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A TAXONOMIC STUDY OF THE GENUS  
*HETEROMORPHA* CHAM. & SCHLECHTD. (APIACEAE)

by

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THESIS

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## SUMMARY

### A Taxonomic study of the genus *Heteromorpha* Cham. & Schlechtd. (Apiaceae)

The species delimitation in *Heteromorpha* Cham. & Schlechtd. has until now been unsatisfactory, and the relationship and placement unclear for several plants which have variously been referred to either *H. arborescens* (Spreng.) Cham. & Schlechtd. or *H. trifoliata* (Wendl.) Eckl. & Zeyh. The present revision has resulted in the recognition of seven species (including seven varieties) across the African mainland from the south-western Cape to the Yemen Arab Republic, and westwards to Nigeria. Eight species from Madagascar are excluded. The name *H. stenophylla* Welw. ex Schinz is reinstated and *H. transvaalensis* Schlechter & H. Wolff is considered a variety of the latter. A new species, *H. occidentalis* Winter, is described. A narrower view of *H. arborescens* (Spreng.) Cham. & Schlechtd. than that of recent authors is applied, and the species is subdivided into five varieties to accommodate the diversity. Two of these are described for the first time, namely var. *frutescens* Winter and var. *montana* Winter. *H. stolzii* H. Wolff is added to the synonymy of *H. involucrata* Conr., and the circumscription is broadened to accommodate other central African forms of the species. Data are analyzed cladistically and the supposed phylogeny is presented in the form of a cladogram. Keys to the recognized species and varieties respectively, as well as the known geographical distribution for each of the taxa, are presented.

## OPSOMMING

### 'n Taksonomiese studie van die genus *Heteromorpha* Cham. & Schlechtd. (Apiaceae)

Die spesie-afbakening in *Heteromorpha* Cham. & Schlechtd. was tot dusver onbevredigend, en die verwantskap en plasing was onduidelik vir verskeie plante wat na *H. arborescens* (Spreng.) Cham. & Schlechtd. of *H. trifoliata* (Wendl.) Eckl. & Zeyh. verwys is. Die huidige hersiening het aanleiding gegee tot die erkenning van sewe spesies (insluitend sewe variëteite) regoor die vasteland van Afrika vanaf die suidwes Kaapprovinse tot by die Jemen Arabiese Republiek, en weswaarts tot by Nigerië. Agt spesies van Madagaskar word uitgesluit. Die naam *H. stenophylla* Welw. ex Schinz word heringestel en *H. transvaalensis* Schlechter & H. Wolff word beskou as 'n variëteit van laasgenoemde. 'n Nuwe spesie, *H. occidentalis* Winter, word beskryf. 'n Nouer beskouing van *H. arborescens* Cham. & Schlechtd. as díe van onlangse outeurs word toegepas, en die spesie word onderverdeel in vyf variëteite om die diversiteit daarvan te akkomodeer. Twee hiervan word nuut beskryf, nl. var. *frutescens* Winter en var. *montana* Winter. *H. stolzii* H. Wolff word tot die sinonimie van *H. involucrata* Conr. gevoeg, en die omskrywing word verbreed om ander sentraal Afrika vorme te akkomodeer. Data word kladisties ontleed en die vermeende filogenie word in die vorm van 'n kladogram aangebied. Sleutels tot die spesies en variëteite onderskeidelik, sowel as die bekende geografiese verspreiding vir elk van die erkende taksons, word aangebied.

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## CHAPTER 1

## INTRODUCTION

*Heteromorpha* Cham. & Schlechtd. (*sensu stricto*) is a genus of predominantly woody plants (trees, shrubs or suffrutices) in the subfamily Apioideae of the Apiaceae. The species occur throughout most of temperate and subtropical Africa. Whereas seven species are restricted to the African continent and Yemen, Humbert (1956) broadened the generic concept to include eight Madagascar species. The African contingent share the woody habit with the related *Polemannia* Eckl. & Zeyh. from the Drakensberg region as well as fruit characters with the Western and Northwestern Cape genus *Polemanniopsis* B.L. Burtt (Burtt 1988), which have been included here as potential outgroups.

The last revision of this genus was published almost ninety years ago (Wolff 1910). Since then several more species have been described so that there is now a need for a systematic treatment which could provide descriptions, keys and distribution maps of properly delimited and correctly named taxa. The species delimitation in *Heteromorpha* Cham. & Schlechtd. has until now been unsatisfactory, and the relationship and placement unclear for several plants which have variously been referred to either *H. arborescens* (Spreng.) Cham. & Schlechtd. or *H. trifoliata* (Wendl.) Eckl. & Zeyh. Several authors have pointed out the need for further work in this genus

(Brenan 1954; Cannon 1978; Townsend 1985, 1989; Burtt 1991).

Burtt (1991) mentioned the problems with *H. arborescens*, and the uncertainty of the relevance of the wide range in habit seen in the genus as a whole.

Burtt (1991) identified the southern African region with its high occurrence of woody genera as an important focal point for a systematic study of the Apiaceae. This study is therefore intended to form the basis for further work on the African Apioideae, particularly concerning the relationships among woody genera, as well as the generic and tribal delimitations within the subfamily.



## Chapter 2

# MATERIALS AND METHODS

### 2.1 Herbarium material

Due to the distribution of the species in several practically inaccessible parts of Africa, this study is based mainly on material from various international herbaria. Specimens were obtained on loan from the following herbaria: B, BM, G, GOET, GRA, K, L, MO, NY, P, PRE, S, WIN and Z. Other collections studied on site include BOL, JRAU, NBG, NH, NU, SAM and STE. Apart from morphological and historical data, these collections provided locality data which, together with information from literature sources (Gunn & Codd 1981; Leistner & Morris 1976; Polhill 1988), enabled the plotting of distribution maps for each species and infraspecific taxon.

### 2.2 Fieldwork

An excursion was undertaken to the northern and eastern Transvaal to study the plants *in situ* and to collect fresh material for analysis. Fresh seeds were collected for cytological investigation and greenhouse cultivation of plants. Fresh flower, fruit, stem, leaf and root material was fixed in FAA (Sass 1958) for anatomical studies. Fruit, leaf and root material was collected for chemical analyses. Voucher specimens

were collected at each population. Photographs were taken to illustrate habit, habitat and certain features of gross morphology. A population of *Heteromorpha arborescens* in the vicinity of the RAU campus was studied and sampled in the same manner. A total of fourteen populations representing four different species and two varieties were visited.

### 2.3 Cultivation

To study seedling development and as a source of fresh, comparable material for anatomical investigation, seeds from 10 different populations (representing four of the seven recognized species) were sown in pots on the 9th of June 1992. Germination started after 18 days and was complete after 26 days.

#### Provenances of seed-grown *Heteromorpha* plants:

##### *H. involucrata*:

Transvaal, Lydenburg, Winter 61 (JRAU); Transvaal, Barberton Winter 68 (JRAU); Transvaal, Weltevreden, Winter 67 (JRAU).

##### *H. pubescens*:

Transvaal, Rosehaugh, Winter 66 (JRAU); Transvaal, Barberton, Winter 69 (JRAU).

##### *H. arborescens* var. *arborescens*:

S. Cape, Kamanassieberg, Vlok 2633 (JRAU).

*H. arborescens* var. *trifoliata*:

Transvaal, Melville Ridge, Winter 71 (JRAU).

*H. arborescens* var. *frutescens*:

Transvaal, Abel Erasmus Pass, Winter 57, 59 (JRAU).

*H. stenophylla* var. *transvaalensis*:

Transvaal, N of Potgietersrus, Winter 50 (JRAU).

#### 2.4 Gross morphology

After an initial check of herbarium material in PRE, the variation was categorized into operational taxonomic units. At least three specimens were selected where possible to represent each unit. Statistical data was analysed according to these categories. Specimens were studied using a WILD M3Z dissecting microscope and drawings were done with the aid of a camera lucida attachment. Pollen was studied by SEM without prior acetolysis. Problems were experienced with pollen grains swelling and developing surface cracks under medium magnification.

## 2.5 Anatomy

### 2.5.1 Epidermal morphology

Leaves from FAA material or from herbarium specimens of all known species of *Heteromorpha* *sensu lato* (including the Madagascar group), as well as the related genera *Polemannia* and *Polemanniopsis*, were treated according to the method described by Ram & Nyar (1974) to obtain epidermal peels of both leaf surfaces. A complete list of voucher specimens is given in Table 2.1. Stomatal densities were determined under the light microscope, by counts over an area along the eyepiece scale bar. Counts were not taken directly adjacent to the margin or midvein, only in the secondary vein interstices. Dispersion was scored according to patterns of local presence or concentration.

TABLE 2.1 Specimens of *Heteromorpha*, *Polemannia* and *Polemanniopsis* that were investigated for leaf epidermal characters.

#### *Heteromorpha* (African species)

1a *arborescens* (Spreng.) Cham. & Schlechtd., unifoliolate,

Cape & Natal:

---var. *arborescens*, Van Wyk 3313 (JRAU); Vlok 2633 (JRAU).

---var. *collina* (Eckl. & Zeyh.) Sonder, Ward 7538 (PRE).

1b *arborescens* (Spreng.) Cham. & Schlechtd., tri- to multifoliolate, Eastern Cape to Arabian Peninsula:

- var. trifoliata (Wendl.) Sonder, Brink 128 (PRE); Winter 71 (JRAU); De Wilde 6041 (K); Semsei 4122 (PRE); Stolz 24699 (PRE).
- var. montana Winter var. nov., Pope & Muller 2075 (PRE).
- 1c arborescens (Spreng.) Cham. & Schlechtd. var. frutescens Winter var. nov., Natal to Malawi, Winter 51, 57 (JRAU); Rogers 22197 (PRE).
- 2 papillosa C.C. Townsend, Namibia, Merxmüller & Giess 28004 (PRE); Dinter 3499 (PRE); Hanekom 135 (WIN).
- 3.1 stenophylla Welw. ex Schinz var. stenophylla, Namibia, Angola & Malawi, Le Roux 295 (PRE); Giess 8602 (PRE); Dinter 5487 (PRE).
- 3.2 stenophylla Welw. ex Schinz var. transvaalensis (Schlechter & H. Wolff) Winter comb. et stat. nov., suffrutex, Winter 50, 52, 55 (JRAU).
- 4 occidentalis Winter sp. nov., West Africa, Letouzey 5680 (K); Meurillon 1396 (K); Milne-Redhead 762 (K).
- 5 gossweileri (Norman) Norman, Angola, Milne-Redhead 3981 (PRE); Mendes 2069 (PRE); Hundt 727 (PRE); Hooper & Townsend 325 (K).
- 6 pubescens Burtt Davy, Transvaal, Winter 66, 69 (JRAU); Junod 143 (PRE).
- 7a involucrata Conr., typical form, Transvaal, Swaziland & Natal, Winter 61, 68 (JRAU); Gerstner 3763 (PRE).
- 7b involucrata Conr., 'kassneri' form, Malawi & Zambia, Quarré 5919 (PRE); Phillips 1295 (MO).
- 7c involucrata Conr., 'Zimbabwe' form, Zimbabwe & Angola, Jacobsen 2891 (PRE); Bayliss 10686 (PRE); Kers 3491 (S).

7d involucrata Conr., 'Malawi' form, Malawi & SA, Torré & Paiva 11897 (PRE); Winter 67 (JRAU).

*Heteromorpha* (Madagascar species)

- M1 laxiflora (Baker) Humb. var. alticola Humb., suffrutescent climber, *De la Bâthie* 15168 (P); *Humbert & Capuron* 25031 (P); --- var. laxiflora, climber, *Schatz* 2655 (MO).
- M2 marojejvensis Humb., thin-stemmed shrub, *Humbert* 22710 (P); *Miller & Lowry* 4160 (MO); *Herbier de l'Alaotra* 3475 (MO).
- M3 tsaratananensis Humb., woody shrub, *De la Bâthie* 6806, 16411 (P); *Humbert* 18374 (P).
- M4 coursii (Baker) Humb., woody shrublet, *Humbert et al.* 24702 (P); *Herbier de l'Alaotra* 3825 (MO).
- M5 betsileensis Humb., suffrutex, *Humbert* 3792 (P); *De la Bâthie* 6815 (P).
- M6 andringitrensis Humb., herbaceous perennial, *De la Bâthie* 6809, 13741, 14430 (P).
- M7 andohahelensis Humb., suffrutex, *Humbert* 6192, 6466, 13654 (P).
- M8 bojeriana (Baker) Humb., suffrutex, *Bojer s.n.* (P); *Dorr et al.* 2889 (MO); *Catat* 332 (P).

*Polemanniopsis* (Woody shrub, NW Cape)

- PO marlothii (H. Wolff) B.L. Burtt, *Venter* 8132 (PRE); *Taylor* 11384 (PRE); *Van Jaarsveld* 5457 (PRE).

**Polemannia (Woody shrubs, Drakensberg)**

- P1    montana Schlecht. & H. Wolff, *Smook 7181* (PRE); *Schmitz 9077* (PRE); *Jacobs 3097* (PRE).
- P2    simplicior Hilliard & B. L. Burtt, *Hoever 2016* (PRE); *Pole Evans 19654 H* (PRE); *Pentz Sub PRE 48118* (PRE).
- P3    grossulariifolia Eckl. & Zeyh., *Ratray 35* (PRE); *Giffen 1296* (PRE); *Galpin 8359* (PRE).
- 

After germinating seeds of four African species (section 2.3), juvenile leaves were available to investigate ontogenetic changes during leaf development. Trichome types were studied by SEM on dry-mounted leaf fragments from one specimen of each taxon. To investigate the structure of each trichome type, mature leaves were embedded in glycol methacrylate (GMA). The samples were initially fixed in FAA for at least 24 h, after which they were embedded in GMA according to a modification (Tilney 1986) of the method of Feder and O'Brien (1968). The dehydration and embedding procedure was as follows:

1. Twice for 4 to 6 h in 50% ethanol.
2. Twice for 4 to 6 h in 100% ethanol.
3. Twice for 4 to 6 h in n-propanol.
4. Twice for 4 to 6 h in n-butanol.
5. Twice for 24 h in GMA monomer mixture.
6. Five days in GMA monomer mixture.
7. 24 h in fresh GMA monomer mixture in tightly sealing gelatin capsules at 60°C.

The embedded material was mounted in the desired orientation on GMA stubs for sectioning on a Porter Blum MT-1 ultramicrotome. Mounted sections were stained according to the so-called Periodic Acid - Schiff / Toluidine Blue (PAS/TB) staining method described below:

1. 30 min in a solution of 2,4-dinitrophenylhydrazine (prepared by dissolving 1 g DNPH in 30 ml acetic acid, adding to 170 ml distilled H<sub>2</sub>O, mixing thoroughly and filtering).
2. 10 min under running H<sub>2</sub>O.
3. 10 min in a 1% (aqueous) periodic acid solution.
4. 5 min under running H<sub>2</sub>O, followed by thorough drying.
5. 30 min in Schiff's reagent.
6. 5 to 10 min under running H<sub>2</sub>O, followed by rinsing with distilled H<sub>2</sub>O.
7. Dry on slide warmer.
8. Stain with toluidine blue, c. 1 min (up to 3 min).
9. Rinse under running H<sub>2</sub>O till most of the colour is leached from GMA surrounding the material, rinsing finally with distilled H<sub>2</sub>O.
10. Dry and complete mounting, using ENTELLAN mountant.

Drawings were done with the aid of a camera lucida attachment on a Zeiss compound microscope. Vestiture (trichome distribution) was studied on several specimens with the aid of a dissecting microscope. The investigation was limited to the laminar region of the leaf.

### 2.5.2 Stem, petiole, root and fruit anatomy

Samples were prepared and mounted for detailed investigation as described in section 2.5.1 for the study of trichome structure. A list of voucher specimens for the material used is given in Table 2.2. Stem sections were sampled from the fourth (from the apex) visible internode of six month old seedlings of four *Heteromorpha* species, as well as from mature stems c. 10 mm in diameter, from which portions were excised only as deep as the outermost xylem. For *Polemannia* and *Polemanniopsis*, seedlings were not available at the time and young stems were sampled. Petioles were sampled by cutting transverse sections from the median area of each petiole. Broader variation patterns were assessed by preparing additional hand sections. Root (hypocotyl) transverse sections were obtained from 10 mm below the stem bases of six month old seedlings.

Sections were photographed using a Leitz Wetzlar compound light microscope with a 35 mm camera attachment using Fujicolor Super HG II (ISO 100) film. The detection of crystals was enhanced by polarized light.

Flowers, young fruit and mature fruit were sampled from FAA material or from herbarium specimens. A complete list of voucher specimens is given in Table 2.3. Dried samples were rehydrated in distilled water just below boiling point (60 min) before further treatment as above. Transverse sections were cut through the middle of each organ.

**TABLE 2.2 List of specimens used for the investigation of stem, petiole and root anatomy (All in JRAU unless otherwise indicated).**

TAXON	VOUCHER SPECIMEN	MATERIAL
<u>H. arborescens</u> (Spreng) Cham. & Schlechtd. var. <u>arborescens</u>	Van Wyk 3313 Vlok 2633	Pet. (2x) Pet.
<u>H. arborescens</u> (Spreng) Cham. & Schlechtd. var. <u>trifoliata</u> (Wendl.) Sonder	Winter 53 Winter 71	Pet. Rt. (12/9/92) St.(sapling) St.(10 mm) Wd. Pet. (3x)
<u>H. arborescens</u> (Spreng) Cham. & Schlechtd. var. <u>frutescens</u> Winter, var. nov.	Winter 51 Winter 57	Wd. Rt.(12/11/92) St.(sapling) St.(10 mm) Wd. Pet.
<u>H. stenophylla</u> Welw. ex Schinz var. <u>stenophylla</u>	Le Roux 295 (PRE)	Pet.
<u>H. stenophylla</u> Welw. ex Schinz var. <u>transvaalensis</u> (Schlecht. & H. Wolff) Winter, comb. et stat. nov.	Winter 50  Winter 52	Rt.(12/11/92) St.(seedling) St.(7 mm) Pet.
<u>H. pubescens</u> Burtt Davy	Winter 65  Winter 69	Wd. Pet. Rt. (11/12/92) St.(sapling) St.(10 mm) Wd. Pet.
<u>H. involucrata</u> Conr.	Phillips 1945 (Z) Stolz 2086 (PRE) Winter 61 Winter 67 Winter 68	Pet. Pet. Pet. (3x) Pet. (2x) Pet. (3x)
<u>Polemannia simplicior</u> Hilliard & B.L. Burtt	B & M v Wyk 2879	St.(young st.) St.(10 mm) Wd. Pet.
<u>Polemanniopsis marlothii</u> (H. Wolff) B.L. Burtt	Winter 87	St.(bud shoot) St.(10 mm) Wd.

Legend: Rt. = root; St. = stem; Wd. = wood segment; Pet. = petiole

**TABLE 2.3 Specimens of *Heteromorpha* from which material was sampled for the investigation of fruit morphology (including anatomy) and development.**

TAXON	VOUCHER SPECIMEN	FLOWERS	YOUNG FRUIT	MATURE FRUIT
<b><i>Heteromorpha sensu stricto</i> (African species)</b>				
<u><i>H. arborescens</i> (Spreng.) Cham. &amp; Schlechtd. var. <u><i>arborescens</i></u></u>	<i>Van Wyk 3313 (JRAU)</i> <i>Vlok 2633 (JRAU)</i>	+	-	-
<u><i>H. arborescens</i> (Spreng.) Cham. Schlechtd. var. <u><i>trifoliata</i></u> (Wendl.) Sonder</u>	<i>Winter 56 (JRAU)</i> <i>Winter 71 (JRAU)</i>	+	-	-
<u><i>H. arborescens</i> (Spreng.) Cham. Schlechtd. var. <u><i>frutescens</i></u> Winter</u>	<i>Winter 51 (JRAU)</i> <i>Winter 57a (JRAU)</i>	+	+	-
<u><i>H. involucrata</i> Conr.</u>	<i>Winter 61 (JRAU)</i> <i>Quarré 5919 (PRE)</i> <i>Jacobsen 2891 (PRE)</i> <i>Torre &amp; Paiva 11897 (PRE)</i> <i>Stoltz 24699 (PRE)</i>	+	+	+
<u><i>H. papillosa</i> C.C. Townsend</u>	<i>Merxmüller &amp; Giess 28004 (WIN)</i> <i>Seydel 3948 (WIN)</i> <i>Kers 149 (WIN)</i>	+	-	-
<u><i>H. pubescens</i> Burtt Davy</u>	<i>Winter 66 (JRAU)</i>	+	+	+
<u><i>H. stenophylla</i> Welw. ex Schinz var. <u><i>stenophylla</i></u></u>	<i>Giess 15120 (WIN)</i> <i>Giess 15169 (WIN)</i> <i>De Winter 2914 (WIN)</i> <i>Brummit 9316 (PRE)</i>	+	-	-
<u><i>H. stenophylla</i> Welw. ex Schinz var. <u><i>transvaalensis</i></u> (Schlecht. &amp; H. Wolff) Winter</u>	<i>Winter 50 (JRAU)</i> <i>Winter 54 (JRAU)</i>	-	-	+
<b>Madagascar species</b>				
<u><i>H. andohahelensis</i> Humb. var. <u><i>andohahelensis</i></u></u>	<i>Humbert 13654 (P)</i> <i>Humbert 6192 (P)</i>	+	-	-
<u><i>H. andringitrensis</i> Humb.</u>	<i>Perrier de la Bâthie 6809 (P)</i> <i>Perrier de la Bâthie 14430 (P)</i>	-	-	+
<u><i>H. betsileensis</i> Humb.</u>	<i>Perrier de la Bâthie 6813 (P)</i> <i>Rarivo 11038 (P)</i>	-	+	+
<u><i>H. bojeriana</i> (Baker) Humb.</u>	<i>Bojer s.n. (P)</i> <i>Baron 5185 (P)</i>	-	+	+
<u><i>H. coursii</i> (Baker) Humb.</u>	<i>Cours &amp; Humbert 24702 (P)</i>	+	+	+
<u><i>H. laxiflora</i> (Baker) Humb. var. <u><i>laxiflora</i></u></u>	<i>Keraudren 266 (P)</i> <i>Humbert &amp; Capuron 25427 (P)</i>	+	+	-
<u><i>H. marojejvensis</i> Humb.</u>	<i>Humbert 22710 (P)</i>	+	+	+
<u><i>H. tsaratananensis</i> Humb.</u>	<i>Perrier de la Bâthie 6806 (P)</i> <i>Humbert 18374 (P)</i> <i>Perrier de la Bâthie 16411 (P)</i>	-	+	-

### 2.5.3 Wood anatomy

Wood anatomy of *Polemanniopsis*, *Polemannia* and the woody species of *Heteromorpha* was studied by SEM. Voucher specimens are listed in Table 2.2. Surfaces were prepared by cutting small blocks out of dried stems of approximately 15 mm in diameter. Radial and tangential surfaces were exposed by splitting the blocks along the grain, and transverse surfaces were cut with a sharp blade.

### 2.6 Cytology

Seeds of four taxa (section 4.5) were soaked in a KAPTAN fungicidal solution and germinated by laying in a petri dish between two layers of filter paper similarly treated in KAPTAN. Temperature was maintained at 25°C, and filter paper was kept moist until roots were harvested. Root tips were obtained during active growth of the hypocotyl and treated with 8-hydroxyquinoline sulphate (0,02%) for 3 h to inhibit spindle formation during mitosis. The tissue was fixed in Carnoy's solution (ethanol, chloroform & glacial acetic acid - 6:3:1) for 48 h, and transferred to 70% ethanol for storage at -4°C. The tissue was hydrolyzed to separate cells (5 N HCl; 7 to 8 min), and placed in a drop of lacto-propionic orcein (Dyer 1963) solution (45% of concentrate in H<sub>2</sub>O) on a microscope slide. The root tip was cut off right behind the rootcap and squashed beneath a cover slide to spread the cells.

