b. Disk hairy: **ala. arb.** aus. **cam. car. cau. cru. cup. gig. hil. hir. lar. lep. lon. myr. ooc. pee. pet. ram. rha.** rhy. **sol. spn. vag.**
8 a. Stamens 5 (or 6): (arb). **cam. car. cau. cru. cup. hil. hir. lar.** lep. **myr.** ooc ?. **pee. pet. ram. rha. rhy. sol. vag.**
  b. Stamens (7 or) 8: **ala.** arb. **aus. fru. gig.** (lep). **lon.** ooc ?. **pen. spn.**
9 a. Ovary, number of locules 2: **ala.** arb. **cam.** car. **cau. cru.** cup. **fru. gig.** hil. **hir. lar. lep. lon. myr. ooc.** pee ?. pen. **pet. ram. rha. rhy. sol. vag.**
  b. Ovary, number of locules 3 (exceptionally 4): (arb). **aus.** car. (cup). (hil). pee ?. (pen). **spn.**
10 a. Ovules 1 per locule: arb. **cam. car. cau. cru.** cup. hil. **hir.** lar. lep. **myr. ooc.** pee ?. pen. **pet. ram. rha. sol. spn.**
  b. Ovules 1 in one locule, 2 in the other: arb. (cup). hil. (lep). (lon). pee?. pen. **vag.**
  c. Ovules 2 per locule: **ala.** arb. **aus. fru. gig.** hil. lon. pee ?. **rhy.**
11 a. Style length up to 10(–12) mm: **ala. aus.** cam ?. **car.** cau ?. **cru. cup. fru. gig. hil.** hir ?. **lar. lep. lon.** myr ?. **ooc.** pee ?. **pen. pet. ram. rha. rhy.** sol ?. **spn.** vag ?.
  b. Style length more than 12 mm: **arb.** cam ?. cau ?. hir ?. myr ?. pee ?. sol ?. vag ?.
12 a. Fruit lobes more or less erect, axis long: **ala. aus. cam. cau. cru. cup. fru. gig.** hil. hir ?. **lar. lon. myr.** pee ?. pen. **pet. ram. rha.** rhy. **sol.** spn. ?. **vag.**
  b. Fruit lobes spreading, axis short: **arb. car.** hil. hir ?. **lep. ooc.** pee ?. pen. (rhy). spn ?.
13 a. Aril only a sarcotestal ring around the hilum: **arb.** hir ?. pee ?. **pen.** spn ?.
  b. Aril partly free, enveloping (nearly) the whole seed: **ala. aus. cam. car. cau. cru. cup. fru. gig. hil.** hir?. **lar. lep. lon. myr. ooc.** pee ?. **pet. ram. rha. rhy. sol.** spn ?. **vag.**

3. THE INTUITIVE SYSTEMS

There are two intuitive systems of *Harpullia* worth mentioning, viz. the one by Radlkofer and the more recent one by Leenhouts & Vente, both of which will be cited here in full. The delimitation of the species in the two revisions differs in many cases. Accordingly, the species of Radlkofer's system had to be adapted to the species concept of Leenhouts & Vente; the species mentioned are those accepted by us, whereas the names used by Radlkofer are added in brackets.

A. The system of Radlkofer (1933-34)

subg. 1. *Euharpullia*
  sect. 1. *Thanatophora*
    H. camptoneura (camptoneura)
    H. cauliflora (cauliflora)
    H. crustacea (crustacea)

H. cupanioides (thanatophora, macrocalyx, fraxinifolia, fruticosa, cupanioides, leichhardtii, obscura)
H. hillii (hillii)
H. hirsuta (hirsuta)
H. largifolia (largifolia)
H. leptococca (leptococca)
H. oococca (oococca)
H. petiolaris (petiolaris)
H. ramiflora (ramiflora, angustifolia, reticulata, aeruginosa, weinlandii)
H. rhachiptera (rhachiptera)
sect. 2. *Harpulliastrum*
H. alata (alata)
H. austro-caledonica (austro-caledonica)
H. frutescens (holoptera, frutescens)
subg. 2. *Otonychium*
sect. 3. *Otonychidium*
H. arborea (mellea, pedicellaris, divaricata, sphaeroloba, arborea p.p.)
H. pendula (pendula)
sect. 4. *Euotonychium*
H. arborea (arborea p.p., glanduligera)
(sect. 5, *Dysotonychium*, with one species, viz. *H. parviflora*, does not belong here but is a synonym of *Sinoradlkofera*.)

B. The system of Leenhouts & Vente (1982)

Leenhouts & Vente (1982: 1) gave a provisional arrangement into rather loosely to clearly coherent groups, as follows:

'The genus is ...... divided into two subgenera, namely a supposedly more primitive one, *Otonychium*, with only two species, *H. pendula* and *H. arborea*, and the other one, *Harpullia*, with the further 24 species, ... The first rather loose group of supposedly relatively primitive species encompasses *H. austro-caledonica, H. giganteacapsula, H. longipetala*, and *H. species nova.* Next comes a mainly Australian group of species characterised by winged petioles and leaf rachises, viz. *H. frutescens, H. alata, H. rhyticarpa,* and probably the New Guinea *H. rhachiptera*. The likewise Australian species *H. hillii* seems to take a position in between some groups ...... Included in the third group are *H. cupanioides, H. vaga, H. crustacea, H. camptoneura*, and *H. hirsuta.* To the fourth group belong three New Guinea species characterised by deeply lobed fruits, viz. *H. leptococca, H. carrii*, and *H. oococca.* The fifth and last group, considered to be the most derived one, is characterised by rami- or cauliflory. This group encompasses 6 or 7 mutually closely allied species, viz. *H. solomonensis, H. ramiflora, H. myrmecophila, H. cauliflora, H. petiolaris, H. largifolia,* and probably *H. peekeliana.*'

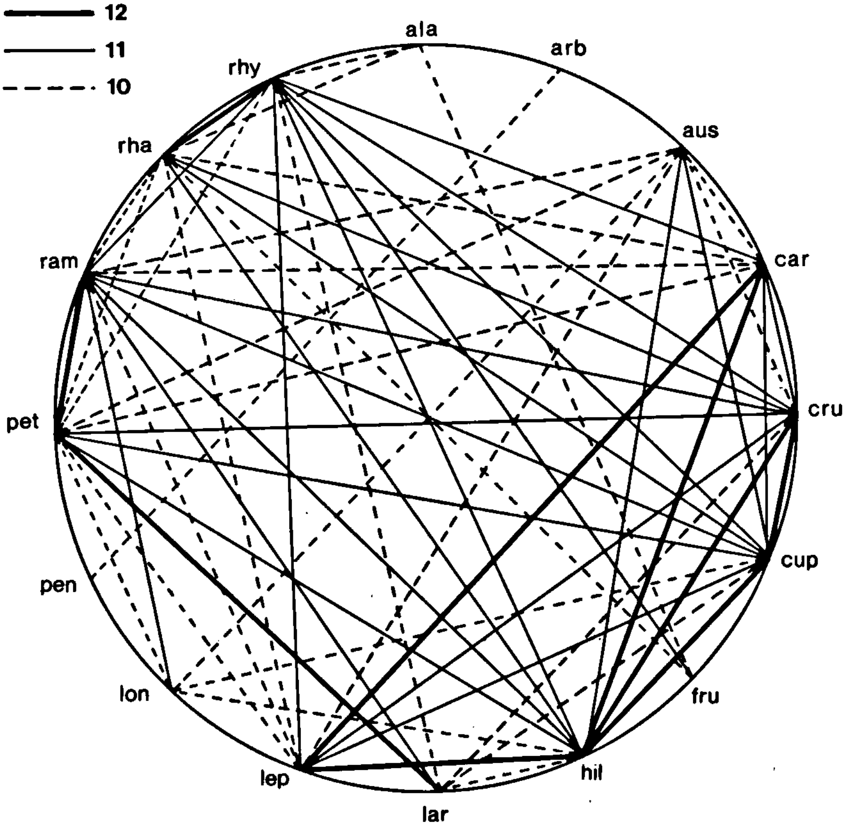

Fig. 1. The main connections between the sufficiently known species expressed in numbers of 'heavy' characters shared. Drawn by Mr. M. Groeneveld.

4. A PHENETIC APPROACH

Contrary to the mainly subjective way in which the original intuitive system was achieved it is tried here to define the connections between the species in a more objective way. For this purpose a simple numerical comparison has been used based upon the characters 1–9 and 11–13 of the synopsis of chapter 2.

The main connections between those 16 species of which all 12 characters used are known are represented in figure 1. Examination of this figure leads to the following comments:

1. Like in the intuitive systems as a first group the pair *H. arborea–pendula* is clearly differentiated from the rest of the genus.
2. The further species can be arranged into three groups, but these are mutually connected in many points. These groups are: 2) *H. alata, frutescens, rhyticarpa*, and *rha-*

chiptera; 3) *H. carrii, crustacea, cupanioides, hillii, leptococca*, and more loosely, mainly connected via *H. cupanioides* and *hillii, H. austro-caledonica*; 4) *H. largifolia, petiolaris, ramiflora*, with more loosely *H. longipetala*, which has also connections with the triangle formed by the species *H. austro-caledonica, cupanioides*, and *hillii*.