## 2.7 Chemotaxonomic survey

### 2.7.1 Flavonoids

The following samples were surveyed for flavonols (vouchers specimens all in JRAU):

*H. arborescens* var. *trifoliata*: Winter 53 (roots)

Winter 71 (leaves & fruits)

*H. involucrata* - typical form: Winter 68 (leaves, fruits & roots)

A standard extraction and hydrolysis method (Harborne 1973) was applied to extract flavonol aglycones. Samples were prepared for HPLC analysis by adsorption onto a C-18 pre-column (EXTRASEP 1000 mg), washing with distilled water and eluting with methanol. Samples were analyzed on a Beckman System Gold HPLC apparatus with a 5 µm Ultrasphere ODS 4,5 mm x 250 mm column. Sample volume was 20 µl; flow-rate 1,0 ml min<sup>-1</sup>; solvent A = 1% acetic acid; solvent B = methanol. The following solvent mixing time program was run: 1 min. at 30% B, 20 min gradient to 100% B, 12 min at 100% B. Detection and on line characterization was done by means of a diode array detector. Separation was monitored at a wavelength of 254 nm (bandwidth 10 nm). Peak retention times and UV-VIS spectra were compared with those of commercial standards of quercetin, kaempferol & luteolin.

### 2.7.2 Coumarins

Samples are listed in Table 5.2. Dried leaf, fruit or root material (1 g) was ground up with a mortar & pestle with the aid of a minimal quantity of pure sand (acid washed). Ethyl acetate (20 ml) was added and left to extract for 20 min. The extract was filtered through Whatman no. 113 paper into a glass column containing celite (5 g), and the filtrate collected in a 250 ml roundbottom flask. The pestle was twice rinsed with ethyl acetate (10 ml), and the rinsings filtered as above. A further 20 ml of ethyl acetate was used to rinse the filter paper and celite. Ethyl acetate was removed under vacuum at 60°C. The flask was rinsed with 95% aqueous methanol (2x 10 ml), transferring rinses into a separation funnel. The solution was washed with n-hexane (3x 30 ml), and the methanol was removed under vacuum (40°C), before partitioning between water (3 ml) and diethyl ether (10 ml). Separation was enhanced with the aid of a bench centrifuge. The ether fraction was transferred into a weighed vial and evaporated to dryness to determine the yield of total extracted material.

Analysis of extracts was done by TLC with UV detection. Some compounds were detected under UV light at 254 nm as quenched spots on plates with fluorescent indicator, and others at 365 nm as bright blue fluorescent spots.

A bulk extract (5.57 g) was prepared by Soxhlet extraction (36 h) of a sample of leaves (121 g dry weight) from *Heteromorpha*

*arborescens* var. *frutescens*. [Voucher specimen in JRAU: Winter 57a]

Isolation of some of the detected compounds from this extract was attempted by column chromatography using silica gel as adsorbent and the following eluent systems:

System 1. Hexane + ethyl acetate (3:7)

System 2. Chloroform

Rough fractions were obtained initially using system 1. Extreme non-polar and polar fractions were eliminated and two impure fractions containing an unknown compound X2 (2,15 g), and unknown compounds Y1, Y2 and Y3 (0,52 g) respectively were collected. Y1, Y2 and Y3 were rechromatographed (system 1), and successfully separated as amorphous solids. X2 was obtained as an oily substance using system 2, as it co-eluted with four impurities on system 1.

These isolates were analyzed by mass spectrometry (MS) and gas chromatography (GC), and later by GC-MS, as they were found to be impure. For GC studies a DB1 fused silica capillary column (30 m x 0,25 mm internal diameter) was used under the following conditions: N<sub>2</sub> as carrier gas at 4 ml min<sup>-1</sup>; column temperature 150°C to 250°C at 7°C min<sup>-1</sup>, 16 min isotherm; injector 250°C; FID detector 300°C. Samples were dissolved in chloroform for injection.

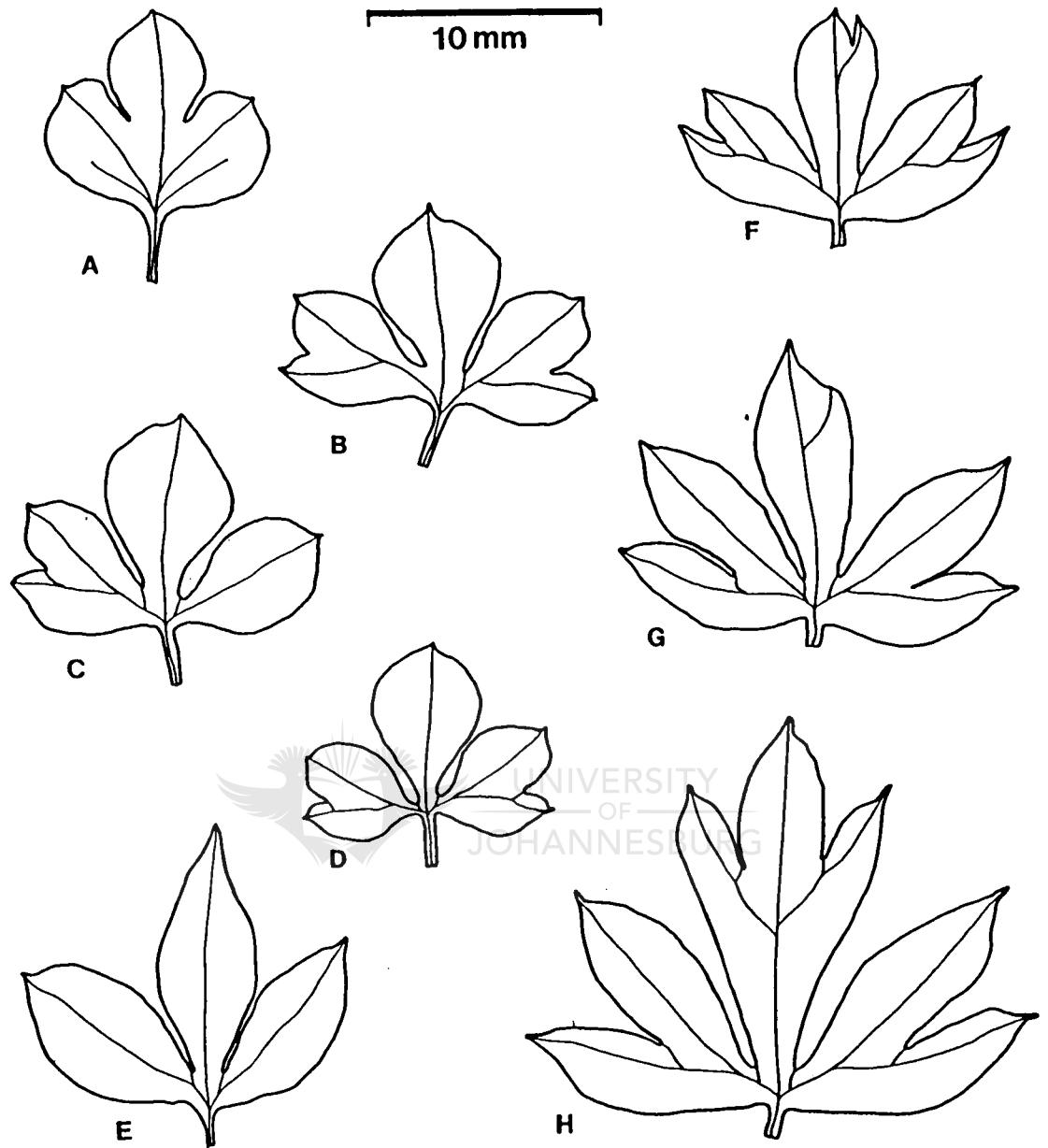
## Chapter 3

### Vegetative Morphology

#### 3.1 Morphology of seedlings

Seedling characters have been used in the classification of the Apiaceae by Cerceau-Larrival (1962). She recognized two main evolutionary lines (L and R) in the family, based on the shape of the cotyledons. Her grouping seems to work generally, but is problematic in *Peucedanum* L., where L types and R types both occur with no abrupt division (Burtt 1991). The cotyledons of *Heteromorpha* are 15 to 19 mm long and 4 to 7 mm wide with an elliptic outline. They were classified as R by Cerceau-Larrival (1962).

Burtt (1991) noted in his discussion on the relationship between *H. trifoliata* and *H. arborescens* that the first seedling foliage leaves illustrated by Cerceau-Larrival (1979) were trifoliolate, and that he expected that seedlings of *H. arborescens* would be different. The variation in seedling leaf outline and progression along the shoot is shown in Figure 3.1. In all the seedlings investigated, the first foliage leaf is three-lobed or deeply trisect, with secondary incisions sometimes present (Figure 3.1 F). From the second leaf, incision is almost complete, and in the fourth, a rachis or petiolule may become evident. Leaves of *H. arborescens* var. *frutescens* are more distinctly petiolulate at this stage than those of other



**Figure 3.1** *Heteromorpha* seedling leaves. A--D, a progression of the first four foliage leaves of *H. arborescens* var. *trifoliata*. E, the first leaf of *H. arborescens* var. *arborescens*. F--H, a progression of the first three leaves of *H. involucrata*. Voucher specimens (all in JRAU): A--D, Winter 71; E, Vlok 2633; F--H, Winter 68. Scale bar: 10 mm.

varieties of *H. arborescens*, but a wider survey could show more variation. In general appearance they seem more like those of *H. stenophylla* var. *transvaalensis*. The number of incisions generally reflect the mature state, but not in the typically

simple leaved *H. arborescens* var. *arborescens* (Figure 3.1 E). Seedlings of this variety have trifoliolate leaves, contrary to Burtt's expectation, with simple leaves appearing only sporadically in the second year. The late occurrence of simple leaves in the development of this taxon serves to corroborate the idea that it is conspecific with var. *trifoliata*. It would be interesting to see, when viable seed becomes available, whether *H. arborescens* var. *collina* and forms of *H. gossweileri* with simple leaves follow a similar ontogenetic sequence.

Seedling leaves of all species studied had hairs of the papillate type along the margins, midrib and primary veins. Similar papillae were found in mature leaves of *H. gossweileri* and *H. occidentalis*, while other species either lose these papillae, or acquire a more specialized type of trichome as they mature.

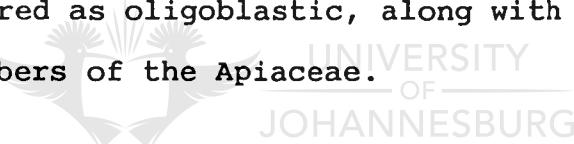
The seedling root and hypocotyl develop into a typical dauciform tuber during the first year. Root anatomy is discussed in further detail under section 3.2.2. The root has a contractile function, so that the lower part of the stem is underground by the end of the first year, affording protection of the future innovation zone against desiccation, frost and fire. The formation of innovation buds at the base of the stem, directly above the root, can be seen at this stage. These either remain dormant until the main axis is disturbed, or produce shoots at the start of the second season.

### 3.2 Morphology of the mature plant

#### 3.2.1 Stem

##### Habit and growth pattern.

Burtt (1988) discusses habit in woody southern African genera using Corner's (1949) terms lepto- and pachycaul, and relates these to Mangenot's (1969) system based on the number of buds produced. Using these terms, he describes *Heteromorpha* as a leptocaul, and as polyblastic, with numerous buds giving rise to the much branched state. Although this is certainly the case in *H. arborescens* and *H. papillosa*, the other species would be better considered as oligoblastic, along with many of the herbaceous members of the Apiaceae.



Burtt (1991) gives a broader analysis of habit under the apt heading: "patterns of growth and of flower and fruit production". The relation of vegetative and reproductive phases of growth is important in assessing habit, particularly in the Apiaceae. Burtt describes the following patterns (with examples) for herbaceous members of the Apiaceae:

- I: Apical bud remains vegetative (strictly monopodial stems).  
*Hydrocotyle L.*
- II: Main stem terminating in an umbel, lateral branches similarly terminated, branching sometimes repeated (monopodial branching terminated by an umbel). *Annesorhiza* Cham. & Schlechtd., *Peucedanum*.

III: Main stem ends in an umbel at an early stage, growth continues from the uppermost axillary bud (sympodial pattern). Species of *Sonderina* H. Wolff, *Ciclospermum* La Gasca.

*Heteromorpha* can be grouped in the second type, covering the whole range in the extent of branching, from the simple and mostly single stems of *H. gossweileri*, where the only aerial branching occurs in the reproductive phase, to the repeated branching found in *H. arborescens*.



**Figure 3.2** The juvenile habit in *Heteromorpha*. Young saplings of *H. arborescens* var. *trifoliata* with simple stems and dauciform tubers. Age was estimated at approximately five years (left) and seven years (right), by counting growth increments along the stem. Both are from Melville ridge, Johannesburg. Scale bar: 100 mm.

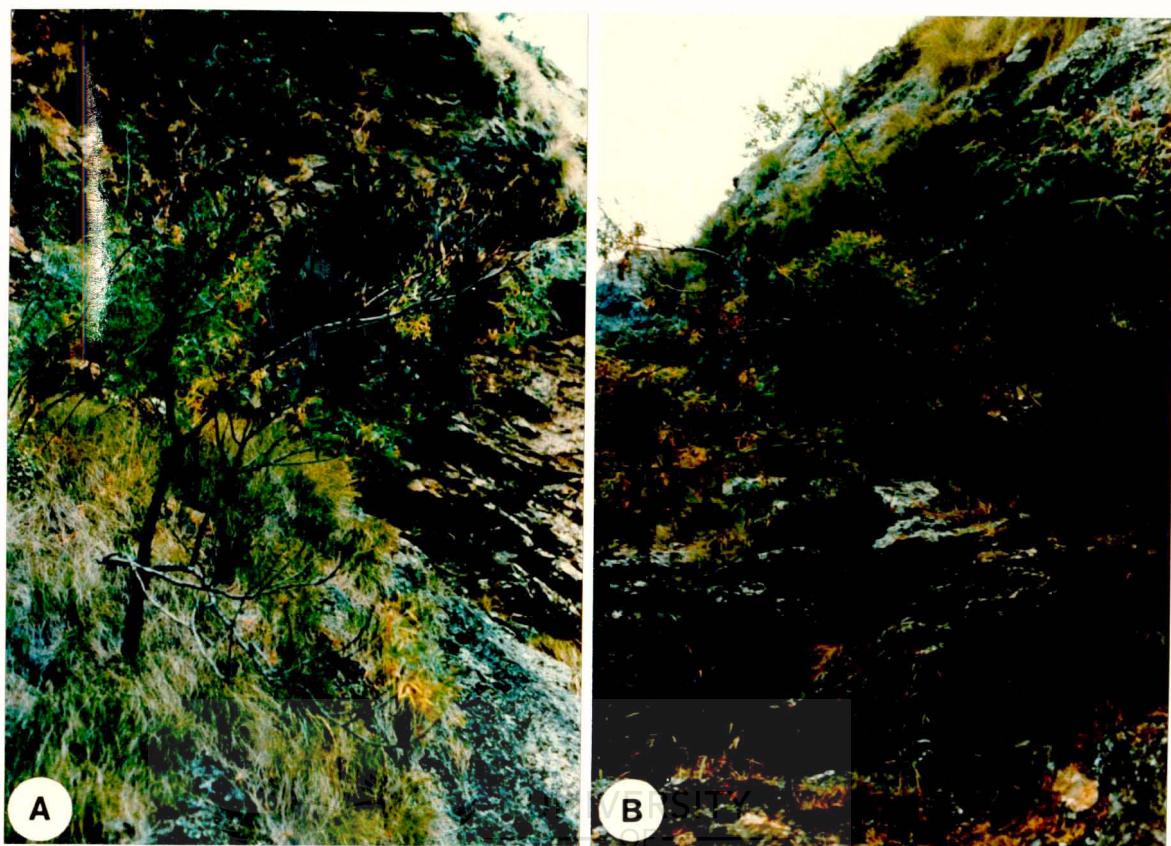
After the first year, the basic pattern of the juvenile state (as in Figure 3.2) can either be maintained as in Figure 3.7 B, with simple stems being replaced from the subterranean stem and hypocotyl region, or the aerial system can be extended apically

and eventually laterally through branching. Adventitious shoots are often formed at the base, and additional tuberous lateral roots may develop from the hypocotyl region in some species. The resultant underground habit is a woody caudex, with a few fascicled roots.

To describe the variation in habit observed in this study, three main categories are defined, namely those of tree, shrub and suffrutex. The criteria chosen to characterize these types are:

1. Extent of branching (vegetative only) above ground.
2. Degree of suckering.
3. Number and distribution of proliferation buds  
(location of renewal zones).
4. Variation in internode length.
5. Woodiness (relative proportion of xylem to pith).

The tree category may include shrubby forms, but these are probably extremes in the range of ecotypic adaptation. The tuberous taproot of the young plant becomes obscured after a few years by the increase in general dimensions as the plant matures and the branching system develops. *Heteromorpha arborescens* is generally a small tree, 3 to 9 m tall (Figure 3.3), with a trunk diameter of 50 to 250 mm [Phanerocorm or caulocarpic habit of various authors, e.g. Troll (1964), Weberling (1989), Radford (1986)]. It has been likened to *Bupleurum fruticosum* L. in habit (Sonder 1862, Burtt 1988). Branching is untidy, unbalanced or



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**Figure 3.3** Examples of the tree habit in *Heteromorpha*. *H. arborescens* var. *montana* growing in the Chimanimani mountains in Zimbabwe. Note the leaves clustered at the ends of branches in the foreground (A), while plants in the background have long adventitious shoots, leafy along the entire length, causing a virgate appearance as in (B).

"top-heavy", often giving the plant a virgate appearance (Figure 3.3 B). There is a characteristic vascular thickening where one branch arises from another, with the vascular system of the younger branch encircling the older branch. Apical dominance is strong, leading to the production of long, slender branches during periods of active growth (Figure 3.3 A). This pattern is broken by terminal inflorescences or physical damage such as herbivory or drought stress, and persistent lateral growth ensures a lasting well-branched habit relative to other species. Depending on the growth disturbance history, it may develop either a single trunk or several thinner trunks from a basal

rootstock, the latter situation commonly resulting from fire in grassland habitats. This plasticity is evident in Figure 3.4 A and B, for two plants growing in close proximity in adjacent habitats.

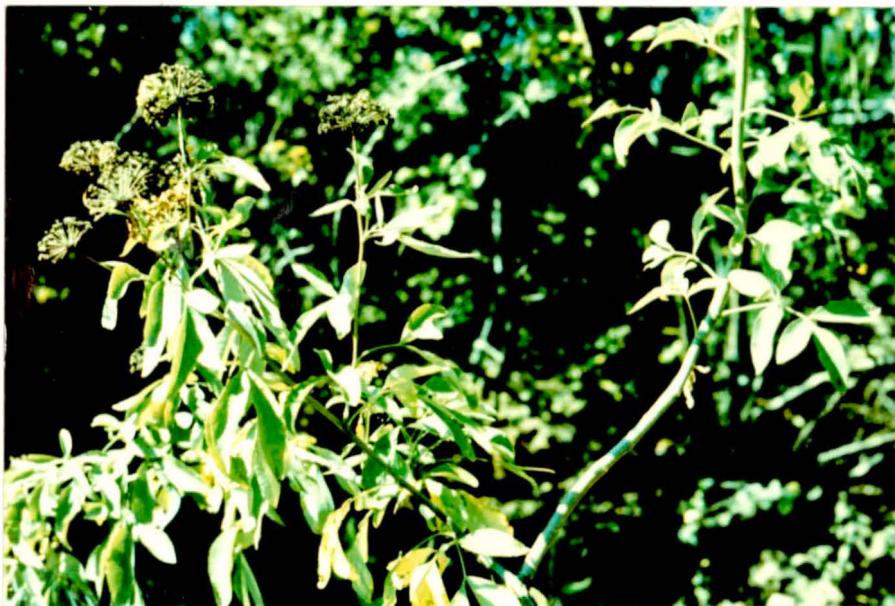
From well-branched herbarium specimens it is clear that *H. papillosa* has a similar habit, but tends to be smaller, only reaching 1,8 m. In mature stems of both these species, the amount of secondary xylem is much greater than pith, short shoots occur, and internode length varies tremendously with growth rate.

The synflorescences of *H. arborescens* and *H. papillosa* are produced terminally or pseudo-laterally (terminal on short shoots of previous growth cycle), whereas those in the other species are all terminal. Branching within the synflorescence is discussed in the following chapter. A new main axis is usually derived from a shoot which develops from the first vegetative bud directly below the synflorescence (Figure 3.5), while branching occurs lower down. Deciduousness has been observed in plants of *H. arborescens* var. *trifoliata* on the Transvaal highveld, but this phenomenon appears to be restricted to areas with a pronounced dry (cold) season.

The climbing habit reported for *H. arborescens* plants is here considered a variation of the tree habit, presumably resulting from low light intensities in dense vegetation. As this habit occurs in at least two varieties which are found in different



**Figure 3.4** The effect of fire disturbance on the habit of *Heteromorpha arborescens* var. *trifoliolata*. The plant in (A) is growing among rocks, protected from fire and has a well-developed trunk and is well-branched. The branches of the same plant are just visible on the skyline in (B). In the foreground in (B), the plant was exposed to fire in the previous season and has produced many unbranched stems from the caudex. (C) shows a plant two or three years after a fire, having regained its crown. A and B are at Chloorkop, NE of Johannesburg, and C is at the Wolkberg.

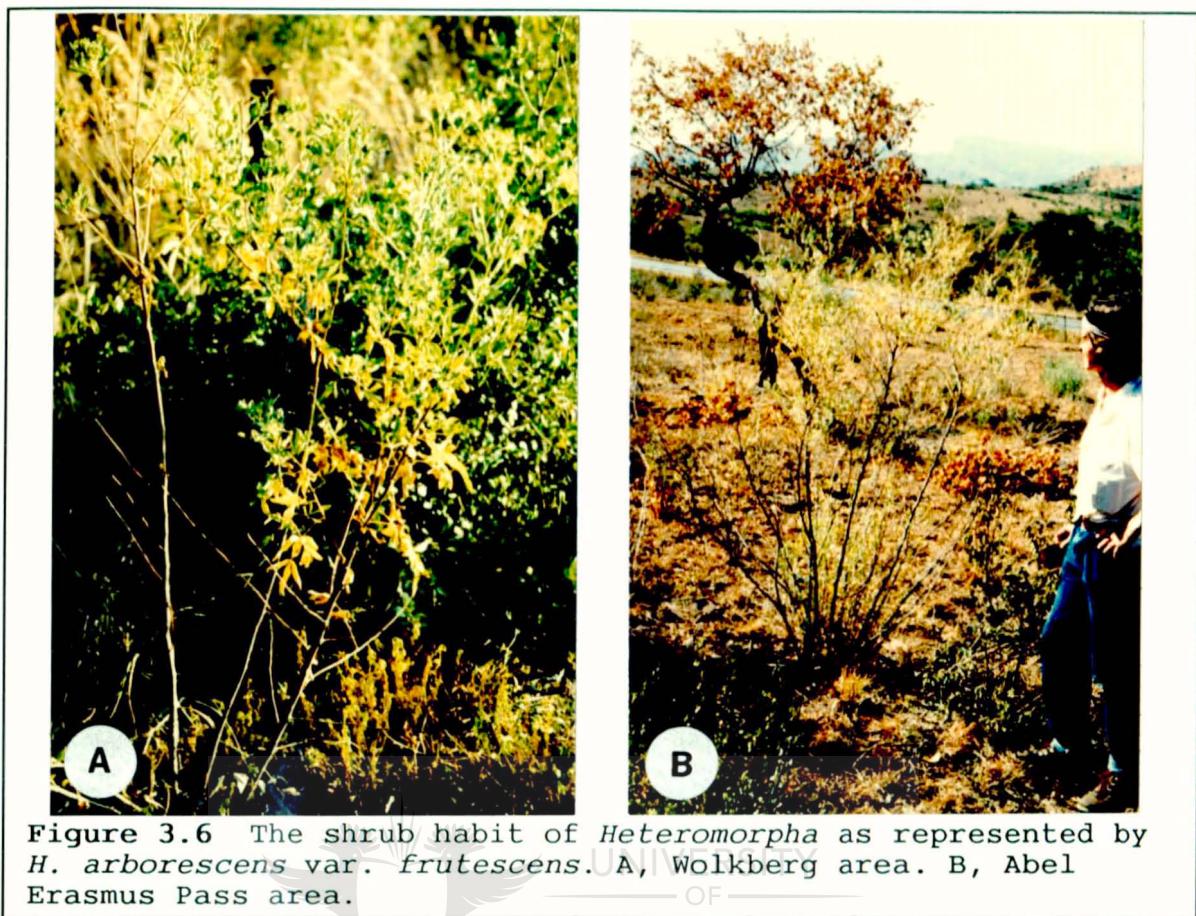


**Figure 3.5** Innovation growth in *Heteromorpha arborecens* var. *trifoliata*. The main growth impetus has been taken over by a shoot which has developed from the first vegetative bud directly below the terminal synflorescence.



habitats in the same areas, this phenomenon is not accorded any taxonomic significance.

*H. arborescens* var. *frutescens* represents the shrub category, and the plants are rarely taller than 2 m (Figure 3.6). If growth is not disturbed, a single trunk of c 50 mm in diameter may develop, which may branch with age. Lateral growth is not as strong as in the other varieties of *H. arborescens*, so that the growth of a vegetative stem or trunk is preferentially terminated after flowering and fruiting. The innovation buds seem to be concentrated below ground rather than on above-ground stems. After the reproductive stems have died, leaving few or no vegetative shoots to continue growth, new stems are usually



**Figure 3.6** The shrub habit of *Heteromorpha* as represented by *H. arborescens* var. *frutescens*. A, Wolkberg area. B, Abel Erasmus Pass area.

produced as suckers from the caudex. Fire seems to play a role in the life-cycle of the stem.

The suffrutescent habit (Figure 3.7), also termed semi-shrub, cryptocorm, and/or rhizocarpic habit by various authors, e.g. Troll (1964), Radford (1986) and Weberling (1989) is present in *H. stenophylla*, *H. occidentalis*, *H. gossweileri*, *H. pubescens* and most forms of *H. involucrata*. A caudex directly above a well-developed tuberous taproot (Figure 3.7 B) gives rise to one or more innovation shoots, which results in the renewal of the complete branching system above ground (normally simple, often solitary stems, which die back after one or two growth cycles). These stems are unbranched unless physically damaged, the growth



**Figure 3.7** The suffrutescent habit type in *Heteromorpha*. A, a multi-stemmed plant of *H. stenophylla* var. *transvaalensis*, from the Potgietersrus district, with slight branching due to growth disturbance. B, a single-stemmed plant of the same population, showing caudex and tuberous root. C, a multi-stemmed plant of *H. involucrata* from Saddleback Pass near Barberton, showing how stem growth is terminated by a single compound umbel.

of each stem being terminated by flowering. The straight and erect stems are thin, with a large spongy pith, but are sufficiently woody to defy description as a herbaceous perennial. The vegetative plant is usually 0,5 to 1,0 m tall, and may reach 1,8 m when flowering or fruiting. In *H. involucrata* the roots seem to be less tuberous and more woody in the plants excavated. *H. occidentalis* could not be studied *in situ*, but from descriptions (Jacques-Felix 1970a & 1970b) appears to be a more robust plant up to 2,5 to 3 m high. Plants of *H. involucrata* grown from seed (Winter 61) flowered after less than two years, similar to many biennial herbaceous plants in the family.



**Figure 3.8** The weakly branching shrub habit of *H. pubescens* from the Rosehaugh area.

A fourth type of habit which is actually a special case of the shrub category, is displayed by *H. pubescens* (Figure 3.8), and *H. involucrata*, both of which are otherwise suffrutescent. Although subterranean innovation buds are present, some innovation activity in these species occurs in the above ground portion of the plant, and they are therefore characterized by weak lateral branching rather than resprouting. This could depend on disturbance history, however. The forms of *H. involucrata* which

resemble *H. arborescens* in other characters, seem to fall into this category (judging from a single plant seen in the Barberton district of South Africa, and from descriptions on herbarium labels). The evolution of this somewhat woody habit is considered to be independent of that of other arborescent habits in the genus, although the possibility of introgression in the case of *H. involucrata* must be allowed for.

Taxonomically, habit is particularly useful for distinguishing *H. stenophylla*, *H. occidentalis* and *H. gossweileri* from most forms of *H. arborescens* var. *trifoliata*.

#### **Woodiness vs herbaceousness**



The family Apiaceae is widely considered to have arisen from the same basic stock as the Araliaceae (Rodríguez 1957, Burtt 1988), the common ancestor probably having a woody habit.

The distinction between the Araliaceae and the Apiaceae is traditionally based on the predominantly woody habit in the former and general herbaceousness of the latter. From a northern hemisphere perspective, this is understandable, but not when the woody genera of the Apiaceae from the tropics and southern hemisphere are considered. Rodríguez (1957) argues that if the three subfamilies of the Apiaceae do form a phylogenetic sequence as assumed, the sporadic occurrence of woodiness in all three precludes the idea that woodiness indicates primitiveness

in the family. This argument seems to be based on the notion that common equals primitive, which is debatable.

Rodríguez (1957) studied *Myrrhidendron* Coulter. & Rose and compared it with other woody genera. Burtt (1988) mentions that woodiness seems to be secondarily derived in *Myrrhidendron* (suggested by its strong resemblance to herbaceous Apiaceae in other characters). In *Heteromorpha* however, this interpretation of woodiness seems incongruent with other characters (see cladistic analysis), and there may have been repeated reversals in the family as a whole (see below).

Rodríguez (1957) could find no evidence to support the argument for secondary derivation of woodiness in *Myrrhidendron*. He compared *M. donnell-smithii* Coulter. & Rose with *M. glaucescens* (Benth.) Coulter. & Rose, a suffrutescent species, and interpreted the shorter vessel elements of the latter as a reflection of a reduced habit thus conditioned by a harsher environment. According to Rodríguez, it is likely that woody genera in the Apiaceae would have evolved along many divergent lines. This may be the case in the southern African woody genera, which show a very limited affinity among themselves and with other genera (Burtt 1991). However, Burtt (1991) pointed out that these genera may also represent relicts from an earlier diverse Apiaceae flora in the region.

### Stem surface features

Stems of *H. arborescens* and *H. involucrata* are either glabrous or pilose, *H. involucrata* usually being more pilose than *H. arborescens*. Young stems are particularly pilose, even in some of the forms where the mature stems are glabrous. In *H. pubescens*, the stems are invariably densely pilose with multicellular hairs. Stems of *H. papillosa*, *H. stenophylla* and *H. occidentalis* are always glabrous. In *H. gossweilerii*, stems can be either glabrous, papillate or shortly conically pilose.

Rodríguez (1957), reports a condition infrequent in the Apiaceae but common in the Araliaceae and in *Myrrhidendron*, namely the smooth surface of the stem, resulting from an unbroken cylinder of collenchyma under the epidermis. This is also evident in *Heteromorpha*, which in addition has a definite periderm around this cylinder (in *Heteromorpha* the periderm tends to obscure the underlying layers). This character is confined to the distinctly vegetative stems of woody *Heteromorpha* species, and those of some of the suffrutescent species e.g. *H. stenophylla*. Reproductive stems, and stems of species without distinct (lasting) vegetative aerial stems, have longitudinal striations corresponding to strands of collenchyma to the outside of secretory canals. These strands alternate with green chlorenchyma strands, to which the occurrence of stomata is limited. Such striations have been seen in *H. gossweileri*, *H. involucrata*, *H. stenophylla* and *H. occidentalis*. In the latter, the striations seem much finer.

A useful criterion to differentiate stem types is the presence of a distinct periderm vs a well-developed collenchymatous sheath (outer layers of the cortex). Peeling bark is normally only evident in *H. arborescens* (Figure 3.9). The freshly exposed (through peeling) periderm in *H. arborescens* lends a characteristic sheen (Figure 3.9 B) to the stem not seen in other species. The outer periderm layers tend to roll back in horizontal bands corresponding to the full length of an internode (Figure 3.9 A & B). These layers are parchment-like in appearance and are translucent when held up against the light. This feature enables light transmission to the chlorenchymatous layer on the inside of the periderm, which has been observed even in trunks of 250 mm in diameter. In some cases the underlying tissues are even visible through the periderm. It is not clear whether this has any adaptive advantage for the plant, e.g. efficiency of photosynthesis while in a leafless state. So far only slight peeling has been seen on stems of *H. arborescens* var. *frutescens* (Figure 3.9 C), but this could be merely a necessary correlation with the longevity / persistence of the plant or at least the aerial system, which is limited in this variety. The exact nature of the periderm and its relation to the development of the plant requires more study, using plants from populations of known age, as the only populations seen in the field had an uncertain fire history.

The surface of older stems of other woody species of *Heteromorpha* tends to be slightly rougher than that of *H. arborescens*, with a granular texture and is more persistent,



**Figure 3.9** Stem surfaces of *H. arborescens*. A, *H. arborescens* var. *montana* in the Chimanimani mountains. B, *H. arborescens* var. *trifoliata* at Melville, Johannesburg. C, *H. arborescens* var. *frutescens* on the Abel Erasmus Pass.

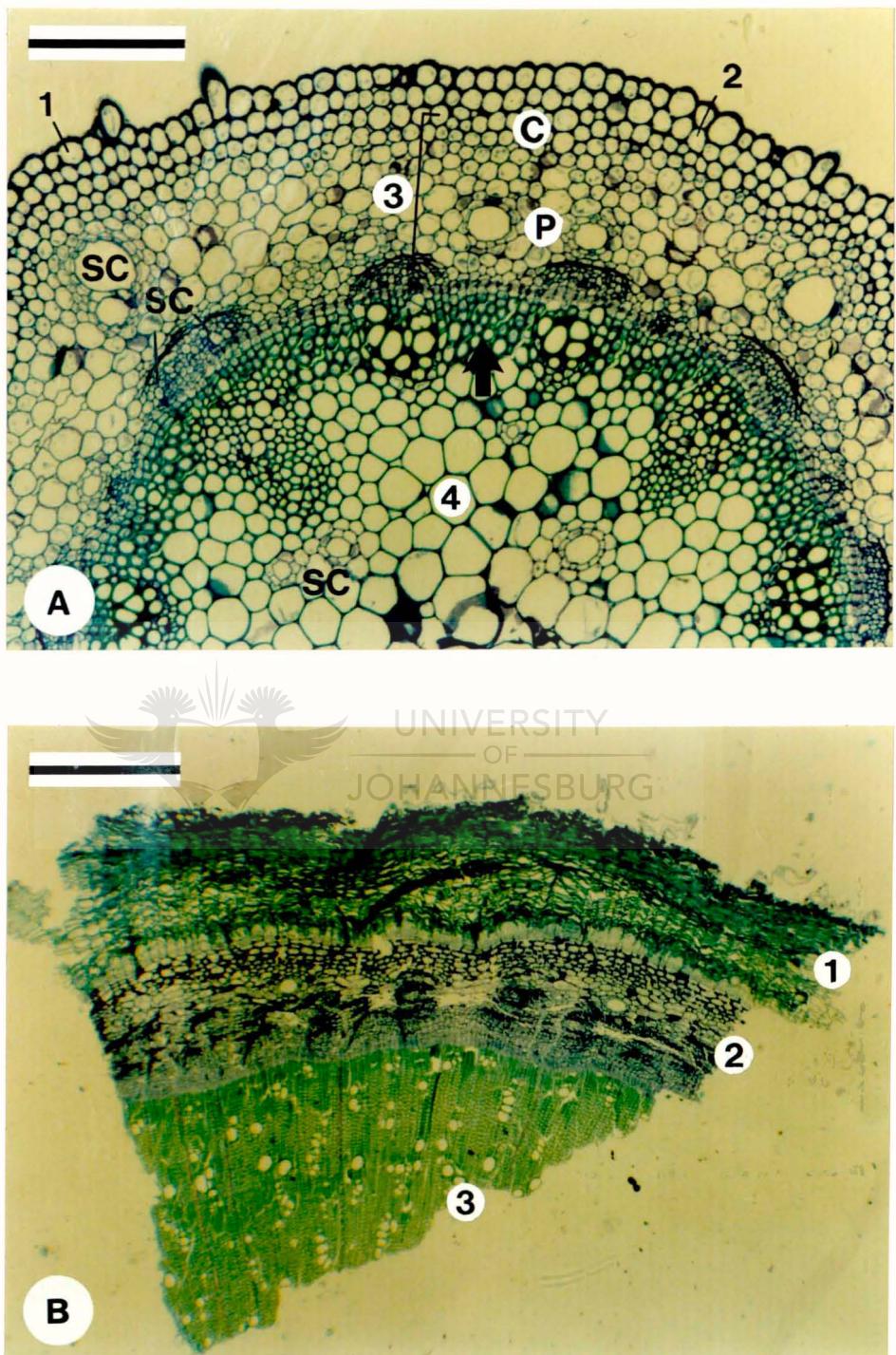


although one herbarium label for *H. pubescens*, Venter 8534 (PRE) reads: "glossy brown, flaking in rings".

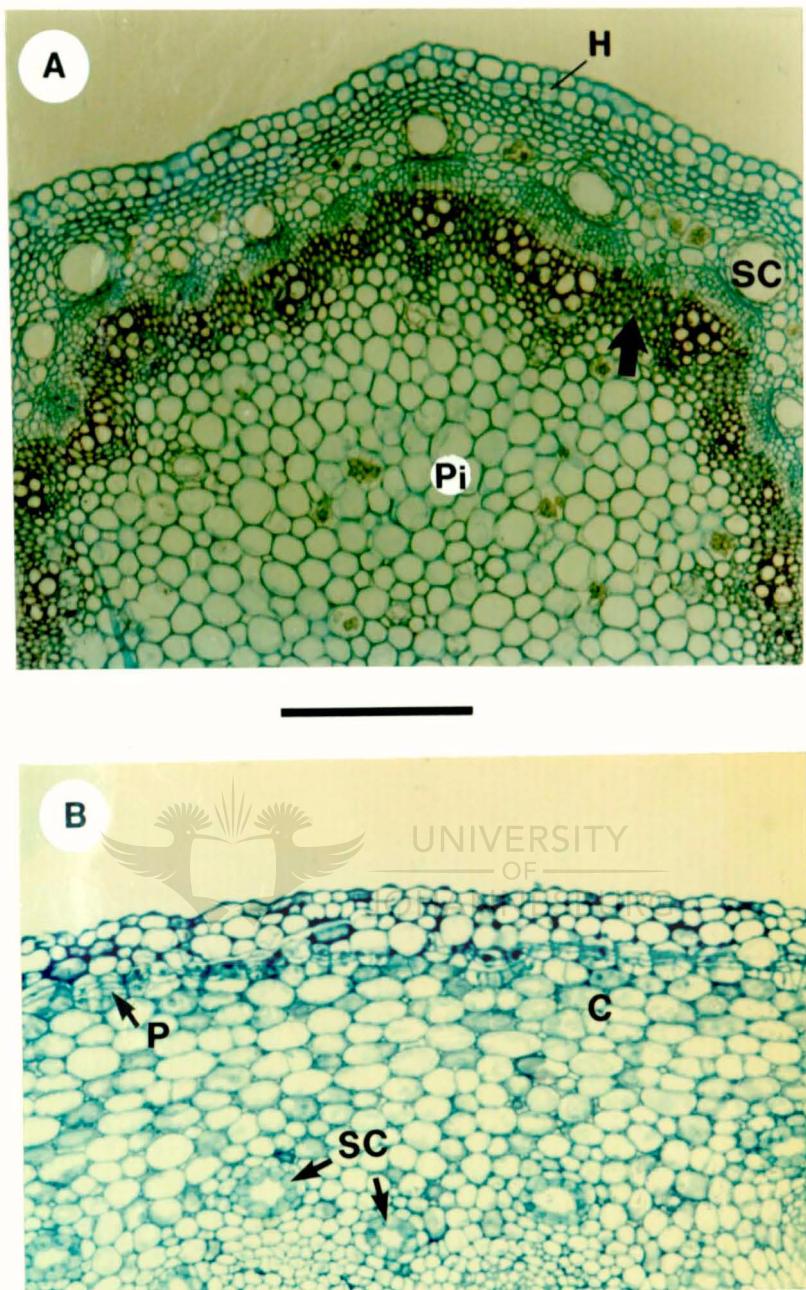
### **Stem anatomy**

The outer region of the stem consists of an epidermis (Figure 3.10 A<sub>1</sub>), a hypodermis (Figure 3.10 A<sub>2</sub>), and cortex (Figure 3.10 A<sub>3</sub>). The hypodermal layer becomes meristematic, forming a phellogen (Figure 3.11 A) which produces the periderm (Figure 3.10 B<sub>1</sub>). In this respect *Heteromorpha* differs from *Polemanniopsis* (Figure 3.11 B), where the phellogen (P in Figure 3.11 B) originates in the cortex (C in Figure 3.11 B).

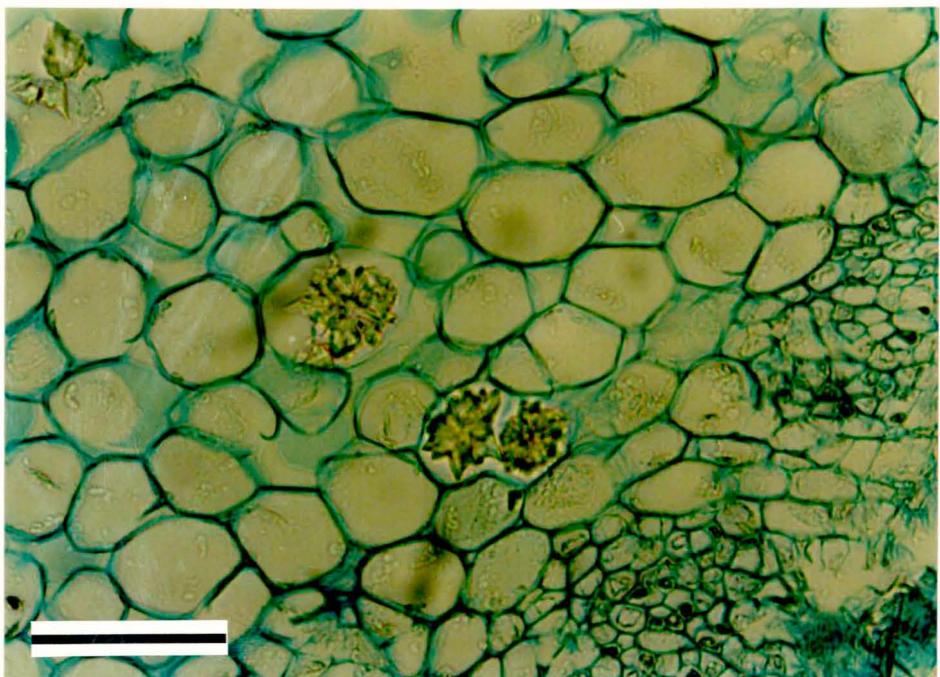
The cortex comprises collenchymatous outer layers (C in Figure 3.10 A) with chloroplasts and radial wall thickening, and parenchymatous inner layers (P in Figure 3.10 A), which are interspersed with secretory canals (SC in Figure 3.10 A; Figure 3.11 A & B). Secretory canals are arranged so that there is usually one to the outside of each primary vascular bundle (Figure 3.10 & 3.11). These canals are markedly larger in *Polemannia* than in *Heteromorpha*. The inner region is made up of a ring of vascular bundles surrounding a parenchymatous pith (Figure 3.10 A<sub>4</sub>; Pi in Figure 3.11 A). The interfascicular regions consist of libriform fibres (Rodríguez 1957) from an early stage (Arrows in Figure 3.10 A & Figure 3.11 A). Secretory canals are also found among the phloem elements and even in the pith (SC in Figure 3.10 A).



**Figure 3.10** Transverse sections through a young (A) and mature (B) stem of *H. pubescens*, Winter 69 (JRAU). A<sub>1</sub>, epidermis; A<sub>2</sub>, hypodermis; A<sub>3</sub>, cortex with collenchyma (C) and parenchyma (P) containing secretory canals (SC); A<sub>4</sub>, pith; B<sub>1</sub>, periderm, B<sub>2</sub>, secondary phloem; B<sub>3</sub>, secondary xylem; Arrow, libriform fibres. Note secretory canals in pith. Scale bars: A, 200 µm; B, 500 µm.



**Figure 3.11** Transverse sections through young stems of (A) *H. involucrata*, Winter 67, and (B) *Polemanniopsis marlothii*, Winter 87 (all in JRAU). In A, several hypodermal cells (H) are dividing tangentially to form a phellogen, while in B cortical cells undergo division [SC = secretory canal; C = cortex; P = phellogen; Arrow = libriform fibres]. Note crystal druses in the parenchyma of the cortex as well as in the pith (Pi) of A. Scale bar: 200 µm.



**Figure 3.12** Crystal druses in the cortex of *H. arborescens* var. *trifoliata*, Winter 71 (JRAU). Scale bar: 50 µm.

Crystal druses (Figure 3.11 A & 3.12), of calcium oxalate (Lemesle 1926), are occasionally observed in large numbers in the cortex and pith of *H. arborescens* var. *trifoliata* and *H. involucrata* (Figure 3.11 A), and are rare in *H. pubescens*. Such crystals are uncommon in the Apiaceae (Metcalfe & Chalk, 1950) but do occur in *Steganotaenia* Hochst. and in the Araliaceae (Rodríguez, 1957), three genera of Saniculoideae, and some five genera of herbaceous Apioideae (cf. Meyer 1937, cited by Rodríguez, 1957 and Metcalfe & Chalk, 1950). No crystals could be found in *Polemanniopsis*. The larger number of crystal-containing cells in the cortex of *H. involucrata* [as *H. glauca*] than in *H. arborescens*, was previously recorded as a diagnostic feature by Lemesle (1926), but this character was found to be inconstant for both *H. involucrata* and *H. arborescens*. The sporadic occurrence of calcium oxalate crystals in *Heteromorpha*,

and the observation of more numerous crystals in the cortex of *H. arborescens* var. *frutescens*, precludes any taxonomic inference based on this character.

The pith in the stems of all *Heteromorpha* species is unbroken and solid, but may disintegrate in older stems of *H. arborescens*. Secretory canals were seen in the pith of *H. involucrata*, *H. pubescens* (Figure 3.10 A) and *H. arborescens* var. *frutescens*, but not in *H. arborescens* var. *trifoliata*. The occurrence as observed is incongruent with other characters, but further investigation could reveal taxonomically useful characters.

Wood anatomy



Rodríguez (1957) surveyed the wood anatomy of most woody genera in the Apiaceae, and compared it with that of the Araliaceae. He found that *Heteromorpha* showed the most primitive character states (similar to *Myrrhidendron*) of all the Apiaceae members investigated, especially in length and perforation of vessel elements. The results for the two specimens of *Heteromorpha* from his survey are summarized in Table 3.1. The longest vessel elements in the Apiaceae were reported in *Steganotaenia* and *Heteromorpha*, and matched those found in what are considered specialized members of the Araliaceae.

Table 3.1 Wood anatomical characters of *Heteromorpha*, compared to average figures for the other members of the Ammineae-Carinae as surveyed by Rodríguez (Modified from Rodríguez 1957, Table 4).

CHARACTER	<i>H. arborescens</i> Schlieben sub. <u>Yale wood</u> 27537	<i>H. trifoliata</i> Brass 17342 (UC 951557)	OTHER CARINAE
<u>Vessels:</u> frequency / mm <sup>2</sup>	43	130	50--114
outline wall	angular to round thin; helical thickenings	angular to round thin; helical thickenings	round 3--10, thin; helical thickenings
pitting	scalariform to alternate	opposite to alternate	opposite, transitional
length	(290--)502(--670)	(160--)349(--600)	(55--)205(--520)
width	(25--)60(--105)	(20--)35(--60)	(8--)44(--120)
l/w ratio	8.4:1	10:1	3.5:1 to 8.7:1
end-wall angle	39 deg.	40 deg.	41--60 deg.
perforation	simple; 5 % double perfor.	simple; 0.5 % vestigial bars	simple
<u>Rays:</u> type	Het. II B	Het. II B	Het. II B
height	120--1300	---	100--2100

Rodríguez (1957) recorded a relatively high frequency of double perforations and vestigial bars in the perforation plates of *H. arborescens* (Thunb.) Cham. & Schlechtd. and in *H. trifoliata* (Wendl.) Eckl. & Zeyh., herein both treated as *H. arborescens*. This condition is also found in many of the Araliaceae, but is extremely rare in the Apiaceae (Rodríguez 1971). Vessel end walls showed the primitive state, i.e. with relatively sharp angles. Specialized states observed included whorled or helical tertiary thickening of vessel walls, shared only with *Bupleurum fruticosum* L. in the Ammineae-Carinae, and opposite to alternate pitting (Rodríguez 1971). There are about 6 to 12 rays per mm, sometimes without marginal (upright) cells. Fibres were reported to be 470 µm long (Rodríguez 1957).