On the same numerical basis the ten incompletely known species can be added to these four groups, as follows:

H. camptoneura comes near to *H. crustacea, cupanioides*, and *hillii*, hence to group 3.

H. cauliflora comes nearest to *H. petiolaris* and *ramiflora*, hence to group 4.

H. giganteacapsula comes nearest to *H. austro-caledonica, crustacea*, and *cupanioides*, hence to group 3.

H. hirsuta comes nearest to *H. camptoneura, carrii, crustacea, cupanioides, hillii*, and *leptococca*, hence falls completely within group 3.

H. myrmecophila comes nearest to *H. cauliflora, petiolaris*, and *ramiflora*, hence to group 4.

H. oococca comes nearest to *H. carrii, hillii*, and *leptococca*, hence to group 3.

H. peekeliana comes nearest to *H. cauliflora* and *ramiflora*, hence to group 4.

H. solomonensis comes nearest to *H. cauliflora*, hence to group 4, with on the second place some species of group 3.

H. species nova comes nearest to *H. austro-caledonica*, hence to group 3.

H. vaga comes nearest to *H. camptoneura, crustacea, cupanioides*, and *hillii*, hence to group 3.

5. A PHYLOGENETIC APPROACH

A. The characters

The choice of characters that can be used in phylogenetic speculations will always be arbitrary to some degree, can hardly be done in a strictly objective way. Still, I am of the opinion that one or two out of the several methods used seem theoretically sound and accordingly deserve more confidence. A critical review of several methods in more or less common use has been given by P.F. Stevens (Evolutionary polarity of character states. Annual Rev. Ecol. Syst. 11, 1980, 333–358). In the present case I used in the first place out-group analysis, the out-group being mostly the tribe Harpullieae (11 genera), sometimes the Sapindaceae as a whole; secondly in a few cases correlation (see the discussion on the position of the inflorescence); and in the third place in some cases Hennig's thesis that a character state scattered over several not distinctly closely allied taxa must be accepted as primitive, one restricted to some closely allied taxa only as derived.

Making use of these methods, five out of the 13 characters included in the synopsis of chapter 2 could with reasonable certainty be used phylogenetically. These characters are: couplet 8 (from 8 to 5 stamens), 9 (ovary from 3-merous to 2-merous), 10 (from 2 ovules per locule to 1), 12 (harmonious development of the fruit is considered primitive, growing of the lobes only whereas the axis remains short derived), and 13 (presence of a small sarcotesta only should be primitive, of a complex aril consisting of the sarcotesta and a loose arilloid enveloping the whole seed is accepted as derived).

As to the further characters it seems beyond doubt that the numbers 1, 7, and 11 cannot simply be valued phylogenetically.

As to character 2, petiole and leaf rachis winged or not, it is not self-evident what state is primitive, what derived. Arguments favouring the opinion that a winged petiole and leaf rachis are primitive are: 1) pollen morphologically at least *H. alata, frutescens,* and *rhyticarpa* appear relatively primitive (*H. rhachiptera*, however, has a very aberrant pollen type); 2) the occurrence in several genera scattered throughout the family (however, this could also mean that this is a relatively unstable character, developing parallel and fixed only late in ontogeny). Counterarguments favouring a winged petiole and rachis as derived are: 1) this character state is restricted to a single phenetic group of species; 2) these species are macromorphologically moderately (*H. alata* and *frutescens*; phylogenetic value without this character 2) to distinctly (*H. rhyticarpa*; phylogenetic value 3–4) or even highly (*H. rhachiptera*; phylogenetic value 4) derived. (For 'phylogenetic value' see part C of this chapter.) Summarising, I have the impression that the argumentation in favour of a winged petiole and rachis being derived is somewhat more convincing. Accordingly, I have accepted it as such in the construction of figure 2. However, I have also worked out the opposite conclusion; this appeared to lead to one difference only: *H. rhachiptera* shifted to the group of *H. camptoneura* and *crustacea.*

Character state 3 a, leaflets incised, occurs only in *H. alata.* Following Hennig this should mean that it is derived. This is in contrast to the relatively primitive pollen type. As it regards one species only and has no influence on the structure of the phylogenetic scheme it can better not be used.

Character 4, the position of the inflorescence, might be of phylogenetic value, but it is not reasonably self-evident what state is primitive, what derived. I have tried to solve this problem in two ways, both by looking for correlation between different positions of the inflorescence and some phylogenetically probably reliable characters. The first table is restricted to *Harpullia.* The species are divided into two groups, those with exclusively axillary inflorescences versus at least partly rami- or cauliflorous. Under both groups the percentages of correlation are given with the derived states of the five phylogenetically most reliable characters.

	axillary s. s.	*at least partly rami- or cauliflorous*
Stamens 5 or 6	67%	67%
Ovary 2-celled	77%	78%
Ovules 1 per locule	43%	67%
Fruit lobes spreading	17%	11%
Arilloid present	92%	89%
Totals	296	312

This comparison leads to the conclusion that rami- and/or cauliflory seems slightly more derived than exclusively axillary inflorescences. However, only the third character gives a clear indication in that direction, and this is even partly neutralised by the 4th and the 5th character.