Apart from the amount of secondary xylem formed, no differences in the wood anatomy were detected among the three species of *Heteromorpha* (with two varieties) investigated in this study. This discussion is therefore limited to the value of wood anatomical characters at the generic and suprageneric level. The only distinguishing character observed in the study was the prominent large-celled rays seen in transverse sections of mature wood in *Polemanniopsis*. The rays of both *Heteromorpha* and *Polemannia* have smaller cells.

In the eight *Heteromorpha* specimens sampled for this study, only simple perforations were seen in the end walls of the vessel elements. An in-depth study of macerated wood samples could reveal the double perforations and vestigial bars which were not seen in this study, but were reported by Rodríguez (1957, 1971).

Large pits resembling perforations were seen in *H. pubescens* and in *Polemannia* in the acute angled ends of vessel tracheids (Figure 3.13). These conducting elements seem to be transitional between tracheids and vessel elements. Rodríguez (1957) discusses various forms of multiperforate vessel types, but nothing similar to that found in the present study is reported. These conducting elements are closest in resemblance, at least superficially so, to the Gnetalean foraminata type of primitive perforation plate (Fahn 1982), which has to the best of my knowledge not yet been recorded in Angiosperm wood. This character state may be a further synapomorphy justifying the use of *Polemannia* as outgroup for *Heteromorpha*, but a wider survey and better understanding of the character is required.

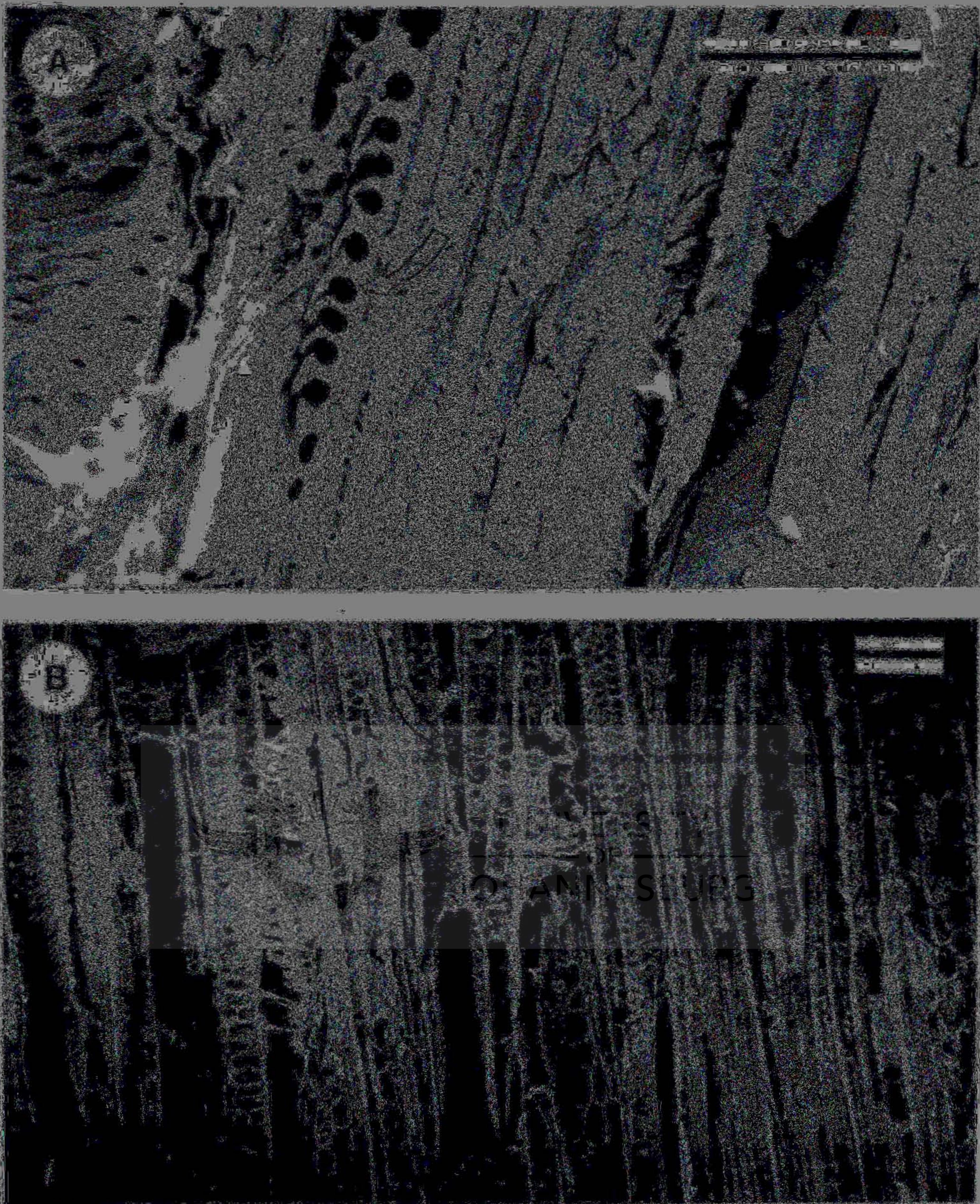


Figure 3.13 SEM micrograph of (A) a radially broken surface of secondary xylem of *H. pubescens*, Winter 69 and (B) a tangentially broken surface of *Poliemannia simplicior*, B.-H. & M. van Wyk 2872, showing large pits resembling perforations (arrows) in the acute angled ends of vessel tracheids. Vouchers in JRAU. Scale bars = 100 µm.

### 3.2.2 Root system

The storage root in the Apiaceae was studied in detail by Esau (1940) for *Daucus carota* L. It was shown that the storage root is a secondary development of the hypocotyl together with the primary root (Esau 1940). As



**Figure 3.14** An example of the simple, tuberous storage root in the suffrutescent species *H. stenophylla* var. *transvaalensis*. Scale bar: 500 mm.

discussed above under habit, a similar dauciform tuberous root develops in *Heteromorpha* soon after germination. *Heteromorpha* seedlings show the ability to resprout from the hypocotylar region of the root when the main stem is damaged, which would not be expected if the root was derived only from primary root tissue. It could be noted here that even the adventitious roots formed in *Heteromorpha* cuttings become tuberous at their bases.

The mature plant of suffrutescent species of *Heteromorpha* typically has a

simple tuberous root (Figure 3.14) representing the juvenile state (Figure 3.2) in the genus, while shrubby and arborescent species have a more branched system in accordance with the aerial system, with fleshiness diminishing further away from the caudex. In *H. arborescens* var. *trifoliata*, the fleshy nature is

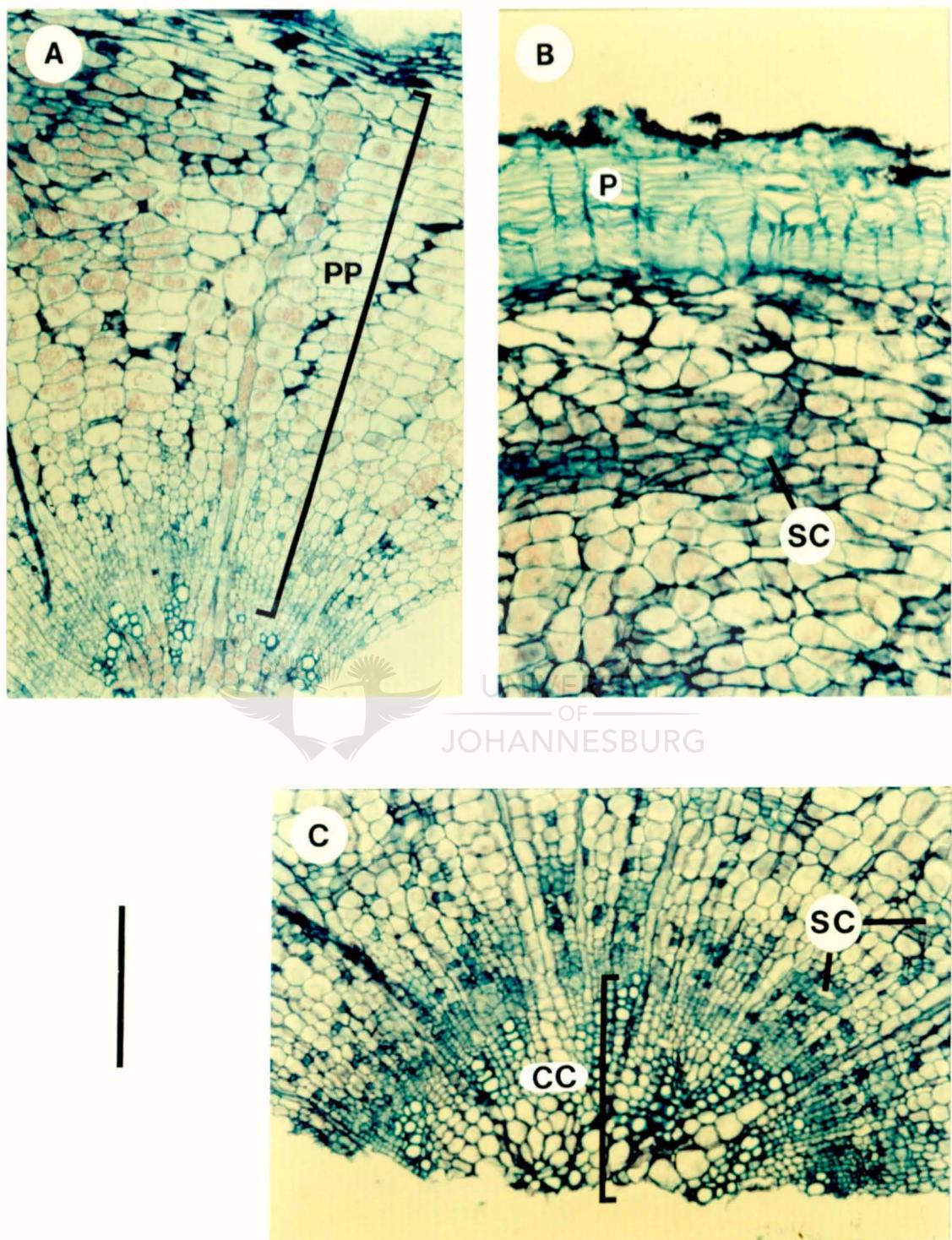
lost at maturity, in contrast with *Polemanniopsis* plants of similar dimensions, where even the secondary and tertiary roots are fleshy.

No differences were found among the roots of all four of the species of *Heteromorpha* investigated in the anatomical survey. Typical sections are shown in Figure 3.15. The storage root consists primarily (about 75 % of radial extent) of phloem and pericyclic tissue (PP in Figure 3.15 A), and is rich in large-celled storage parenchyma, though the distinction between phloem and pericycle, and hence their relative proportion is not clear. The proportion of parenchyma to other tissues in the central cylinder (CC in Figure 3.15 C) is also high. Simple and multiple starch grains (stained dark blue with iodine in potassium iodide) were present in the storage tissue (Figure 3.15). The periderm (P in Figure 3.15 B) is well developed and characteristically flaky, similar to that of stems with well-developed periderm. Secretory canals (SC in Figure 3.15 B & C) are present in the pericycle and phloem.

### 3.2.3 Leaves

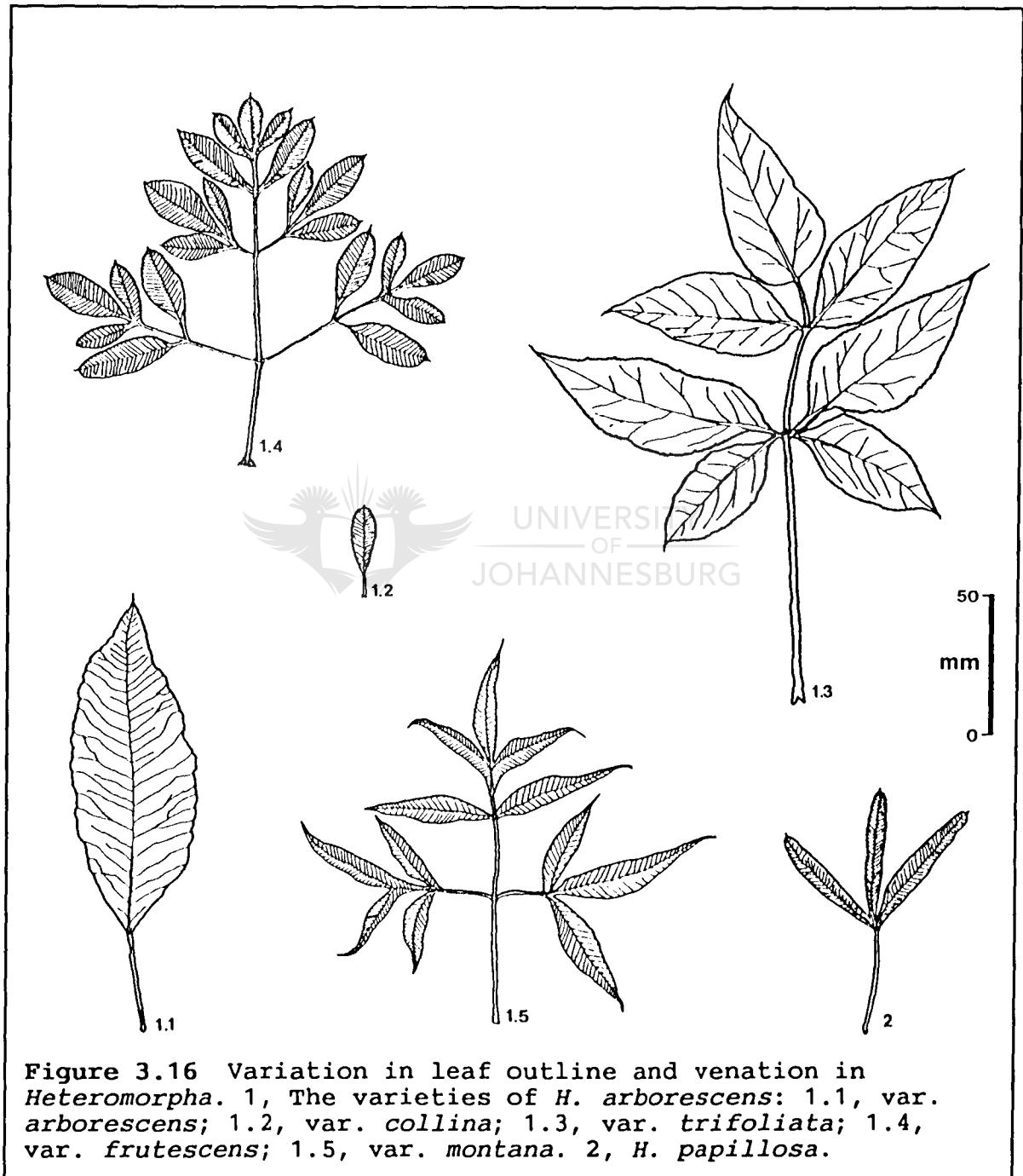
#### 3.2.3.1 Gross morphology

The leaflets of *Heteromorpha* have entire margins (Figure 3.16), a feature supporting the exclusion of the species from Madagascar which were included in the genus by Humbert (1955, 1956). These plants all have serrate leaflet margins. This is



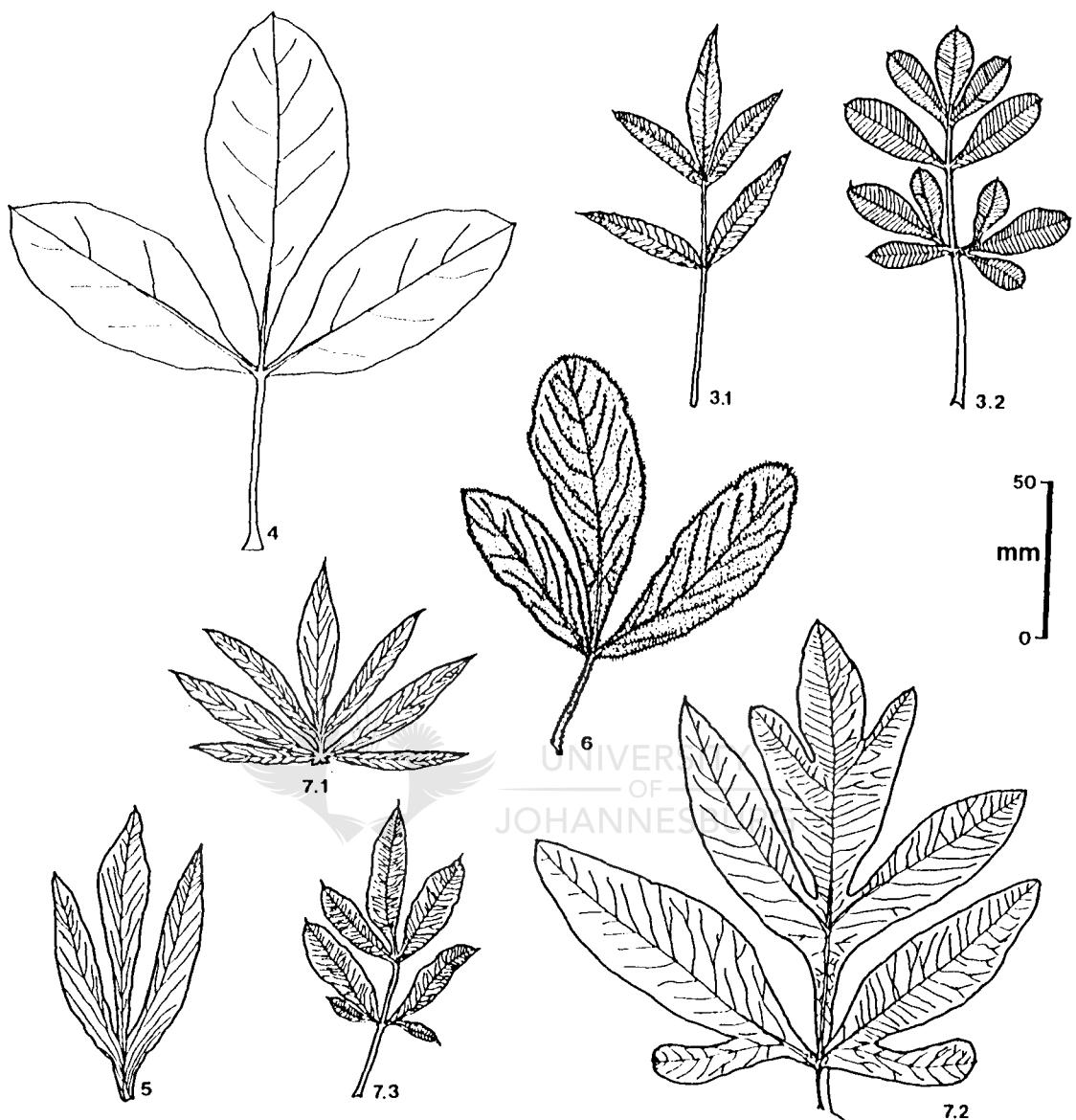
**Figure 3.15** Transverse sections through roots of *Heteromorpha*. A, *H. pubescens*, Winter 69 (JRAU). B & C, *H. arborescens*, Winter 71 (JRAU). Starch grains are stained red. [P = periderm; PP = phloem & pericyclic tissue; CC = central cylinder; SC = secretory canal] Scale bar: 200 µm.

also why *Heteromorpha* is considered to be more closely related to *Polemannia* than *Polemanniopsis*. The former genus has entire leaflets, while the latter has serrate leaflets.



**Figure 3.16** Variation in leaf outline and venation in *Heteromorpha*. 1, The varieties of *H. arborescens*: 1.1, var. *arborescens*; 1.2, var. *collina*; 1.3, var. *trifoliata*; 1.4, var. *frutescens*; 1.5, var. *montana*. 2, *H. papillosa*.

The large range of variability (polymorphism), which is characteristic of *Heteromorpha*, is probably best illustrated in



**Figure 3.16 (continued).** Variation in leaf outline and venation in *Heteromorpha*. 3, *H. stenophylla*: 3.1, var. *stenophylla*; 3.2, var. *transvaalensis*. 4, *H. occidentalis*. 5, *H. gossweileri*. 6, *H. pubescens*. 7, *H. involucrata*: 7.1, typical form; 7.2, 'kassneri' form; 7.3, 'Zimbabwe' form.

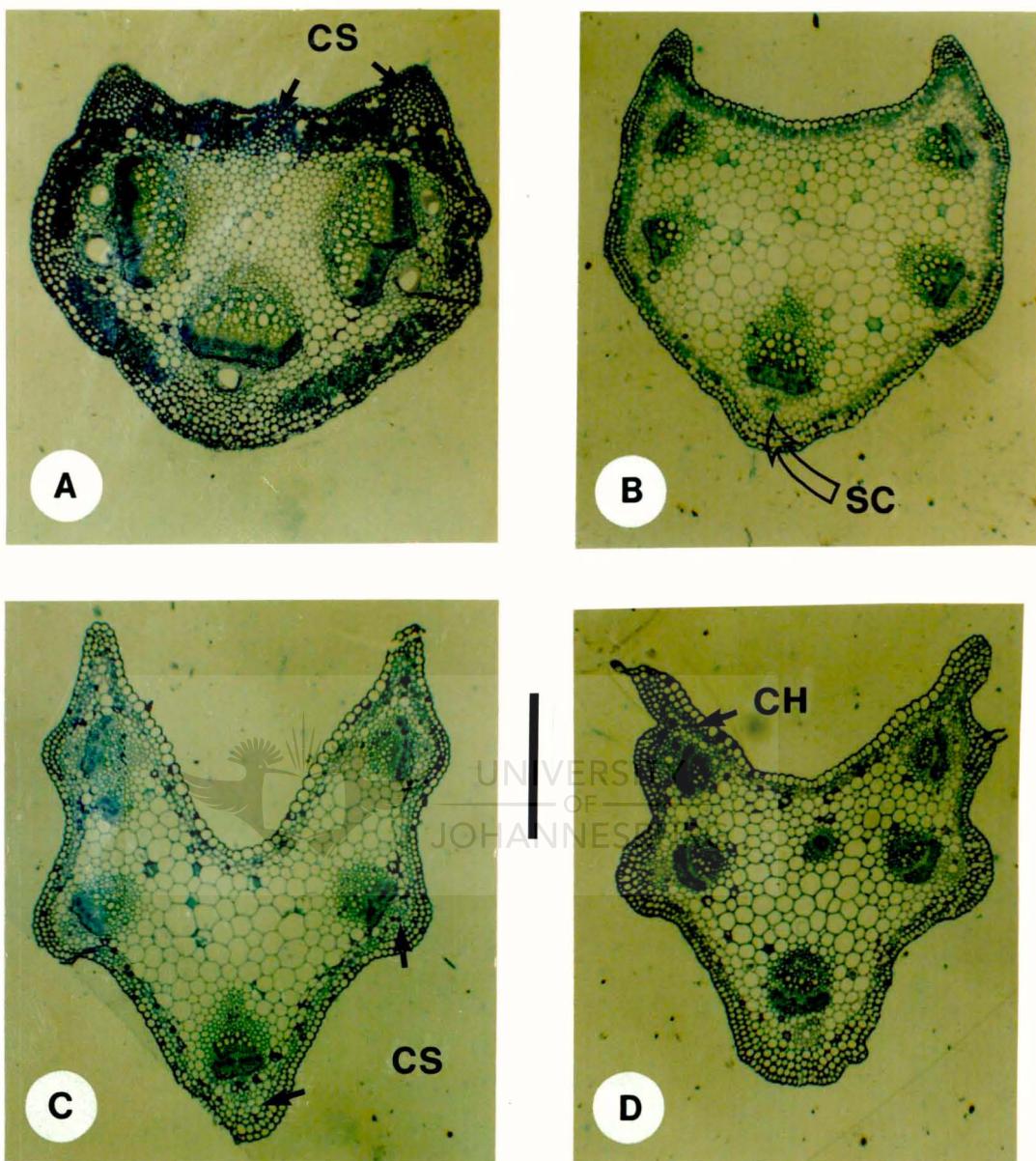
the leaves (Figure 3.16). The basic leaf shape is trifoliolate, the variations of which are simple (reduced), or further divided. When further divided, they are either pedately or pinnately (Figure 3.16: 1.4, 1.5, 3.1) compound, or various combinations of these two types (Figure 3.16: 1.3, 3.2, 7.1,

7.2, 7.3). The above variation is sometimes repeated in further subdivisions (Figure 3.16: 1.4). The incisions can be complete (with petiolules as in Figure 3.16: 1.3, 1.4, 1.5, or without petiolules as in Figure 3.16: 3.1, 7.1, 7.2, 7.3), decursive (Figure 3.16: 1.5, 7.2), parted or merely lobed (Figure 3.16: 7.2), leading to an immense range of leaf outlines. Although there are general trends for each taxon, there are no abrupt discontinuities. Distinct petiolules, for example, are typical for *H. arborescens*. Pronouncedly decursive lateral leaflets are likewise typical for *H. involucrata*.