This conclusion is strengthened, however, by the results of a second trial, which is based upon a former study in which all 111 sufficiently known genera of the Sapindaceae were included. This time, the genera were divided into three groups: exclusively terminal; axillary and sometimes also rami- or cauliflorous, and exclusively rami- or cauliflorous. For each of these three groups the percentage of correlation with the primitive states of the seven phylogenetically most reliable flower characters was calculated*.

	terminal	*axillary*	*rami- or cauliflorous*
Flowers actinomorphic	75%	76.5%	40%
Calyx 5-merous	94%	94%	100%
Sepals free	60%	42%	30%
Petals 5	42%	50%	33%
No petalar scale	36%	30%	33%
No crest to the scale	10%	58%	33%
Pistil 3-merous	77%	72%	63%
+	394	422.5	332

This second comparison leads to the conclusion that in the Sapindaceae as a whole rami- and cauliflory are clearly derived characters. As this is in accordance with the results gained from *Harpullia* alone and strengthens it, it seems warranted to use the inflorescence character in the phylogenetic discussion.

The phylogenetic evaluation of the characters 5 and 6 is not clear. The character state 5 a (sepals in fruit at least partly deciduous) occurs mainly, 6 a (petals with claw and auricles) exclusively in *H. arborea* and *pendula*. Within *Harpullia*, these two species take a rather isolated position and are among the most primitive (see figure 2). Accordingly, correlation would lead to the conclusion that these character states are primitive. According to a more Hennigian argumentation, however, the same facts, character states (nearly) restricted to a pair of mutually distinctly allied and within the genus rather isolated species would lead to the conclusion that they are derived.

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* A direct mutual comparison of the two tables is impossible because of some in itself unessential differences. These differences were partly for practical reasons, partly they were caused by the fact that the second table was made several years ago and could not easily be reconstructed. The main difference is that in the first table *derived*, in the second *primitive* character states are the basis of comparison. Furthermore, 'axillary' stands in the first table for exclusively, in the second for at least partly axillary. Accordingly, the last column of the first table regards 'at least partly rami- or cauliflorous', of the second table 'exclusively rami- and/or cauliflorous' ('terminal' is important among the genera of the Sapindaceae, but does not play a part in *Harpullia*). The really important point, the correlation of the position of the inflorescence with some characters that appear phylogenetically reliable, is as well served by the one table as by the other.

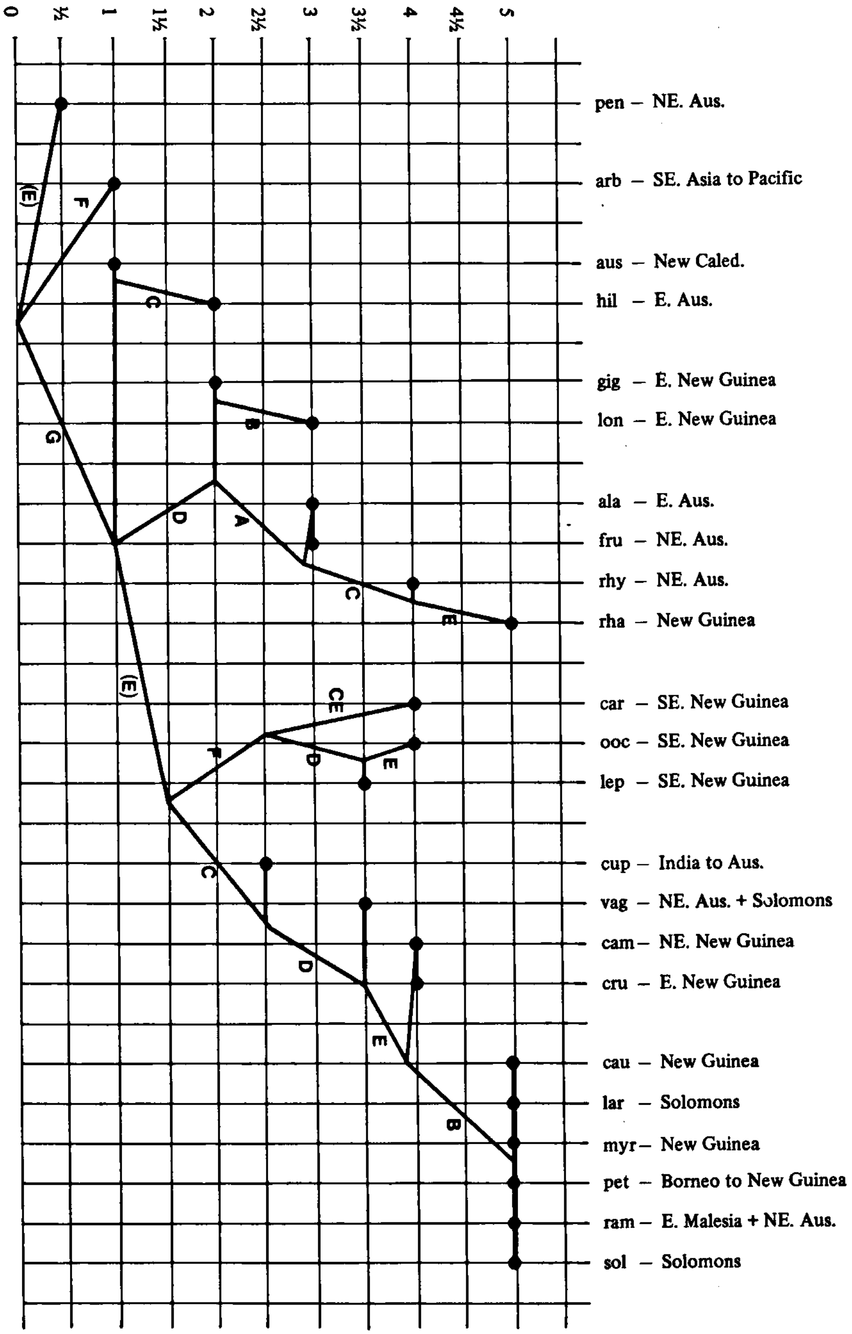

Fig. 2. Phylogenetic scheme. At left the phylogenetic value is given; the capitals along the lines represent the derived character states added. Executed by Mr. M. Groeneveld.

If we do not restrict our outgroup analysis to the genus *Harpullia*, however, but draw the whole family Sapindaceae into the comparison it appears that at least clawed and auricled petals occur in many genera throughout the family. This might lead to the conclusion that this is a primitive character state, but parallel development, e.g. in adaptation to some pollination syndrome seems as well possible. With conclusions so much in conflict it seems unwarranted to pass judgment on the phylogenetic value of these characters.

B. The methods

The final intention of the present study is the construction of a phylogenetic scheme. The way of construction of that scheme mainly follows W.H. Wagner Jr (see his paper 'Origin and Philosophy of the Groundplan-divergence Method of Cladistics' in Systematic Botany 5, 1980, 173–193), mixed up with some of Hennig's ideas and methods.

The building stones of the scheme are the species and their respective characters. In order to make these building stones easier to handle all species got a phylogenetic formula, expressing the important character states, and a phylogenetic value.

The *phylogenetic formula* is composed of the letters A to G incl., each representing one of the characters that could be interpreted phylogenetically. A character present in the primitive state is indicated with a lower case letter, if in the most derived state it is indicated with a capital; a character present in a state in between is represented by a capital in brackets; variation of a character is indicated by two letters connected by a hyphen. The letters stand for the following character states:

a = leaf rachis and petiole not winged
A = leaf rachis and mostly also petiole winged
b = inflorescences axillary to terminal
B = inflorescences at least finally rami- or cauliflorous
c = stamens 7 or 8
C = stamens 5 or 6
d = ovary with 3 or 4 locules
D = ovary with 2 locules
e = 2 ovules per locule
(E) = locules partly with 1, partly with 2 ovules
E = 1 ovule per locule
f = fruit axis long, fruit lobes more or less erect
F = fruit axis short, fruit lobes spreading
g = aril restricted to a sarcotestal ring around the hilum
G = aril composed of a sarcotestal and a free part, together enveloping (nearly) the whole seed

The *phylogenetic value* of a taxon can be derived from its phylogenetic formula. The most primitive condition of a character gets the value 0, the most derived state gets 1, in between is valued ½. With a phylogenetic formula of seven letters as in the present case the value may vary from 0 to 7 accordingly.

The phylogenetic formulas and values for all species are included in the list, chapter 2 A.

The final phylogenetic scheme, published as figure 2, has been constructed in the following way. Along the vertical axis the phylogenetic value is set out, from 0 at the bottom to 5 (the maximum reached) at the top. The species are arranged along the horizontal axis, in principle according to their minimal phylogenetic value, from the most derived one at the right to the most primitive one at the left. This original sequence has been partly disturbed later on as a consequence of the grouping of the species. Along the connecting lines the derived character states added are mentioned so that the building up of the phylogenetic formula of each species can be followed.