It is not unusual to find trifoliolate leaves together with several variations of pedately or pinnately compound leaves on a single shoot of *H. arborescens* var. *trifoliata*. Apart from the initial development of the shoot from the bud state, when earlier leaves are the simplest, the variation does not follow a set sequence along the stem. With the material available, trifoliolate leaves seem to be a constant character for *H. occidentalis* (Figure 3.16: 4). All other species either show some degree of simplification, or of further pinnate and/or pedate division of the lamina. The typical pattern is pinnate with five leaflets (Figure 3.16: 3.1), the lower pair of leaflets often slightly larger than the upper leaflets, and sometimes (Figure 3.16: 1.3, 7.1, 7.3) with subsidiary basiscopic (pedate) leaflets. Complex patterns of division on this basic pattern are found in *H. arborescens* var. *trifoliata*, var. *montana*, var. *frutescens* (Figure 3.16: 1.4), and *H. stenophylla* var. *transvaalensis* (Figure 3.16: 3.2). The pedate division sometimes superficially approaches the palmate division

as in *Polemanniopsis*, but in general the division is close to that of *Polemannia*, where the midveins of the lowest pair of "pinnae" of a five membered leaf join those of the next pair of true pinnae just before the junction with the petiole, similar to 1.3 in Figure 3.16. Leaves of *H. gossweileri* are simple or tripartite (Figure 3.16: 5) to trifoliolate, usually with decurrent margins.

Leaves are subsessile in *H. gossweileri* (Figure 3.16: 5) with marginal and secondary venation and chlorenchyma continuing uninterrupted to the leaf base (winged petiole), or shortly petiolate only when trifoliolate. In some forms of *H. involucrata*, leaves are subsessile, with a short petiole dilating to form a leaf base (Figure 3.16: 7.1). The degree of amplexicauly varies, but leaf bases in *H. papillosa* and *H. arborescens*, except in *H. arborescens* var. *collina*, generally encircle the stem for two thirds of the circumference or more, while in other species, and also in *Polemannia* and *Polemanniopsis*, they generally encircle only half the circumference or less. Both *Heteromorpha* and *Polemannia* lack the broad sheathed base present in *Polemanniopsis*. Simple leaves of *H. arborescens* are always petiolate (Figure 3.16: 1.1), the general state in the genus. Petiole length distinguishes *H. gossweileri* (0 to 5 mm, rarely up to 30 mm) from *H. stenophylla* (35 to 43 mm, with extreme values of 25 mm and 102 mm---Figure 3.16: 3.1 & 3.2). In *H. involucrata*, the range is from 0,5 mm (Winter 61) to 94 mm (Torré & Paiva 10763). Forms of this species from Zimbabwe and Malawi (Figure 3.16: 7.3) have longer petioles (more than 25 mm) than other, more typical forms.



**Figure 3.17** Median transverse sections of petioles of some *Heteromorpha* species. A, *H. arborescens* var. *arborescens*, Van Wyk 3313. B, *H. arborescens* var. *trifoliata*, Winter 71. C, *H. involucrata*, Winter 61. D, *H. pubescens*, Winter 69. Vouchers all in JRAU. [SC = secretory canal; CH = chlorenchyma; CS = collenchyma strand] Scale bar: 500  $\mu\text{m}$ .

The petioles of *Heteromorpha* species are sulcate (Figure 3.17), similar to those of *Polemannia*, while in *Polemanniopsis* the groove is lacking. In transverse section, petioles vary from carinate in *H. occidentalis*, *H. involucrata*, and *H. pubescens* (Figure 3.17 C & D) or canaliculate in *H. gossweileri* and *H.*

*stenophylla* var. *transvaalensis*, to semiterete in *H. occidentalis*, *H. involucrata* and *H. arborescens* (Figure 3.17 B) or terete in *H. involucrata*, *H. stenophylla* var. *stenophylla*, *H. papillosa* and *H. arborescens* (Figure 3.17 A). In terete petioles of *Heteromorpha* species, the groove is only evident due to the two collenchyma ridges on either side of it. *Polemannia* has a shallow canaliculate petiole, similar to that seen in *H. gossweileri* and *H. stenophylla* var. *transvaalensis*.

The vascular bundle arrangement in the petiole is crescent shaped, V-shaped (Figure 3.17 C), or almost circular (Figure 3.17 B). As in other members of the Apiaceae (Metcalfe and Chalk 1950), one or more medullary bundles may be present (Figure 3.17 D) in addition to the peripheral bundles. Medullary bundles are collateral or centric (Figure 3.17 D). The number of bundles, and occurrence of medullary bundles is variable within a species according to state of growth and seems independent of lamina division. Five vascular bundles are typical (Figure 3.17 B), and the lateral pairs sometimes fuse (Figure 3.17 A), resulting in only three bundles. Secretory canals are present, usually at least to the outside of each bundle and in the phloem, sometimes in the pericycle (SC in Figure 3.17 B). Ridges of collenchyma along the canal border are separated from the nearest bundles by a layer of chlorenchyma (CH in Figure 3.17 D), which is interrupted by subepidermal collenchyma strands (CS in Figure 3.17 A & C) at the abaxial side of each peripheral bundle, and sometimes by a strand of collenchyma in the groove (Figure 3.17 A).

The pinna shape of *Heteromorpha* species is typically elliptic to lanceolate, but varies from very narrowly elliptic in *H. papillosa* (Figure 3.16: 2) to widely obovate in *H. arborescens* var. *trifoliata*, covering most variations in between. Taxonomically, the narrowly elliptic to almost linear pinnae of *H. papillosa* serve to distinguish it from *H. arborescens*. Within *H. arborescens*, var. *collina* is characterized by obovate leaves (Figure 3.16: 1.2), and var. *montana* by falcate, strongly decurrent, lanceolate leaflets (Figure 3.16: 1.5), which are sometimes almost as narrow as those of *H. papillosa*. *H. arborescens* is the only species where the terminal leaflet of a pinnately divided leaf can be distinctly petiolulate with an obtuse or rounded base (Figure 3.16: 1.3). *H. stenophylla* var. *stenophylla* has lanceolate to linear pinnae (Figure 3.16: 3.1), while var. *transvaalensis* has obovate to oblanceolate leaflets (Figure 3.16: 3.2). In some species, notably *H. involucrata*, there is tremendous variation as regards pinna outline. One form [Saddleback Pass, Winter 68] may have a decomound linear to virtually filiform lamina, while on another part of the same mountain range, a trifoliolate form [Malolotja, Braun 614] is found which has widely obovate pinnae. Similar variability was also reported by Townsend (1985) for general leaf form in *Heteromorpha*.

Pinnae dimensions vary from those of *H. collina*, with simple laminae 10 to 44 mm long and 5 to 13 mm wide, to the large leaflets of *H. occidentalis*, with pinnae of up to 115 x 45 mm. [Jaques-Félix (1970b) reports leaf lengths of up to 170 mm in this species]. A robust specimen of *H. stenophylla* from Malawi

has a terminal leaflet of 160 x 10 mm, but this is exceptional. Leaf dimensions are of limited taxonomic value, but may be used for diagnostic purposes in combination with other characters to distinguish *H. arborescens* var. *collina* from *H. arborescens* var. *arborescens*.

### 3.2.3.2 Venation

The primary venation can be either flush with the mesophyll, sunken in channels, partially buried in mesophyll, slightly projecting or extensively projecting. This character state has been used by Wolff (1921) to delimit *H. stolzii* Wolff, which was said to have sunken venation. However sunken veins have now been found to occur regularly in other taxa as well. The venation is pinnate to reticulate and variable within species. In *H. gossweileri*, the angle between the midrib and lateral veins is generally smaller than 45 degrees (Figure 3.16: 5). Venation is concluded to be of no taxonomic use in *Heteromorpha* as there are no discontinuities, but it does have diagnostic value for *H. gossweileri* in combination with other characters.

### 3.2.3.3 Epidermal morphology

Stomatal type has previously only been recorded for one of the woody African Apiaceae, namely *H. arborescens*. The presence of anomocytic stomata, which are considered a primitive type only shared with three other genera in the family, was found to

isolate the genus from its closest putative relatives (*Apium* L., *Trochiscanthes* Koch, *Cnidium* Cusson and *Seseli* L.) in Cerceau-Larrival's proposed tribe Heteromorpheae (Guyot 1971). Based on this evidence, Guyot (1971) suggested that *Heteromorpha* should be separated from the other four genera in this group. This isolation of *Heteromorpha* from other genera in the family is, however, incongruent with my results discussed below.

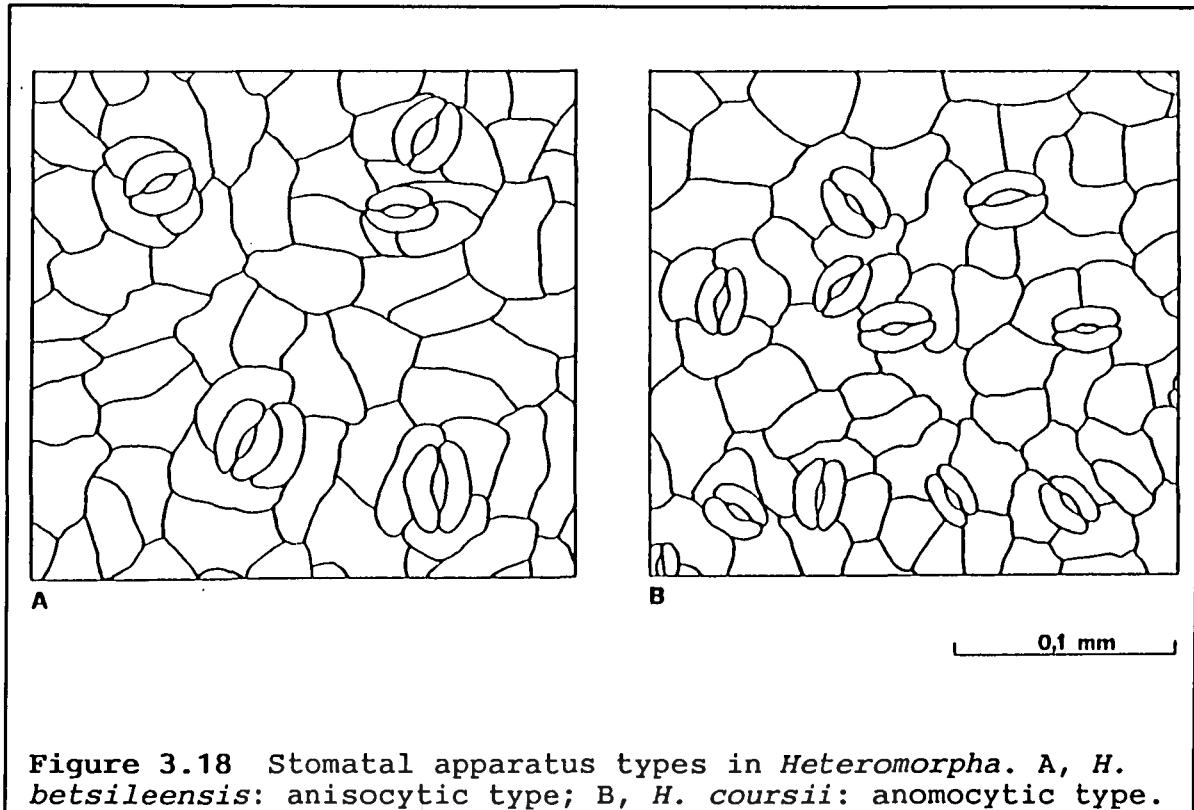
Most species of *Heteromorpha* are either glabrous or have trichomes which are not readily visible to the naked eye. Phenotypic variation as well as the broad species concepts employed in past surveys (mostly Flora treatments and therefore of a limited, regional nature), have tended to obscure the taxonomic relevance of vestiture. However, trichome type and trichome distribution have been used (Townsend 1985, 1989) to distinguish *H. trifoliata* (of that author) from species with basally tuberculate trichomes, and to characterise *H. papillosa* and *H. gossweileri* (Townsend 1985). Epidermal characters are therefore clearly of taxonomic value in *Heteromorpha*, especially when the paucity of information on other characters is considered.

Several characters of the epidermis were chosen for analysis and they were found to vary as described below:

## Stomatal apparatus

The stomatal apparatus proved difficult to interpret because cell boundaries were indistinct in the stomal region and because cells adjacent to the stoma differed superficially from the surrounding epidermal cells. The cuticle appears to be much thicker in this region, making the radial cell walls and guard cell boundary almost indiscernible. This at first suggested a tetracytic or actinocytic arrangement, but the number of surrounding cells was too inconsistent for this to be the case. Stoma are juxtaposed in some instances, or separated by one cell only (Figure 3.18 B), confirming the perigenous anomocytic origin. Cells surrounding the stomata sometimes differ from other epidermal cells in their reaction to staining, but there is no evidence of any structural difference, hence the interpretation that these are not true subsidiary cells.

As found by Guyot (1971) for *H. arborescens*, the rest of the genus (with one exception) as well as the genera *Polemannia* and *Polemanniopsis*, all possess the anomocytic type stomatal apparatus (Figure 3.18 B). The stomata of the Apiaceae are generally considered to be more or less intermediate between anomocytic and anisocytic (Guyot 1971; Ostroumova 1987 in Baranova 1992). The anomocytic type of stomatal apparatus seems conservative, occurring throughout, with the exception of *H. betsileensis*, suggesting a different position for this species. This is also the only Madagascar species with any degree of vestiture on the laminar region. *H. betsileensis* has an anisocytic type stomatal apparatus (Figure 3.18 A). The radial



**Figure 3.18** Stomatal apparatus types in *Heteromorpha*. A, *H. betsileensis*: anisocytic type; B, *H. coursii*: anomocytic type.

cell walls of subsidiary cells are shorter than the tangential walls, giving them a thinner shape than the normal epidermal cells. The characteristic clustering of the stoma with three surrounding cells suggests a common origin from one stomatal initial cell (mesogenous type), although it must be emphasized that the ontogeny was not studied (see Baranova 1992 for a detailed discussion of morphological vs ontogenetic classification of stomata). The occurrence of a second stomatal type could indicate a polyphyletic grouping of the Madagascar species, as this feature appears to be rather conservative in the Apiaceae, and is a potential character for tribal delimitation.

### Stomatal dispersion

Stomata sometimes occur in crypts formed by the prominently raised veins on the abaxial surface, as in *H. pubescens*.

In *H. arborescens* var. *frutescens* the stomata occur in chain-like clusters in the interstitial regions, whereas in the other species they are randomly dispersed in that region, or concentrated along veins.

Four main patterns of stomatal dispersion over the adaxial surface were identified. Stomata can be absent, occur along the margin and/or midrib only, occur mostly along the margin and veins, or occur throughout the entire surface. These data are listed in Table 3.2. In the Madagascar species and the other genera stomata are either absent or dispersed randomly across the entire surface. *Heteromorpha sensu stricto* by contrast, shows great variation. *H. stenophylla* var. *stenophylla* and *H. gossweileri* differ from the other African species and varieties by the occurrence of stomata across the entire adaxial surface. This stomatal dispersion pattern (state 4 of Table 3.2) is shared with all *Polemanniopsis* and *Polemannia* species, but with only two Madagascar species (*H. andohahelensis* and *H. bojeriana*). In *H. papillosa* this state co-occurs with states 2 and 3 of Table 3.2. There may be a logical correlation between this character and the high adaxial stomatal density in these species.

TABLE 3.2 Epidermal character state distribution for leaves of *Heteromorpha*, *Polemannia*, and *Polemanniopsis* surveyed. (Voucher specimens are listed in Table 2.1)

CODE	TAXON	ADAXIAL STOMATAL DISPERSION				TRICHOMES											Distribution							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18					
<i>Heteromorpha</i> (African species)																								
1	<i>H. arborescens</i>	-	+	+	-	-	-	-	+	-	-	-	F	+	-	-	-	-	-	-	-	-	-	
1a	var. <i>arborescens</i>	-	+	+	-	-	-	-	+	-	-	-	-/F	+/F	R	-	R	-	-	-	-	-	-	
1b	var. <i>trifoliata</i>	+	+	+	-	-	-	-	-	-	-	-	-/F	-/B	-	-	-	-	-	-	-	-	-	
1c	var. <i>frutescens</i>	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2	<i>H. papillosa</i>	-	+	+	+	-	-	-	+	-	-	-	B	B	-	-	-	-	-	-	-	-	-	-
3	<i>H. stenophylla</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.1	var. <i>stenophylla</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.2	var. <i>transvaalensis</i>	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	<i>H. occidentalis</i>	+	+	-	-	+	+	-	-	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-
5	<i>H. gossweileri</i>	-	-	-	+	+	-	-	-	-	+	-	+	+	+	-	+	-	-	-	-	-	-	-
6	<i>H. pubescens</i>	+	-	-	-	-	-	-	-	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+
7	<i>H. involucrata</i>	-	+	+	-	+	+	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	-
7a	typical form	-	+	+	-	+	+	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	-
7b	'kassneri' form	+	-	-	-	-	-	+	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	-
7c	'Zimbabwe' form	-	+/	+	-	-	+	+	-	+	-	+	+	+	+	-	+	+	+	+	+	+	+	-
7d	'Malawi' form	+	-	-	-	-	+	+	-	+	-	+	+	+	+	+	+	+	R	-	-	-	-	-

Adaxial stomatal distribution: 1, absent; 2, margin only; 3, mostly margin & veins; 4, across entire surface.

Trichome type: 5, papillate; 6, conical; 7, long cylindric; 8, short cylindric; 9, filamentous; 10, tuberculate; 11, multicellular.

Trichome distribution: 12, margin; 13, adaxial midrib; 14, adaxial lateral veins; 15, entire adaxial surface; 16, abaxial midrib; 17, abaxial lateral veins; 18, entire abaxial surface.

Legend: + = present; - = absent; F = few; R = rare; B = basal only

TABLE 3.2 (continued)

CODE	TAXON	ADAXIAL STOMATAL DISPERSION				TRICHOMES						Distribution						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Heteromorpha</i> (Madagascar species)																		
M1	<i>H. taxiflora</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M2	<i>H. marojejyensis</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M3	<i>H. tsaratananensis</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M4	<i>H. coursii</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M5	<i>H. betsileensis</i>	+	-	-	-	-	-	-	+	+	-	-	-	-	B	R	-	-
M6	<i>H. andringitrensis</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M7	<i>H. andohahelaensis</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
M8	<i>H. bojeriana</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
P0	<i>Polemanniopsis marlothii</i>	-	-	-	+	+	-	-	-	-	-	-	+	-	-	-	-	-
P1	<i>Polemannia montana</i>	+	-	-	+	+	-	-	-	-	-	-	+	-	-	-	-	-
P2	<i>P. simplicior</i>	-	-	-	+	+	-	-	-	-	-	-	+/	+/	-	-	-	-
P3	<i>P. grossulariifolia</i>	-	-	-	+	+	-	-	-	-	-	-	+/	+	IMV	-	-	-

Adaxial stomatal distribution: 1, absent; 2, margin only; 3, mostly margin & veins; 4, across entire surface.

Trichome type: 5, papillate; 6, conical; 7, long cylindric; 8, short cylindric; 9, filamentous; 10, tuberculate; 11, multicellular.

Trichome distribution: 12, margin; 13, adaxial midrib; 14, adaxial lateral veins; 15, entire adaxial surface; 16, abaxial midrib; 17, abaxial lateral veins; 18, entire abaxial surface.

Legend: + = present; - = absent; F = few; R = rare; B = basal only; IMV = intramarginal vein

## Stomatal distribution and density

The distribution and density of stomata (on both leaf surfaces) are diagnostic for some species or varieties. The results of the stomatal density study are presented in Figure 3.19. The data show that the variation in this character is independent of habit and is also not logically correlated with mesophytic or xerophytic habitats. Compared to *Heteromorpha*, the other two genera are relatively invariant in terms of abaxial density (Figure 3.19 A), with values of around 110 per mm<sup>2</sup>. Across *Heteromorpha*, most species have between 100 and 200 stomata per mm<sup>2</sup> on the abaxial surface. There are three Madagascar species with far higher values. These are *H. marojejyensis* (M2: mean=279), *H. tsaratananensis* (M3: mean=293) and *H. coursii* (M4: mean=265). This is a potential grouping character within the Madagascar contingent, and could support the division of this group into two or more genera when these species are investigated further.

In the African *Heteromorpha* group, notable outliers are *H. involucrata* - 'kassneri' form (7b: mean=229), *H. gossweileri* (5: mean=220) and *H. stenophylla* var. *stenophylla* (3.1: mean=88). *H. stenophylla* var. *stenophylla*, previously considered merely a form of *H. arborescens* var. *trifoliata* (Schreiber 1967; Townsend 1985), is distinguished from the latter (1c) by having less than 100 abaxial stomata per mm<sup>2</sup> and a substantially higher adaxial density (3.1: mean=27 in Figure 3.19 B). The other species all have higher abaxial densities (Figure 3.19 A). *H. occidentalis* (4: mean=162) is clearly distinguishable from all the central

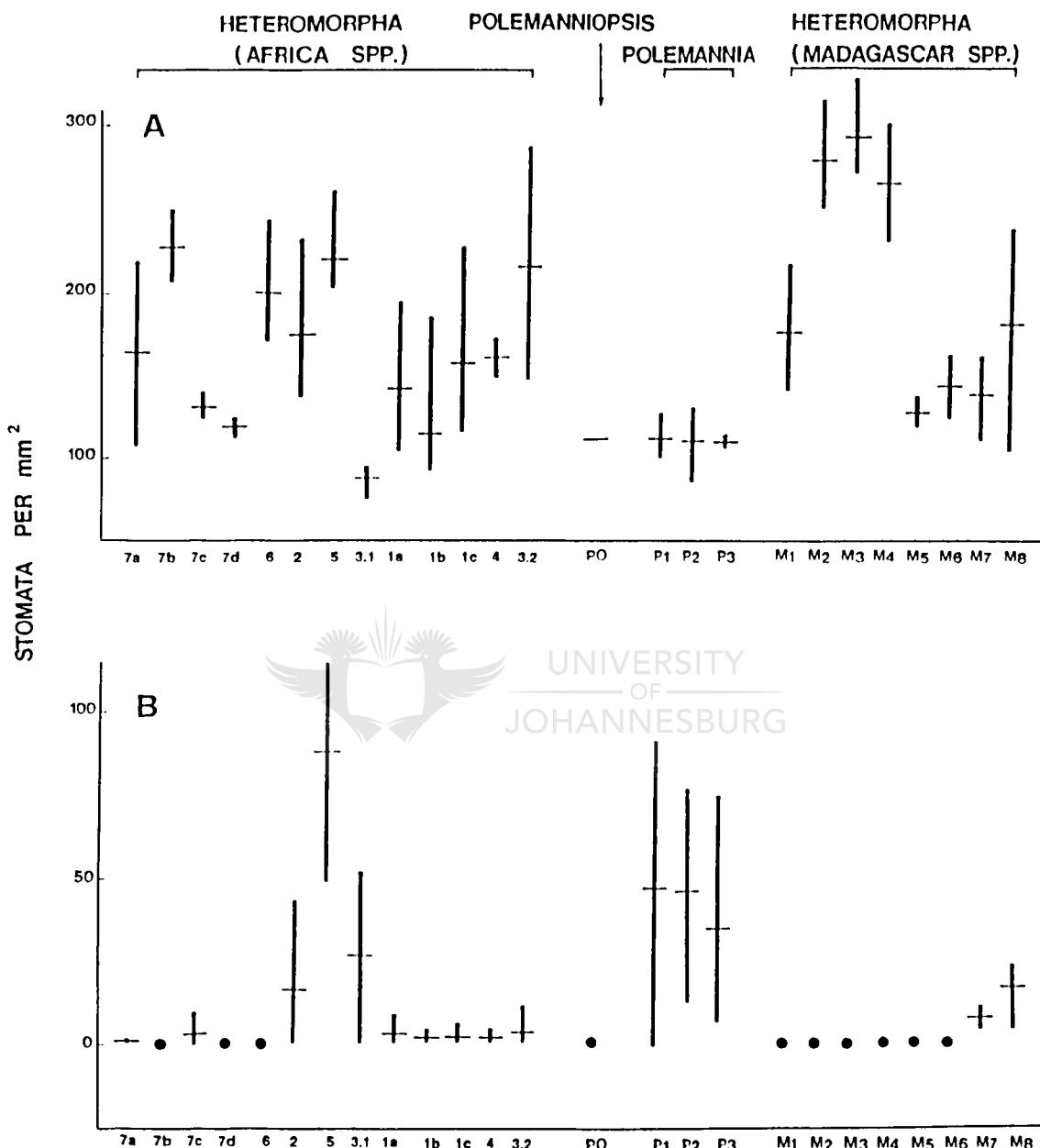


Figure 3.19 A, abaxial density; B, adaxial density of stomata in the genera *Heteromorpha*, *Polemanniopsis* and *Polemannia*. Range and mean values of specimens examined are indicated for each species/form; — = absence of stomata; single values ( $n = 1$ ) are denoted by a horizontal bar only. Taxa numbered and sampled as in Table 2.1. & Table 3.2.