As to the three incompletely known species not included in the scheme, according to their phylogenetic formulas the most probable position of *H. hirsuta* is near *H. camptoneura* and *crustacea*, of *H. peekeliana* it is in the group of *H. cauliflora*, and of *H. species nova* it is either near *H. pendula* or near *H. austro-caledonica*.

In the choice of the scheme, next to theoretical considerations of objectivity, some checks were used, viz. in the first place the coherence of three groups which seems incontrovertible, the *alata* group (2 of chapter 4), the *largifolia* group (4), and the group *H. carrii, leptococca*, and *oococca*, in the second place the logical geographic pattern of the genus as a whole as well as of the different groups (Hennig's 'Chorological Method'). The present scheme meets these requirements to a reasonable degree.

6. CONCLUSIONS

The construction of different systems along different lines and with different methods leads to two questions, in the first place how much agreement or disagreement there is between these different systems, and secondly what are the possible consequences for the taxonomy?

A. Mutual comparison

In this paragraph the intuitive systems of chapter 3, the phenetic system worked out in chapter 4 and depicted in figure 1, the macromorphological phylogenetic system constructed in chapter 5 and figure 2 (called phylogenetic system), and the pollen morphological phylogenetic system by Muller (called palynologic system) are compared mutually.

At first come some species or groups of species where as a whole the different systems show a good agreement.

1. All systems lead to a first subdivision into two taxa, the subgenera *Otonychium* (with *H. pendula* and *H. arborea*) and *Harpullia* (with the further 24 species) of the revisions by both Radlkofer and Leenhouts & Vente. In agreement with the latter revision in both phylogenetic systems the subg. *Otonychium* is considered the more primitive, the subg. *Harpullia* the more derived one. *Harpullia pendula* is according to the phylogenetic scheme the more primitive one of the two species of subg. *Otonychium*; this is in good accordance with the historic-geographic conclusions drawn by Muller (1984, chapter 8).

2. *Harpullia austro-caledonica* takes in both phylogenetic schemes as well as in the intuitive system by Leenhouts & Vente the next position, the basic one in subg. *Har-*

pullia. In the palynologic system this position is rather an isolated one, best in accordance with the geography (endemic to New Caledonia) and accordingly the history. The connections suggested in the other systems are different. Radlkofer combines it with two E. Australian species, *H. alata* and *H. frutescens*, to sect. *Harpulliastrum*, fairly well in accordance with palynology. Leenhouts & Vente suggest loose connections with some relatively primitive species of New Guinea, viz. *H. giganteacapsula*, *H. longipetala*, and *H. species nova*. In the phylogenetic system it is primarily connected with *H. hillii*, the most primitive representative of subg. *Harpullia* in Australia, possibly again with *H. species nova*. In the phenetic system the primary connections are with *H. cupanioides* and *H. hillii*.

3. The first clearly coherent group of species in subg. *Harpullia* is formed by *H. alata*, *H. frutescens*, and *H. rhyticarpa*, all E. Australian. This group occurs in all systems. Radlkofer combined the two species known to him, *H. alata* and *H. frutescens*, with *H. austro-caledonica* to his sect. *Harpulliastrum*, with this connection underlining the relatively primitive position of this group. This is well in accordance with the palynology as mentioned above. Contrary to this, in the intuitive system by Leenhouts & Vente is suggested, in the phenetic and phylogenetic system expressed, a close connection between this group and the more derived *H. rhachiptera* from New Guinea (see nr. 9).

4. *Harpullia cupanioides* takes in the primarily phenetic systems (incl. also the intuitive system of Leenhouts & Vente) a position in between *H. hillii*, considered more primitive, and a more derived group of species the kernel of which consists of *H. camptoneura*, *H. crustacea*, and *H. vaga*. In the palynologic system the first connection is more stressed: *H. cupanioides* is grouped with and placed in between *H. hillii* and *H. carrii*, with *H. camptoneura*, *H. crustacea*, and *H. vaga* forming the more derived sister group. In the phylogenetic system the main point falls to the other side and *H. cupanioides* is considered the most primitive species of the latter group.

5. The group *H. camptoneura*, *H. crustacea*, *H. hirsuta*, and *H. vaga*, referred to in connection with *H. cupanioides*, occurs in all systems. It is considered moderately derived in the phylogenetic systems as well as in the intuitive system of Leenhouts & Vente.

6. Agreement occurs also between the different systems on the coherence as well as the derived position of the ramiflorous group *H. cauliflora*, *H. largifolia*, *H. myrmecophila*, *H. peekeliana*, *H. petiolaris*, *H. ramiflora*, and *H. solomonensis*. In the palynologic system the group is still further divided into two sister groups, the more primitive one formed by *H. ramiflora* and *H. solomonensis*; this is in accordance with the opinion of Leenhouts & Vente (1982: 37 & 39). Moreover, and contrary to all other systems, *H. longipetala* is in the palynologic system added to the more derived subgroup (compare nr. 11).