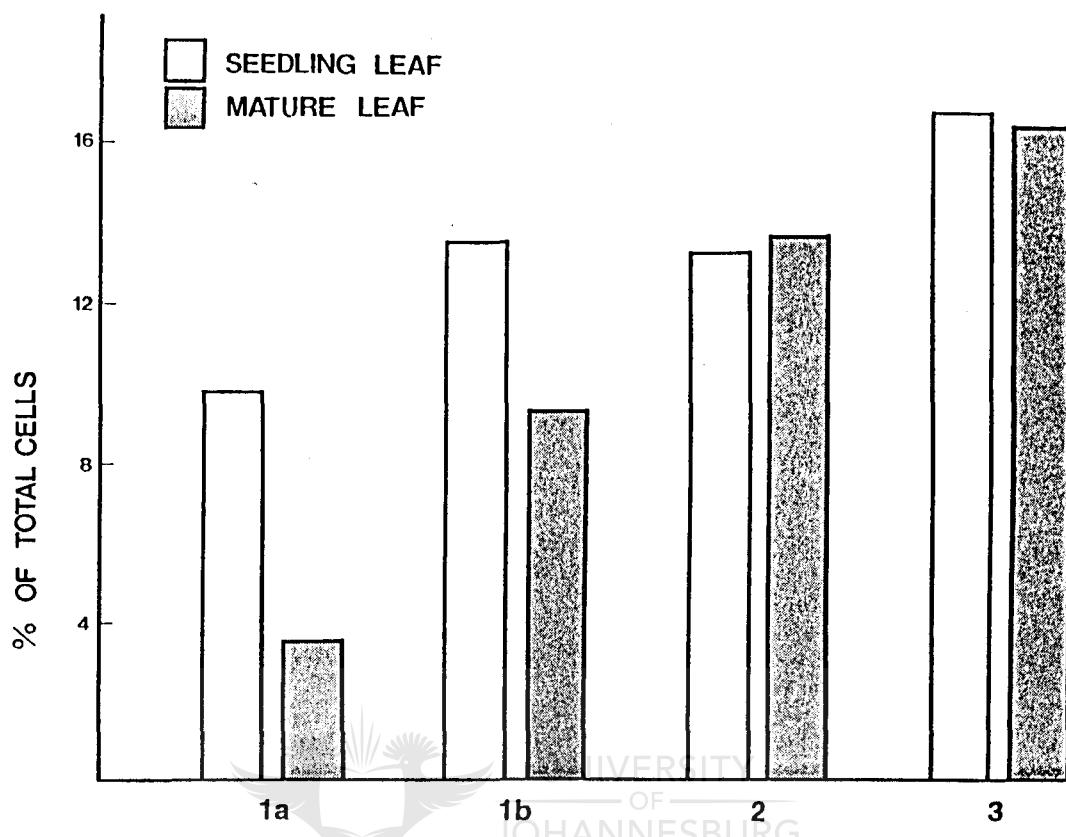
African forms of *H. involucrata* (7b, 7c & 7d; means=229, 131 & 119 respectively).

Most species examined had none or virtually no adaxial stomata (Figure 3.19 B), whereas *Polemannia* has on average just over 40 stomata per mm<sup>2</sup>, and a relatively high variation per species. Adaxial stomata are rare (means less than 5 per mm<sup>2</sup>) or absent in most *Heteromorpha* species except *H. papillosa* (2: mean=16), *H. gossweileri* (5: mean=88), *H. stenophylla* var. *stenophylla* (3.1: mean=27), *H. andohahelensis* (M7: mean=8) and *H. bojeriana* (M8: mean=17).

#### Epidermal ontogeny



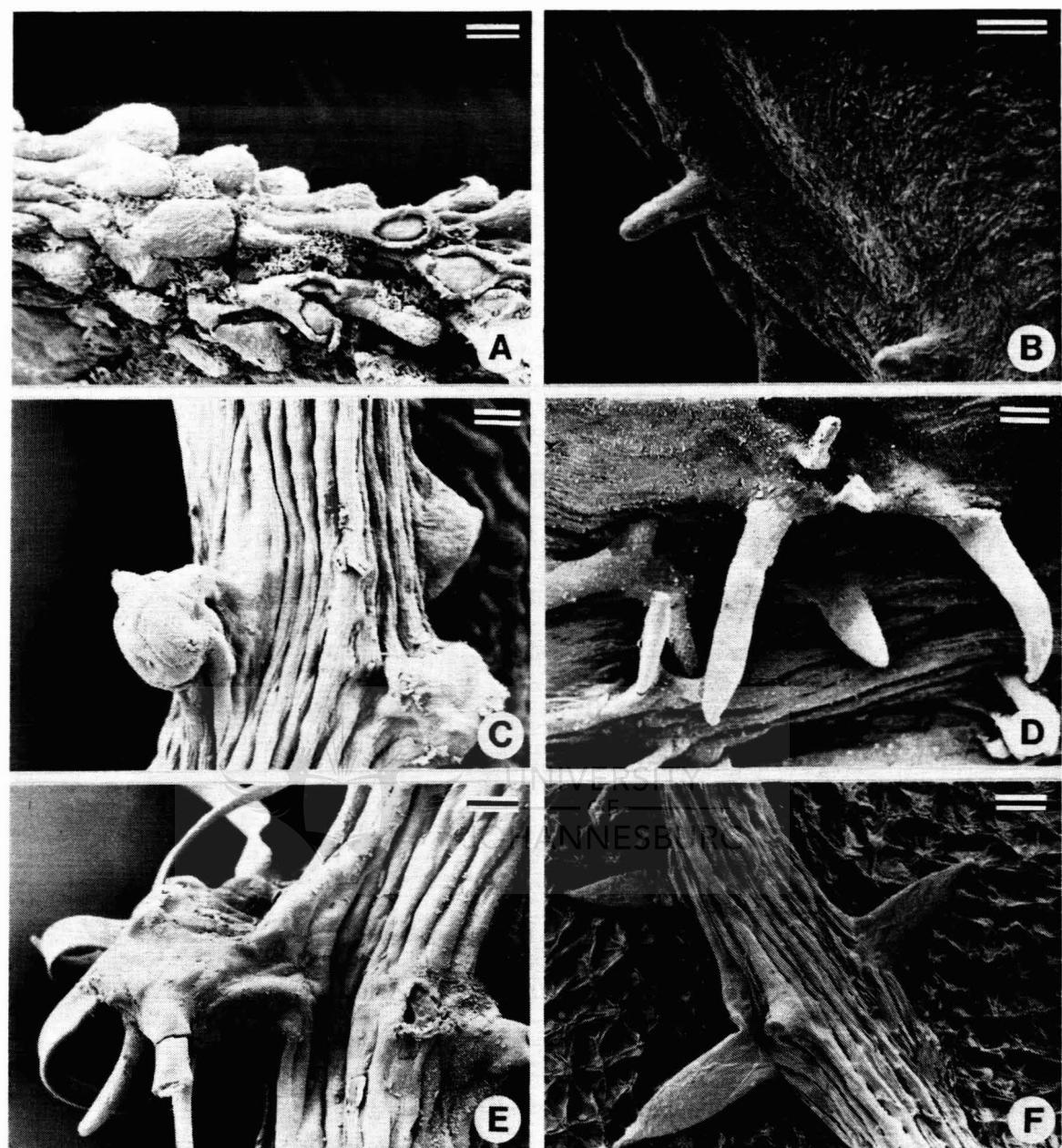
*H. arborescens* var. *frutescens* and *H. arborescens* var. *trifoliata* show an ontogenetic feature not present in *H. pubescens* and *H. involucrata*, namely a decrease in size (Figure 3.20) of normal epidermal cells. The number, size and outline of normal epidermal cells are different in juvenile and adult leaves (Figure 3.20: 1a & 1b). As the leaves develop from the juvenile to the mature stage, the proportion of stomata to normal epidermal cells remains constant in *H. involucrata* and *H. pubescens*, whereas it decreases in the two varieties of *H. arborescens*. This is not due to fewer stomata being formed, but to a reduction in size of the normal epidermal cells and thus a higher epidermal cell density.



**Figure 3.20** Variation in leaf epidermal ontogeny in *Heteromorpha* indicated by differences in proportions of stomata to surrounding cells between seedlings and mature leaves. This is a function of the size and number of normal epidermal cells. [1a = *H. arborescens* var. *trifoliata*, Winter 71; 1b = *H. arborescens* var. *frutescens*, Winter 57; 2 = *H. involucrata*, Winter 61; 3 = *H. pubescens*, Winter 69]

#### Trichomes and their distribution

Several trichome types (Figure 3.21 & Figure 3.22) are recognized which, when combined with dispersion pattern, also serve to characterise certain species and forms. The variation in mature trichome types as well as their distribution is summarized in Table 3.2.



**Figure 3.21** Trichome types in *Heteromorpha sensu stricto*. A, *H. gossweileri*: papillate hairs, resembling juvenile state; B, *H. arborescens* var. *trifoliata*: short cylindric hairs; C, *H. involucrata* - typical form: short conical hairs on tuberculate base; D, *H. involucrata* - 'kassneri' form: multicellular, long cylindrical hairs; E, *H. pubescens*: filamentous trichomes on tuberculate base; F, *H. involucrata* - 'Malawi' form: conical trichome. Scale bars: 10 µm.

#### Trichome type

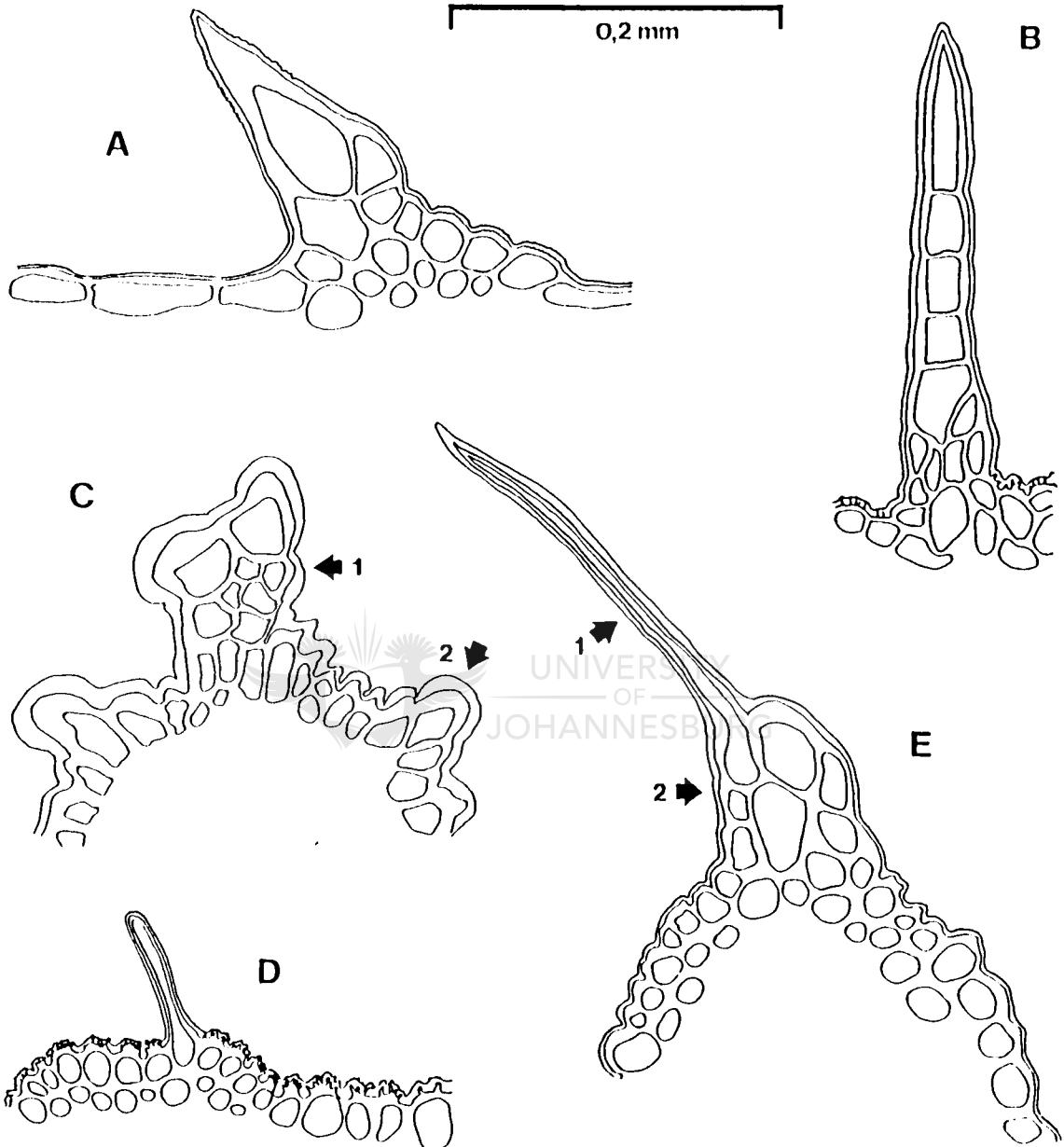
The various types were analysed in terms of seven character states (Table 3.2). The papillate type (Figure 3.21 A & 3.22 C<sub>2</sub>),

which is also the juvenile type, has a wide occurrence (present in all three genera), and is also the only type for *Polemanniopsis* and *Polemannia*. Compared to the Madagascar group where only the long, slender (filamentous), multicellular hair is found in *H. betsileensis* alone, the African species show a high diversity of form.

Papillate trichomes, similar to those shown in Figure 3.21 A & 3.22 C<sub>2</sub>, were observed on the juvenile leaf margins of *Heteromorpha*. These were present on the juvenile leaves in all forms of the five African species investigated. This feature appears to be the primitive state which is variously lost or modified by means of apical and sometimes basal cell differentiation in the ontogeny of the mature types.



Tuberculate trichomes occur either as simple tubercles (Figure 3.22 C) or with one (Figure 3.21 C & 3.21 A, B & E) or many (Figure 3.21 E) trichomes of another type affixed apically, described by Townsend (1985) as papillose. This feature is characteristic of *H. pubescens* and most forms of *H. involucrata*, but the tubercles are limited to a slight cushion in some forms, as well as in *H. occidentalis* and *H. gossweileri*. The term 'verruculose' used by Townsend (1985) to describe the vestiture in *H. gossweileri*, suggests the simple tuberculate type of trichome (Figure 3.22 C<sub>1</sub>). Although the SEM survey only showed the papillate type (Figure 3.21 A), which does bear a superficial resemblance, light microscopy confirmed the presence of some cushioned trichomes (Figure 3.22 C).

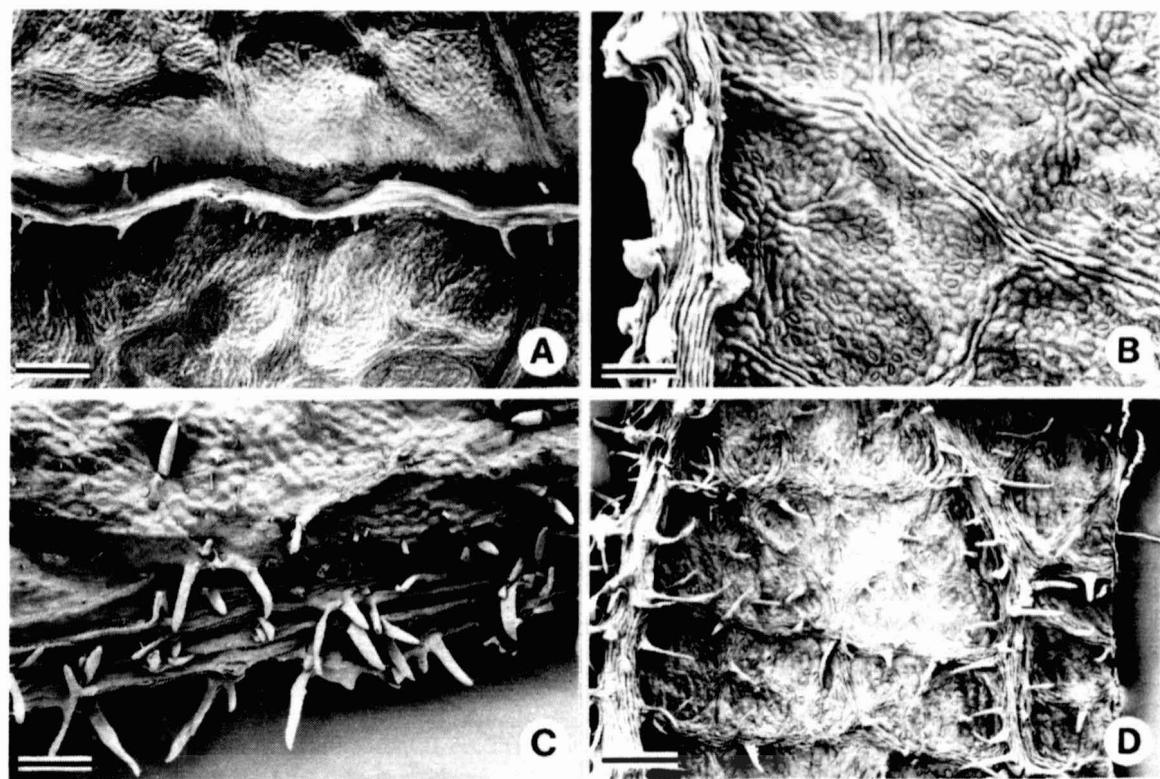


**Figure 3.22** Structure of trichome types, as seen in Figure 3.21, in leaf transverse sections of *Heteromorpha* sensu stricto. A, *H. involucrata*, typical form: conical trichome on a tuberculate base; B, *H. involucrata*, 'kassneri' form: multicellular, long, cylindrical trichome; C, *H. gossweileri*: 1, tuberculate and 2, papillate trichome; D, *H. arborescens* var. *trifoliata*: short, cylindrical trichome; E, *H. pubescens*: filamentous trichome on a tuberculate base.

The filamentous (filiform) type is only found in *H. pubescens* (Figure 3.21 E & 3.22 E) and *H. betsileensis* and, in addition to distribution and density of hairs, characterizes these species. Shorter cylindrical hairs (Figure 3.21 B & 3.22 D) are characteristic of *H. arborescens* var. *arborescens*, *H. arborescens* var. *trifoliata*, but are also found in *H. papillosa*, rarely in *H. stenophylla* and occasionally (with other types) in some forms of *H. involucrata*.

Other types that can be identified are 1, a unicellular conical hair (Figure 3.21 F & 3.22 A), usually present in all forms of *H. involucrata* and in *H. occidentalis*, often cushioned by surrounding cells and slanted toward the leaf apex (Figure 3.22 A), and 2, a unicellular or multicellular long cylindrical hair (Figure 3.21 D & 3.22 B), present in the central African forms of *H. involucrata*.

The presence of small tubercles (although sparse in some specimens) along the leaf margin of *H. occidentalis*, supports its isolation as a suffrutescent species distinct from *H. arborescens* var. *trifoliata*, which sometimes (often only in young growth) has a margin with short cylindrical hairs. This feature suggests a closer affinity with the suffrutescent species *H. gossweileri*, *H. pubescens* and *H. involucrata*.



**Figure 3.23** Some examples of trichome distribution in *Heteromorpha* *sensu stricto*: A, *H. arborescens* var. *trifoliata*: adaxial midrib; B, *H. involucrata*: abaxial view, margin only; C, *H. involucrata* 'kassneri' form: margin and adaxial surface; D, *H. pubescens*: abaxial view, along entire venation. Scale bars: A--C, 50 µm; D, 100 µm.

### Trichome distribution

Patterns of laminar distribution of trichomes are summarized in Table 3.2. Hairs, when present, are usually located at least on the adaxial midrib (Figure 3.23 A). In *H. arborescens* a pilose abaxial midrib is rare. This is, however, the exception in *H. involucrata*, where the abaxial midrib is usually more pilose in the typical form. Forms from Malawi have a glabrous abaxial midrib and appear similar to *H. arborescens* var. *trifoliata* if trichome type is ignored, while in those from Zimbabwe both midrib surfaces are pilose. The presence of trichomes along the

leaf margin is the rule in *H. involucrata* (Figure 3.23 B & C) and the exception in *H. arborescens* var. *trifoliata*.

*H. involucrata* is the only species with trichomes on the areas between the veins (Townsend 1985), and not on the veins and margin only, as in all other species.

*H. pubescens* has morphological features in common with *H. involucrata* and also shares the pilose abaxial midrib and presence of hairs on the adaxial secondary veins (Townsend 1985) in addition to those found elsewhere. The latter feature is only rarely found in other species.

*H. gossweileri* has a vestiture pattern, which for its particular trichome type, is characteristic. The leaf margin, midrib, and major adaxial veins all have a variable number of trichomes, often concentrated apically or basally (Townsend 1985).

### 3.3 General conclusions

Many of the characters surveyed seem to have more value at the generic level than for the purposes of this study. Other characters such as stomatal features, are of limited use for inferring relationships, but are nevertheless invaluable as diagnostic features for the delimitation of the species.

Compared to the other genera surveyed, *Heteromorpha* has a high diversity of trichome types, and these are used to analyze the

phylogeny of the genus. Epidermal characters provide supporting evidence for a less conservative treatment of the African species than those of Cannon (1978) and Townsend (1985, 1989). The degree of woodiness and branching in *Heteromorpha* species is an important character and seems to correlate with other morphological features. Without attention to habit, other characters tend to be difficult to interpret.

As currently circumscribed, *H. involucrata* shows as much if not more variation in the characters surveyed than the *H. arborescens* complex, and formal recognition of infraspecific taxa may be useful.



**CHAPTER 4****REPRODUCTIVE MORPHOLOGY****4.1 Inflorescence**

Weberling (1989) describes an improved, natural typology of inflorescences originally developed by Troll (1964), which allows for a more systematic, if not somewhat complex, interpretation of inflorescence structure, types and evolution than is possible with previous systems. In his definition of inflorescence types, Weberling recognizes the importance of considering the total reproductive branching system (Troll's synflorescence) in relation to the branching system of the whole plant. Burtt (1991) also emphasizes the close relation of growth pattern with pattern of flower and fruit production. In many plants the synflorescence includes structures identical to those of the vegetative system. In *Heteromorpha* this has led to bracts being misinterpreted as foliage leaves and subsequent misidentification when herbarium specimens show only synflorescence leaves and no foliage leaves. In the discussion below, the terminology used follows that of Troll (1964) and Weberling (1989).

**4.1.1 Structure**

Burtt (1991) provides a broad overview of inflorescence structure in the Apiaceae. He notes that Froebe (1964, 1971) has

shown for the Saniculoideae and Hydrocotyloideae that the umbel is basically a highly condensed cyme (a monotelic type of inflorescence), as opposed to a condensed raceme (polytelic type), and explains why he considers the extension of this idea to the rest of the family (i.e. Apioideae) to be the most likely case.

In *Heteromorpha* the synflorescences are produced terminally or pseudo-laterally (terminal on short shoots of the previous season's growth) as in *H. arborescens* and *H. papillosa*, and would classically be described as a paniculate arrangement of compound umbels (Figure 4.1). Each synflorescence consists of a main florescence (the terminal compound umbel on a relatively short peduncle) which develops first, followed by paraclades of the first order (lateral branches of several nodes, bearing compound umbels) and lastly, when present, paraclades of the second or even third order (Figure 4.2 A). It is these paraclades which have often been (and still are) mistaken for vegetative branches with terminal inflorescences. Simple umbels occur sporadically as umbellulae somewhat detached below a compound umbel, as discussed by Burtt (1991) with respect to *Anginon* Raf. The development of paraclades can be suppressed so that the inflorescence normally has only a main florescence, as in some forms of *H. involucrata* (Figure 3.7 C), in *H. papillosa* and sporadically in other species. The number of paraclades is variable and a specimen of *H. arborescens* var. *collina* from Zululand has been seen [Wylie sub Wood 8746 (NH)] with over 40 short paraclades arranged along the main axis.



**Figure 4.1**  
Synflorescence structure in *Heteromorpha*, showing the main florescence (terminal), with lateral paraclades. In (A) the relatively large bracts tend to obscure the boundary between vegetative and reproductive growth, while at a later stage (B) the boundary becomes clear as the synflorescence dies back after fruit ripening and all bracts are shed. [A, *H. pubescens*, Sudwala caves area; B, *H. arborescens* var. *frutescens*, Abel Erasmus Pass]. Scale bar: 100 mm.





A

**Figure 4.2** Variation in *Heteromorpha* synflorescences. A, *H. stenophylla* var. *transvaalensis*, Winter 54: bracts are much reduced and third order paraclades are common. B, *H. arborescens* var. *frutescens* Winter 51: the synflorescence is set apart from the vegetative plant, bracts are slightly reduced and second order paraclades are common. Scale bar: 100 mm.



B

The synflorescence can either blend in with the rest of the vegetative growth as is typical of *H. arborescens* (Figure 3.5) and *H. papillosa*, or it can be set apart from the rest of the plant by longer peduncles, accompanied by a reduction in bract size, as in *H. stenophylla* var. *transvaalensis* (Figure 4.2 A), *H. arborescens* var. *frutescens* (Figure 4.2 B), *H. gossweileri* and most forms of *H. involucrata*. This feature is of slight diagnostic value, but is not taxonomically consistent.

The number of rays in the main florescence compared to lateral umbels, has been used by Townsend (1985) to characterize *H. involucrata*, as well as *H. transvaalensis*, although he points out that this character is variable in *H. involucrata*. Burtt Davy (1932) used the number of rays as a key character to distinguish *H. arborescens* var. *trifoliata* from *H. transvaalensis*, the former with 15 to 40 rays, and the latter with 5 to 13 rays. The results for the present study are shown in Table 4.1.

Whereas other species usually have up to 25 rays, or up to 32 in the case of *H. pubescens*, *H. involucrata* is the only species which can have up to 68 rays. Although there is a definite pattern concerning the average and maximum values, the minimum number is variable and depends on various factors. Aborted rays are often evident among the others. In *H. involucrata*, the South African and Swaziland forms generally have more rays (up to 68) than the central African forms (17 to 24, rarely 34), the exception being forms from Zambia which match the type specimen of *H. kassneri*, with 25 to 41 rays. This supports the notion

**TABLE 4.1** Variation in the number of rays in the main florescence of *Heteromorpha*. (Species and varieties are numbered as in chapter seven; n = number of specimens examined)

LITERATURE					
TAXON	n	MEAN	S.D.	RANGE	VALUES
1.1	4	14,6	3,0	(7--)14--17(--23)	
1.2	9	12,7	5,3	(4--)10--15(--24)	12--18 *
1.3	8	18,5	5,9	(10--)14--23(--30)	(8--)15--40 **, ***
1.4	3	13,1	0,8	10--18	
1.5	6	23,5	4,2	21--23(--32)	
2	5	17,9	4,2	(12--)17--23(--27)	10--12 °
3.1	3	22,6	4,0	(10--)18--25	up to 10 ∞
3.2	3	15,5	1,3	14--16(--17)	5--15 °, ∞∞
4	1	22	-	22	20--25 +
5	3	11,8	3,6	9--10(--16)	(6--)7--10(--14) °, ++
6	3	29,4	2,3	(24--)28--32	
7	10	29,0	14,0	(16--)22--68	(6--)22--55 °, +++

\* Ecklon & Zeyher (1837)  
 \*\*\* Townsend (1989)  
 ∞∞ Schinz (1894)  
 + Jaques-Felix (1970a)  
 +++ Conrath (1908)

\*\* Burtt-Davy (1932)  
 ° Townsend (1985)  
 ∞∞∞ Wolff (1921)  
 ++ Norman (1922, 1933)

that *H. pubescens* and *H. involucrata* are sister groups which speciated in the south. It also indicates divergence within *H. involucrata*, the extent of which cannot be assessed properly in this study, but may well require formal distinction. Both *H. gossweileri* and *H. stenophylla* var. *transvaalensis* have fewer rays (up to 17) than the other suffrutescent species. Variation within *H. arborescens* seems to be correlated with climatic factors, as those with higher numbers generally occur in areas with higher rainfall.

The number of raylets per umbellule generally varies from eleven to twenty one, but may be as high as thirty in *H. involucrata*. The variation roughly follows that of the rays.

The length of rays in the main florescence is 15 to 40 mm long (extreme values of 11 and 80 mm), but shorter rays sometimes occur toward the centre of the umbel. Care must be taken to measure rays at the mature fruiting stage, since growth has been noticed to continue well into the fruit ripening period. *H. gossweileri* can be distinguished from most other species by its long, slender rays, 50 to 70 mm long (sometimes up to 80 mm), those of *H. involucrata* occasionally reaching 75 mm, and those of *H. stenophylla* var. *stenophylla* rarely reaching 50 mm. The type specimen of *Franchetella arborescens* var. *platyphylla*, here included under *H. occidentalis*, has terminal umbel rays of up to 54 mm long.

#### 4.1.2 Bracts

The term as used here includes, in addition to the involucral bracts, all leaf-like organs in the synflorescence. Cannon (1978), referring to the caducous nature of bracts and bracteoles, recognizes only those in the involucre and involucel of the compound umbels. In *Heteromorpha* species, a reduction in size and division of the lamina is typical, as in most leafy plants, going from the vegetative state of growth to the reproductive state [The converse is true in the growth of a vegetative shoot from an axillary lateral bud]. In a synflorescence of *H. arborescens* var. *trifoliata*, it was found that there is usually at least one pair of opposite simple bracts in the paraclades, the opposite arrangement being confined to these paraclades and to the bases of axillary vegetative shoots. A specimen of *H. involucrata* with a single terminal compound umbel, Wilms 563 (Z) has occasional nodes with a verticillate arrangement of four leaves which should probably be interpreted as bracts, signifying the transition to reproductive growth in the stem.

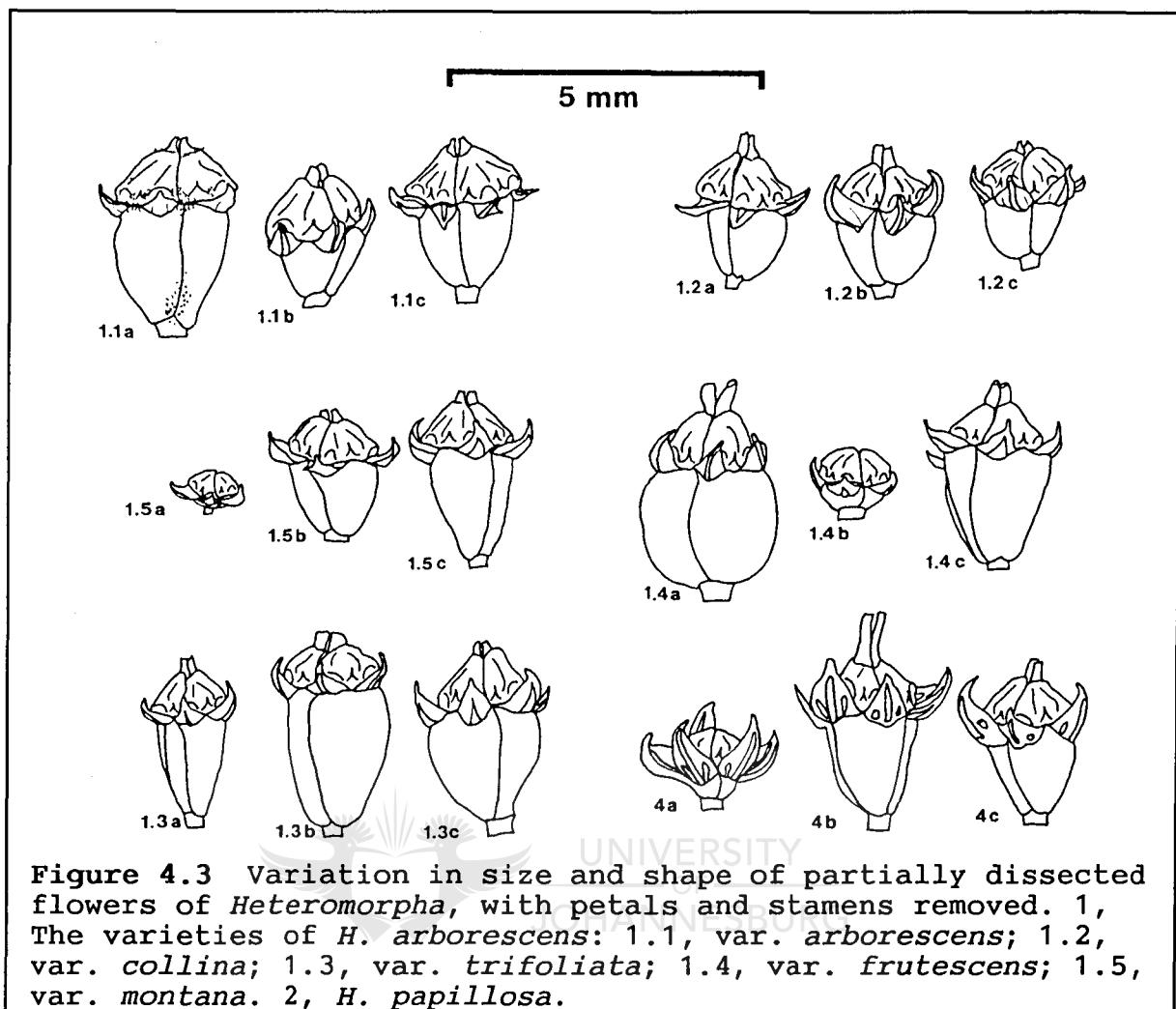
Involucres and involucels are present at the nodes of the umbels as well as umbellules. These consist of bracts which can be all linear as in *H. gossweileri*, or are sometimes interspersed with usually one or two larger, foliose bracts in most species. Foliose bracts are larger and more numerous in the typical form of *H. involucrata*, and in *H. pubescens*, than in the other forms of *H. involucrata* or in any of the other species. These bracts are often dissected in *H. involucrata*. It must be emphasized

that the distinction between foliose and bracteose bracts is not always clear. Forms with narrowly elliptic or linear foliage leaves or divisions tend to have linear bracts, while those with broader laminae tend to have foliose bracts. Where foliose bracts are prominent, these are often the extremes in a range varying from bracteose to foliose. This seems to be a continuation of the reduction observed as the plant develops in the reproductive phase, the most foliose bracts being interpreted as the lower bracts of the condensed inflorescence.

#### 4.2 Flowers

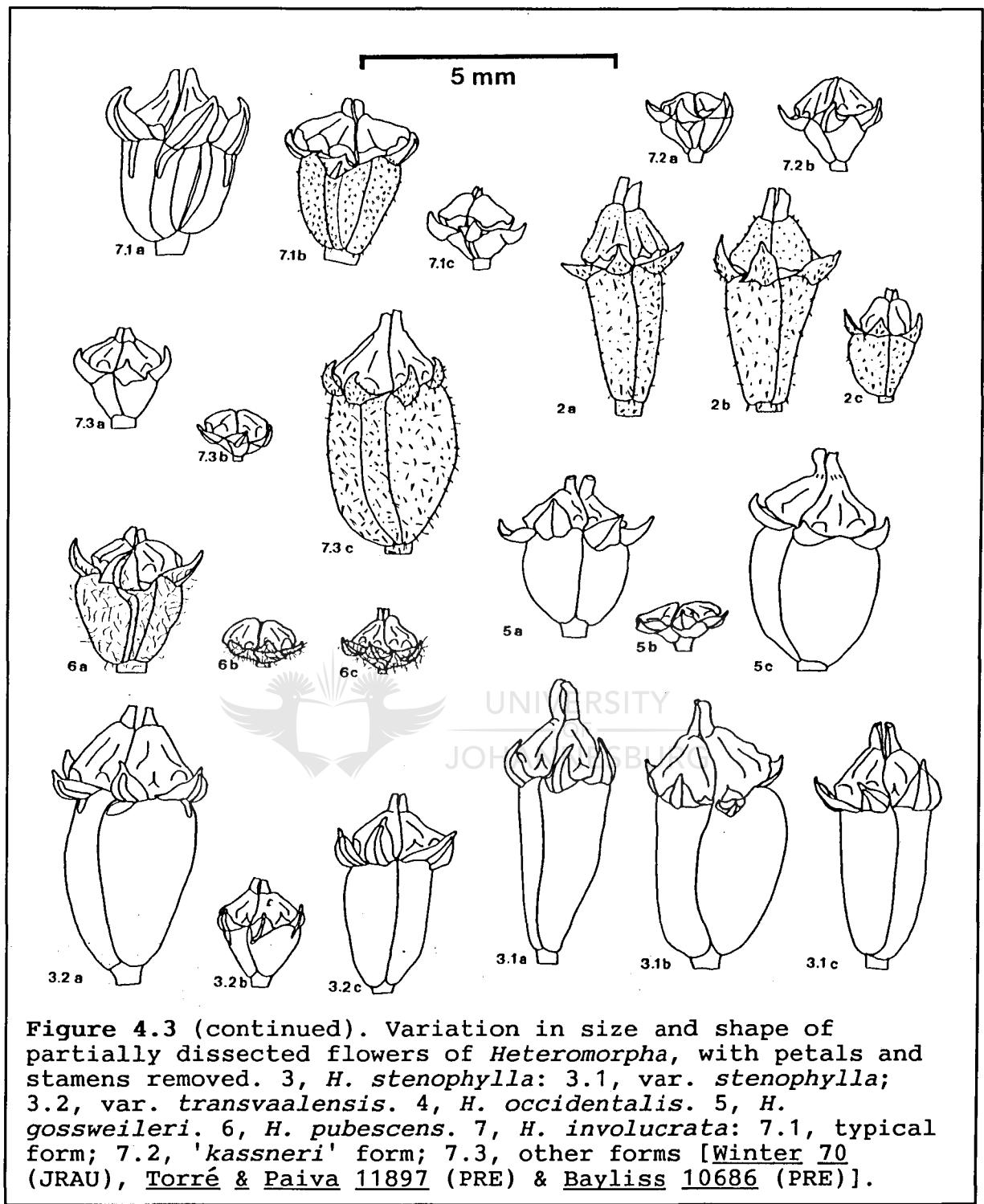
*Heteromorpha* has typical Apiaceae flowers with a bicarpellate, inferior ovary and pendulous ovules, pentamerous outer whorls surrounding a stylopodium ending in two separate simple styles. The calyx lobes are relatively prominent in comparison with other genera, and persist on the ripe fruit.

The range of variation in shape and size of ovary, calyx lobes and stylopodium including style, is shown in Figure 4.3 and that of the petals in Figure 4.4. Some flowers lack an ovary and styles. These occur only sporadically and are interpreted as functionally male flowers. According to Burtt (1991), these could possibly be non-functional abortive flowers. Their presence suggests the phenomenon of temporal dioecism (Cruden 1988), as these staminate flowers are associated with one or two plants in populations where most of the other plants are already in the fruiting stage. They may also occur on paraclades of the



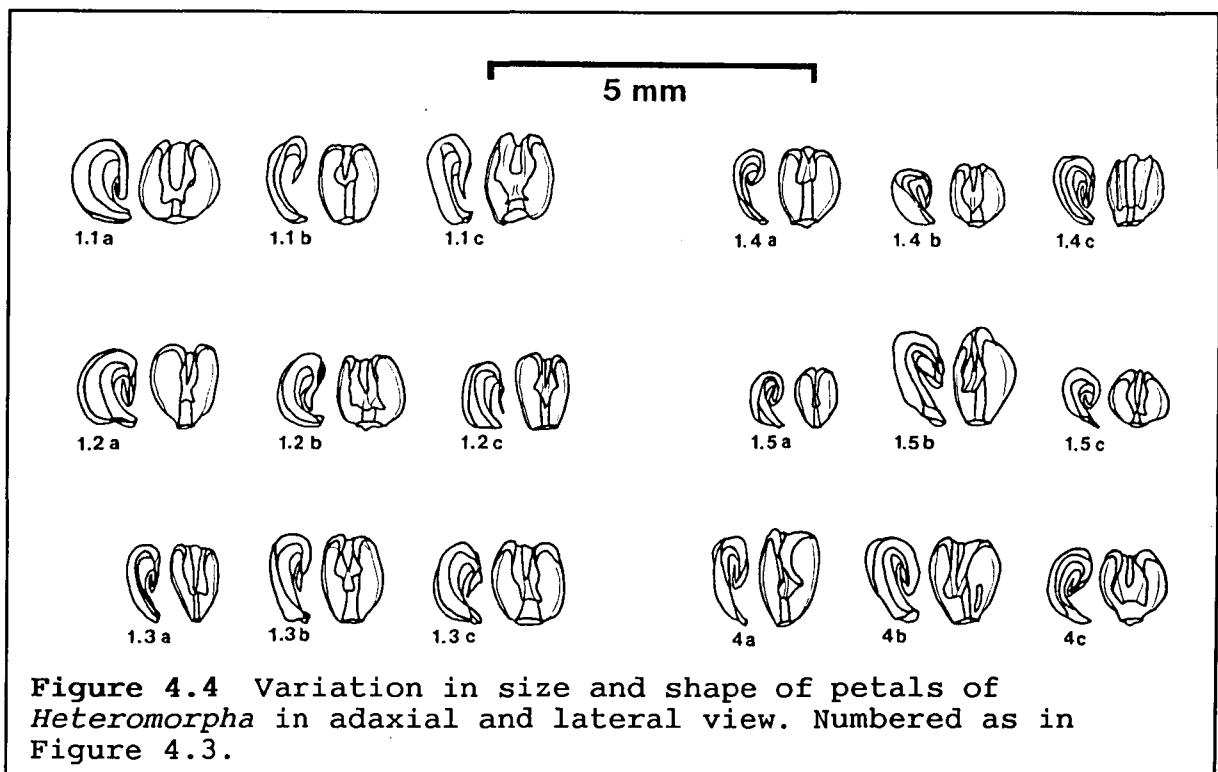
**Figure 4.3** Variation in size and shape of partially dissected flowers of *Heteromorpha*, with petals and stamens removed. 1, The varieties of *H. arborescens*: 1.1, var. *arborescens*; 1.2, var. *collina*; 1.3, var. *trifoliata*; 1.4, var. *frutescens*; 1.5, var. *montana*. 2, *H. papillosa*.

second or higher order, on a plant where the other florescences are similarly in a fruiting state. Burtt (1991) points out that andromonoecism seems to be associated with a growth pattern (in herbaceous members of Apiaceae) where a monopodial axis produces terminal umbels and lateral branches. The observations made for *Heteromorpha* in this study are unfortunately too few, due to the infrequent occurrence and the limitations inherent in the dependence on herbarium material, to confirm his notion that sex forms are linked to the hierarchy of primary, secondary and tertiary order compound umbels which results from such a growth pattern. So far it can only be mentioned that the phenomenon does occur in all species of *Heteromorpha*.



**Figure 4.3 (continued).** Variation in size and shape of partially dissected flowers of *Heteromorpha*, with petals and stamens removed. 3, *H. stenophylla*: 3.1, var. *stenophylla*; 3.2, var. *transvaalensis*. 4, *H. occidentalis*. 5, *H. gossweileri*. 6, *H. pubescens*. 7, *H. involucrata*: 7.1, typical form; 7.2, 'kassneri' form; 7.3, other forms [Winter 70 (JRAU), Torré & Paiva 11897 (PRE) & Bayliss 10686 (PRE)].

The ovaries of *H. stenophylla* (3.1 & 3.2 in Figure 4.3) are usually more than twice as long as the stylopodia. Wings and ribs can be discerned in the hypanthium of all species, and wing development is more pronounced in *H. arborescens* var. *frutescens* (1.4 in Figure 4.3) at this stage than in other taxa. In taxa

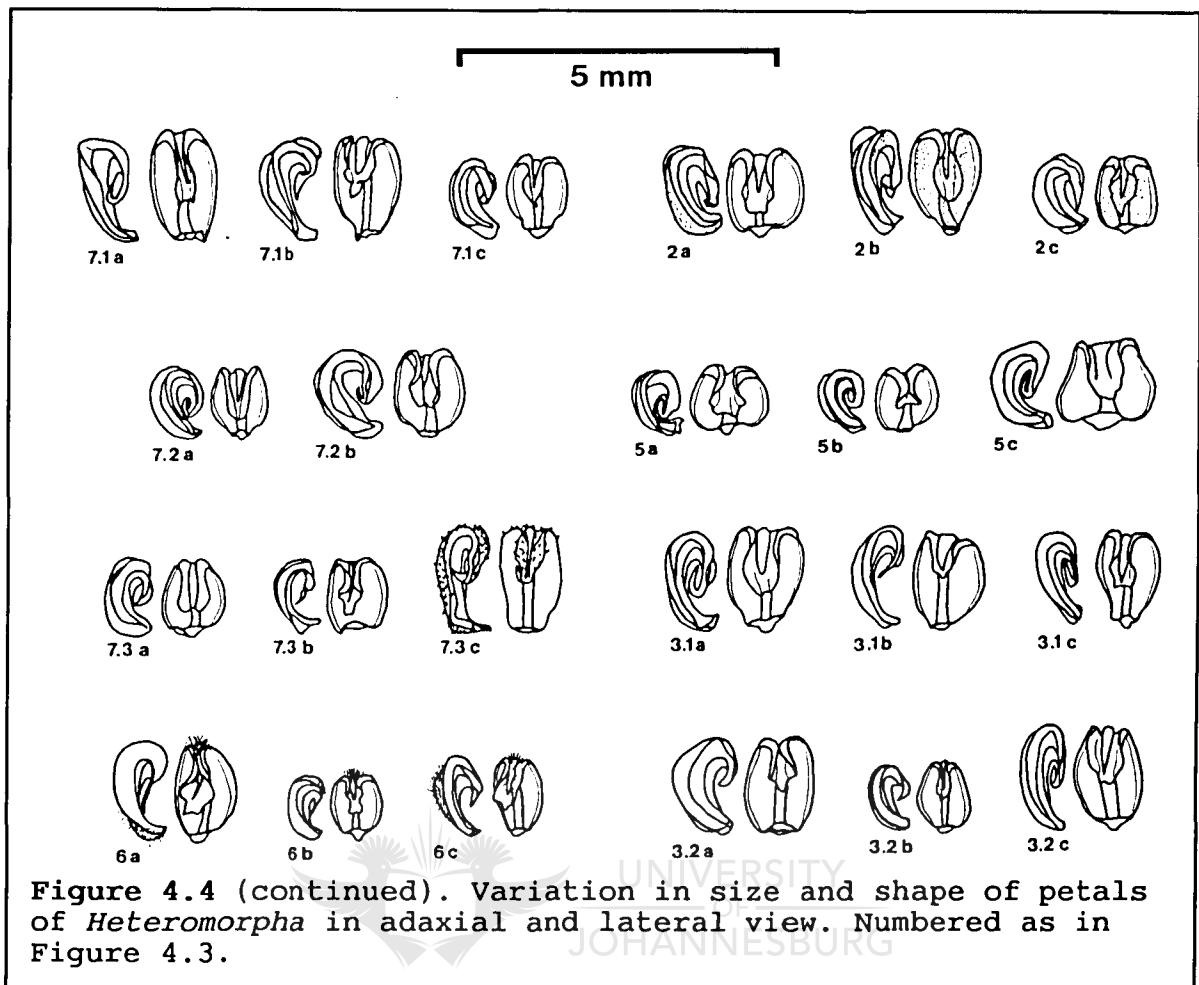


**Figure 4.4** Variation in size and shape of petals of *Heteromorpha* in adaxial and lateral view. Numbered as in Figure 4.3.

where the ovary is pilose, this pilosity is quite variable, except in *H. pubescens* (6 in Figure 4.3) where filamentous trichomes are always present over the entire ovary.