7. Two species, mentioned already but the pollen of which is unknown, are *H. giganteacapsula* and *H. species nova*. Leenhouts & Vente consider these, together with *H. longipetala*, as relatively primitive species, as such belonging to the wider alliance of *H. austro-caledonica*, and place them near the basis of subg. *Harpullia*. This is in reasonably good agreement with the phenetic and the phylogenetic system.

No unanimity exists on the position of a few more species.

8. In the revision by Leenhouts & Vente (1982: 25) *H. hillii* is given a kind of a key position in subg. *Harpullia* with connections to *H. rhyticarpa, H. cupanioides*, and the *H. carrii* group. The latter two connections reoccur in the phenetic scheme. The relatively basic position is stressed in the phylogenetic system where it is connected with the more primitive *H. austro-caledonica*. The connections with more derived groups are lost here. This is mainly caused by the fact that the position of the species in this system is based upon the most primitive character states; if the full variability could be expressed the maximum of *H. hillii* should lie near *H. carrii* and *H. cupanioides*. This is more in accordance with the palynologic system where *H. hillii* is grouped together with *H. cupanioides* and *H. carrii* but separated from *H. austro-caledonica* by the *H. alata* group and not considered very primitive.

9. Systematically, *H. rhachiptera* is possibly the most interesting species of the genus. Leenhouts & Vente added it to the E. Australian group of *H. alata, H. frutescens*, and *H. rhyticarpa* because of the common occurrence of a winged petiole and rachis, hesitatingly, however, as *H. rhachiptera* is endemic to New Guinea. This same combination is to be found in the phenetic and the phylogenetic scheme, in the latter with a note that, if the character 'petiole and rachis winged or not' is not used *H. rhachiptera* would find its place near *H. camptoneura* and *H. crustacea.* Radlkofer included *H. alata* and *H. frutescens* in his sect. *Harpulliastrum* and *H. rhachiptera* in sect. *Thanatophora*, apparently giving more weight to the difference between two ovules per locule in the former two species against one ovule per locule in the latter than to the common character of the wings along petiole and rachis. However, this does not exclude a phylogenetic connection with *H. rhachiptera* as the most derived species. Palynologically, *H. rhachiptera* appears to possess a strongly deviating and unique pollen type and accordingly gets an isolated position, highly derived, as to that in accordance with the phylogenetic system. In connection with this uncertain position and with some pollen characters Muller suggested a hybridogenous origin.

The methodological difficulties met with in the placement of this species may have been caused by the relatively small numbers of characters used, 12 in the phenetic system, 7 in the phylogenetic one, as compared with 26 species. Consequently, in both cases the character 'petiole and rachis winged' may have got too much weight.

10. The intuitive system of Leenhouts & Vente, the phenetic system, and the phylogenetic system recognise a clear and well separated group of species restricted to SE. New Guinea, characterised by fruits with a short axis and widely spreading lobes, and to which belong *H. carrii, H. leptococca*, and *H. oococca*. This group is thought to be connected with, but more advanced than *H. hillii*. Palynologically, only *H. carrii* is known, and in the palynological system that species is connected with *H. hillii* and *H. cupanioides.*

11. A final species the position of which is contradictory in the different systems is *H. longipetala*. Leenhouts & Vente were of the opinion that this belongs to a loosely connected group of rather primitive, all E. New Guinea species together with *H. giganteacapsula* and *H. species nova* and not too far from *H. austro-caledonica*. This is also the position it gets in the phylogenetic scheme where this group is the most

primitive representation of subg. *Harpullia* outside of Australia-New Caledonia. Contrary to this, in the phenetic system *H. longipetala* is primarily connected with *H. ramiflora*, only secondarily with *H. austro-caledonica, H. hillii*, and *H. cupanioides.* This agrees fairly well with the palynologic system where it takes a position with the most derived representatives of the *H. ramiflora* alliance. Here is a clear contrast between the phylogenetic level of some macromorphological characters and the pollen characters.

Summarising, there is a fairly good agreement between the different systems tried. The agreement between the intuitive system of Leenhouts & Vente, the phenetic system, and the phylogenetic system is best, but these are partly based upon the same characters and there has been some inevitable mutual influence. The main points in which the palynologic system differs from the others is the position of *H. longipetala* and *H. rhachiptera* and the relative position of *H. hillii* and the *H. alata* group. Taking the check groups (chapter 5 B) and the geography into account the intuitive system and the phylogenetic one make a somewhat better impression than the others. How well the combined palynologic and phylogenetic systems are in accordance with geography and through this with the geological history has nicely been shown by Muller in his concluding chapter 8.

B. Taxonomy

In principle, taxonomy should reflect the phylogenetic system as well as possible. This formal reflection is hampered by two difficulties, however. In the first place taxonomy is more rigid; in a phylogenetic scheme, and even in a phenetic one, resemblances and differences can be expressed in a more subtle way. In the second place taxonomy should be practical: subdivisions at the same level should differ mutually in one or a few good, preferably conspicuous characters.

All systems agree on a first subdivision of the genus into 2 or 3 groups, viz. *H. pendula* and *arborea*, either combined or also separated, versus the further 24 species. In the phylogenetic system *H. pendula* and *arborea* are also separated at the 0 level as they have none of the characters used in common in the derived state. This correspondence in primitive characters is counterbalanced by their sharing some unique characters that could not be valued phylogenetically, e.g. clawed, auricled, membranous petals, a straight style, and an exclusive pollen type. Summarising, the argumentation on behalf of a subdivision of the genus into two subgenera, *Otonychium* and *Harpullia*, seems convincing.

The difficulties in translating systematics into taxonomy are illustrated already by *H. austro-caledonica*. Systematically, its position is clear enough: the most primitive species of subg. *Harpullia*, whether isolated as in the palynologic system, or more or less loosely connected with other relatively primitive species (*H. giganteacapsula, H. longipetala, H. sp. nova, H. hillii*) or groups of species (the *H. alata* group). Taxonomically, however, one has to draw the line somewhere. In view of the systematic position there is most to be said for a monotypic section. In practice, the definition of such a monotypic section appears difficult. The only macromorphologic characters differentiating this section from the rest of subg. *Harpullia* are the length of the filaments (12.5–17 mm against up to 8 mm) and of the styles (10–12 mm against 1.75–10 mm). An additional combination of characters none of them unique could be: stamens 8, pistil 3-merous (exceptionally even 4-merous), and with 2 ovules per locule. Moreover, it has a pollen type of its own. Sect. *Harpulliastrum* Baillon could be maintained on these characters, though in my opinion they are rather feeble. Combination of *H. austro-caledonica* with one or more of the species mentioned weakens the characters without adding new ones and, accordingly, blurs the delimitation.

The taxonomic arrangement of the further 23 species of subg. *Harpullia* meets still greater problems. Apart from some relatively primitive species that could not well be placed (*H. giganteacapsula, H. longipetala, H. sp. nova*) a subdivision into three or four groups seems possible. These are:

1. *H. alata, frutescens, rhyticarpa*, and possibly *rhachiptera*. Together they are characterised against all other species by their winged petiole and leaf rachis. However, the position of the latter species is unclear (see this chapter, A 9). Without *H. rhachiptera* the character state 'ovules 2 per locule' should be added.
2. *H. carrii, oococca*, and *leptococca*. This group seems well characterised by the fruits with a short axis and spreading lobes, but the same kind of fruit may occur in *H. hillii* and there are no further differences from that variable species.
3. *H. camptoneura, crustacea, cupanioides, hirsuta*, and *vaga*, whether combined with *H. hillii* or not. The main problem is here, like in the foregoing group, the variability of *H. hillii*. The latter species is doubtless closely allied to *H. cupanioides* and differs from it only in some as a whole unimportant characters (see Leenhouts & Vente, 1982: 25, note). The logical solution would be inclusion of *H. hillii* in the present group. This, however, would at least lead to combination with the *H. carrii* group. Theoretically, *H. hillii* is far too variable, especially also in phylogenetically important characters, and primarily on these characters it should be divided into some species. However, *H. hillii* is a distinctly coherent species and any subdivision appears unnatural.
4. The group *H. cauliflora, largifolia, myrmecophila, peekeliana, petiolaris, ramiflora*, and *solomonensis* could be separated on the combination of characters 'inflorescences at least finally rami- or cauliflorous and stamens 5 or 6' (the latter to differentiate it from *H. longipetala*). It does not seem very satisfying, however, to give a relatively young group – Leenhouts & Vente, in their revision of the genus (p. 39) even considered the possibility to combine this into one species, divided into some 12 subspecies – a separate position in contrast to other doubtless much older groups.

Summarising, it appears difficult to express the rather clear phylogenetic subdivision of the genus taxonomically. Contrary to phylogenetic systematics, which stresses connections and aims at a synthesis, taxonomy is primarily phenetic, is analytic, and will aim at separation. Phylogeny may guide taxonomy to some extent, but finally phylogenetic systematics and taxonomy are different ways of tentatively expressing the natural order and have different aims.