*H. occidentalis* (4 in Figure 4.3) has long calyx lobes with two lateral vittae which seem to branch off from the carinal vitta. This character is a useful diagnostic character for *H. occidentalis*. The lateral vittae usually appear as spots or short bars adjacent to, but distinct from the carinal vitta. Similar vittae have been observed only as a rare exception in *H. stenophylla* var. *transvaalensis* (for one fruit on a single specimen which has several florescences covered in fruit).

The petals of *H. gossweileri* tend to be wider toward the base (5 in Figure 4.4, and have a height to width ratio lower than one, whereas the rest are all higher than wide. In addition, the



**Figure 4.4 (continued).** Variation in size and shape of petals of *Heteromorpha* in adaxial and lateral view. Numbered as in Figure 4.3.

carinal vitta is not discernible (not dark) in the *lobulum inflexum*. Although the petals are generally glabrous in *Heteromorpha*, some species do have some form of vestiture. *H. papillosa* (2 in Figure 4.4) has minute papillae, not easily discernible from normal epidermal cells, *H. involucrata* sometimes has short, conical to cylindric trichomes on the dorsal surface (7.3 in Figure 4.4), and *H. pubescens* has a bearded dorsal surface (6 in Figure 4.4), with trichomes concentrated along the keel.

The stylopodium (Figure 4.5) is conical, with indentations in the rim which correspond to the positions of anthers and petals in the bud. The surface sculpture is smooth (Figure 4.5 A & C)

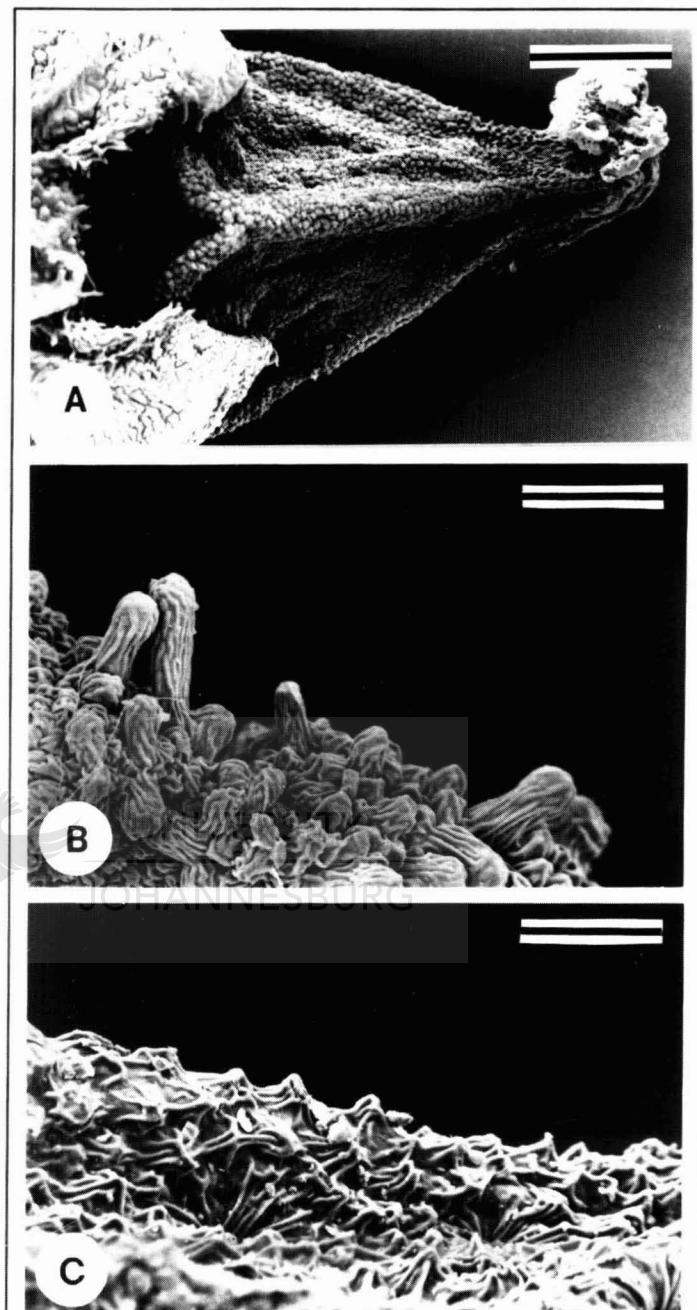
in most species, sometimes papillose in *H. papillosa* (Figure 4.5 B), though this does not seem to be a good character, as both *H. arborescens* and *H. involucrata* are sometimes sparsely short-pilose at the rim, or at the bases of the styles. Furthermore, the distinction between papillose and short-pilose is not practical.



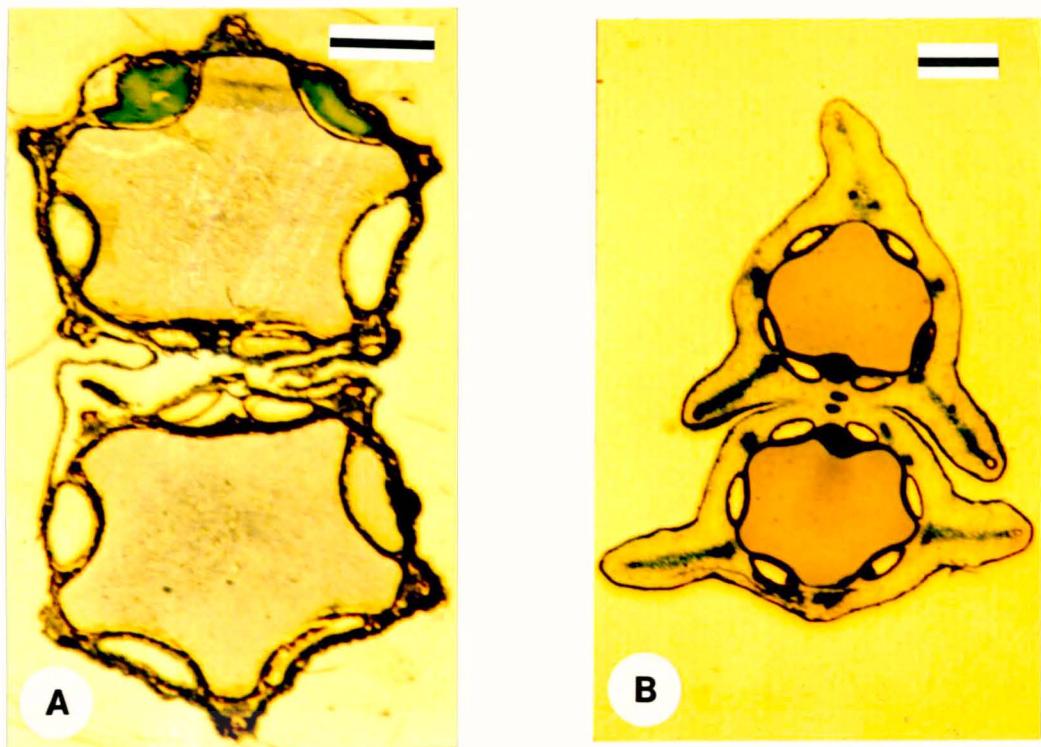
### 4.3 Fruit

#### 4.3.1 External morphology

*Heteromorpha* fruits are typical ribbed cremocarps characteristic of the Apiaceae, but differ from those of most genera (Figure 4.6 A) in that every alternate primary rib (those decurrent from the calyx lobes) develops into a wing (Figure 4.6 B; PS in Figure 4.7). This feature is used in the



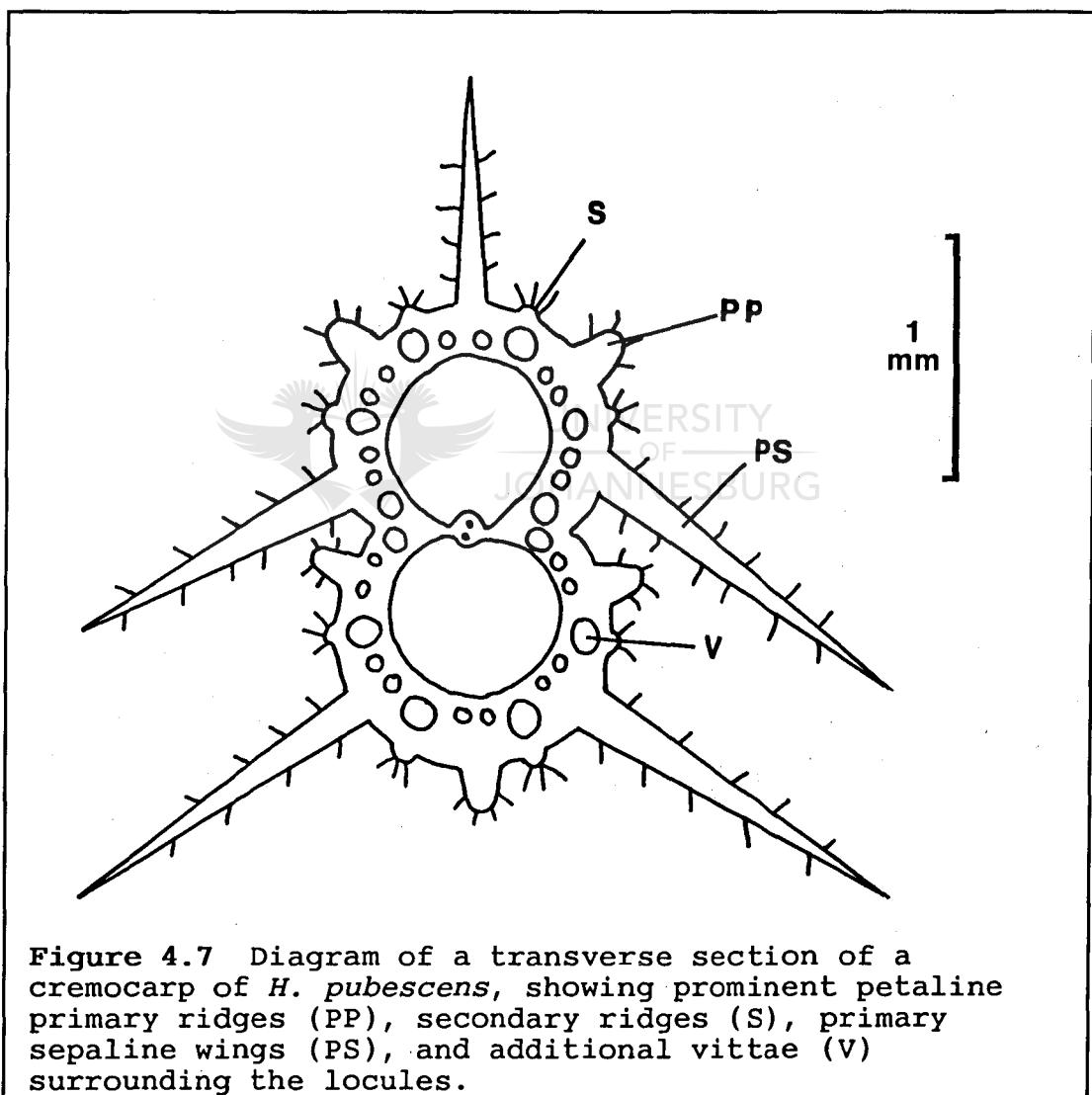
**Figure 4.5** Shape and epidermal sculpture of stylopodia of *Heteromorpha*. A, *H. arborescens* var. *trifoliata*, Winter 53 (JRAU): smooth epidermis. B, *H. papillosa*, Seydel 4423 (MO): papillae on stylopodium. C, *H. papillosa*, Hanekom 135 (WIN): smooth epidermis. Scale bars: A, 500 µm; B & C, 100 µm.



**Figure 4.6** Transverse sections of fruits of *Heteromorpha* *sensu lato*. A, *H. tsaratananensis*, Humbert 18374 (P): the typical state in Apiaceae with mericarps uniformly ribbed. B, *H. arborescens* var. *trifoliata* Winter 71 (JRAU): the configuration with winged sepaline ribs which characterizes *Heteromorpha* *sensu stricto*. Scale bar: 500 µm.

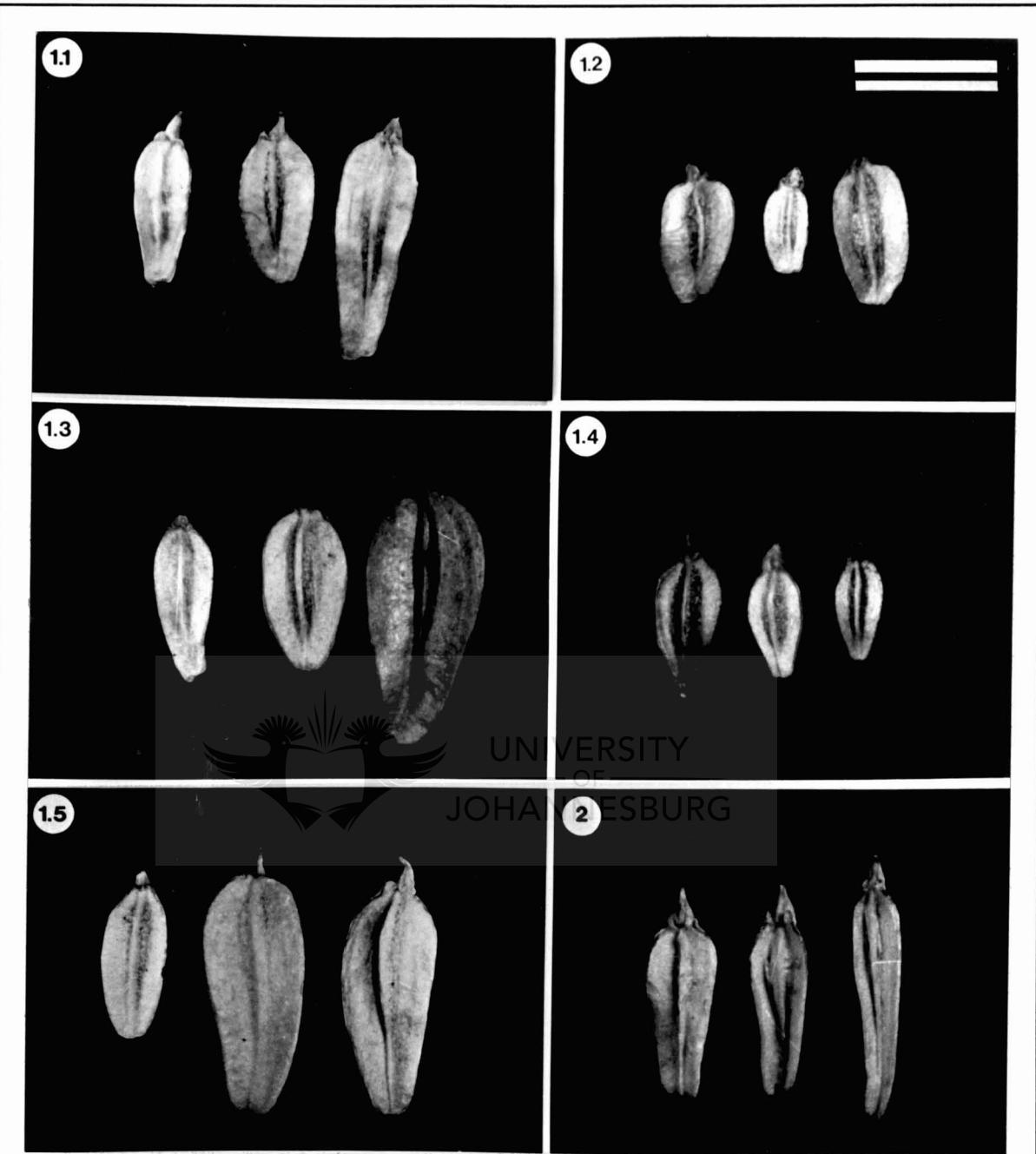
cladistic analysis as the generic synapomorphy supporting the monophyly of *Heteromorpha*, although it is superficially similar to *Polemanniopsis* in this respect. The result of this wing pattern is an atypical zygomorphic fruit (Figure 4.6 B; 4.7) with three wings on one mericarp, and two on the other, to which the name *Heteromorpha* alludes (and not to the generally polymorphic vegetative features of the genus as is often supposed). The two-winged mericarp always faces outward in the umbellule. The wing configuration typical of *Heteromorpha* and its occurrence in the family have been discussed by Burtt (1988) and by Winter et al. (1993). The Madagascar species are excluded from *Heteromorpha* as they do not possess this unique condition.

Petaline primary ribs (PP in Figure 4.7) are normally only visible as slight ridges on the fruit wall, but are well developed (half-winged) in most forms of *H. involucrata*, in *H. pubescens* (Figure 4.7) and in *H. gossweileri*. Secondary ribs are rarely present in *Heteromorpha* as minute ridges in the valleculae, though in *H. pubescens* they occur regularly (S in Figure 4.7), providing a base for a row of trichomes.



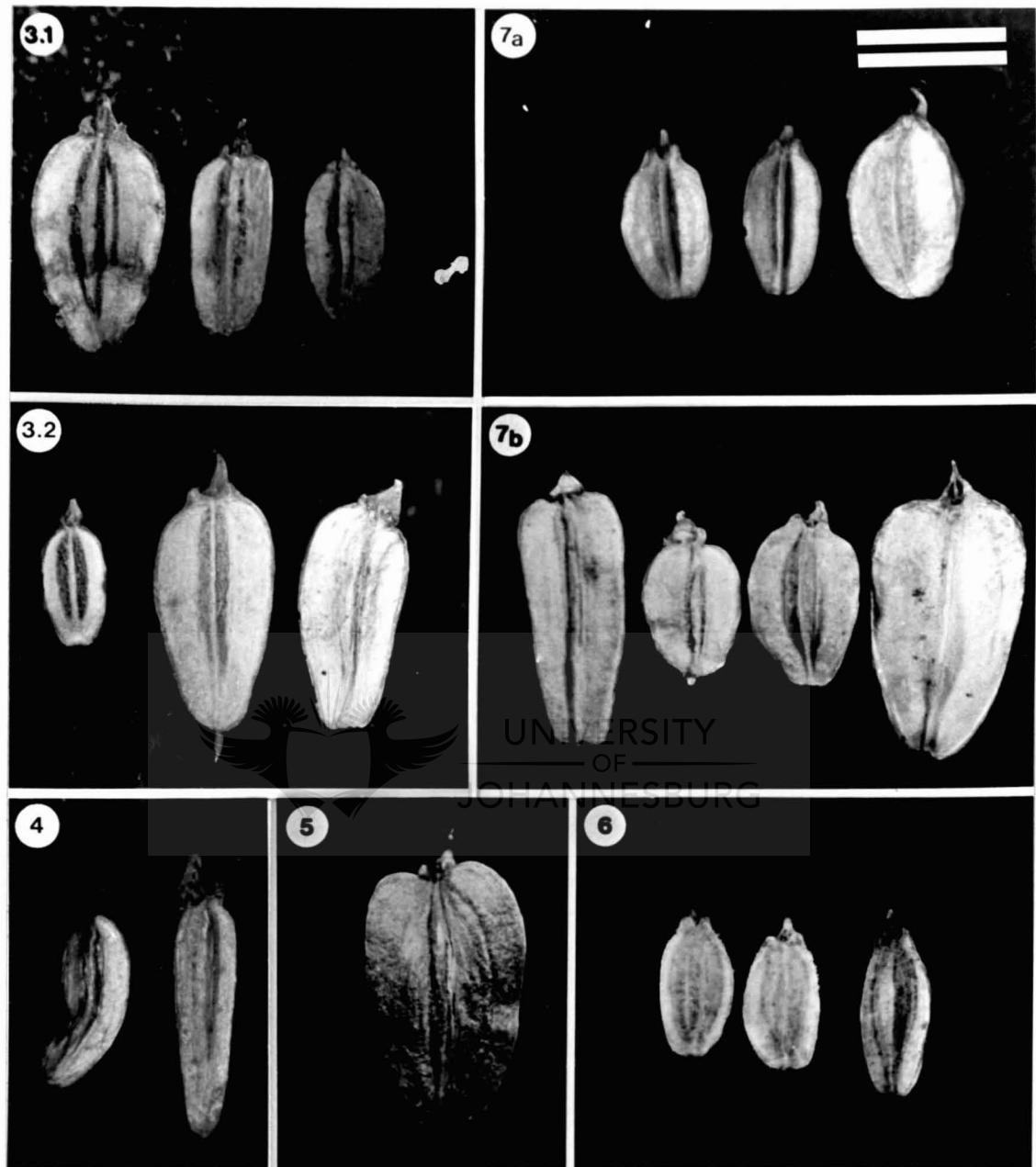
**Figure 4.7** Diagram of a transverse section of a cremocarp of *H. pubescens*, showing prominent petaline primary ridges (PP), secondary ridges (S), primary sepaline wings (PS), and additional vittae (V) surrounding the locules.

Variation in the outlines of fruits of all species of *Heteromorpha* is shown in Figure 4.8. In *Heteromorpha involucrata* the outline is oval in southern forms (7a in Figure 4.8) to



**Figure 4.8** Variation in the outline of *Heteromorpha* fruits. Dorsal views of abaxial mericarps showing two intermediate sepaline wings and one dorsal petaline rib. 1, The varieties of *H. arborescens*: 1.1, var. *arborescens*; 1.2, var. *collina*; 1.3, var. *trifoliata*; 1.4, var. *montana*; 1.5, var. *frutescens*. 2, *H. papillosa*. Scale bar = 5 mm.

obovate in northern forms (7b in Figure 4.8). In *H. gossweileri* the fruit outline is typically more rounded than in other species when young, but mature fruits (seen only in the type



**Figure 4.8 (continued).** Variation in the outline of *Heteromorpha* fruits. Dorsal views of abaxial mericarps showing two intermediate sepaline wings and one dorsal petaline rib. 7a (right) is a lateral view of an adaxial mericarp, showing a dorsal sepaline wing (left side of fruit), intermediate petaline rib and lateral sepaline wing (right side of fruit). 3, *H. stenophylla*: 3.1, var. *stenophylla*; 3.2, var. *transvaalensis*. 4, *H. occidentalis*. 5, *H. gossweileri*. 6, *H. pubescens*. 7, *H. involucrata*: 7a, typical form; 7b, variation [from left to right: Jacobsen 2891 (PRE), Kers 3491 (S), Winter 67 (JRAU) & Stoltz 2086 (L)]. Scale bar = 5 mm.

specimen), are obovate. The fruit outline is not considered to be of any taxonomic importance.

The size of the fruit was used by Wolff (1910) to describe two formae in *H. arborescens* var. *collina*: Fruits of *f. 1. normalis* were up to 8 mm long and 3 to 4 mm wide, while those of *f. 2. anomala* were only 3,5 to 4 mm long and 1,5 mm wide. Townsend (1985) only mentions fruit size with regard to atypical forms of *H. trifoliata* from Mozambique, with fruits up to 10 mm long. The results from the current survey are shown in Table 4.2. Fruits of *H. arborescens* var. *arborescens*, var. *trifoliata* and var. *frutescens* vary in length from 5 to 9 mm, while those of var. *montana* are not more than 5 mm long, and those of var. *collina* only rarely reach up to 6 mm. This places some doubt on the identity of Wolff's var. *collina* forma *normalis*, suggesting that it could in fact have been a variant of var. *arborescens*.

The shape of the fruit seems to be correlated with the distance which the vittae - and probably the locules as well - extend down the length of the fruit. In cases where the fruit is obpyriform (1.1, 1.3 & 2 in Figure 4.8), vittae extend roughly two thirds of the way down, up to the "neck" region, which appears as missing particularly in *H. arborescens* var. *collina* (1.2 in Figure 4.8), *H. involucrata* - southern forms (7a in Figure 4.8), and *H. pubescens* (6 in Figure 4.8), giving the fruit an oval or elliptic outline.

**TABLE 4.2** Variation in the length and width of fruits in *Heteromorpha*. (Species and varieties are numbered as in chapter seven; n = number of specimens examined; underdeveloped fruits not included)

TAXON	n	LENGTH	WIDTH
1.1	3	(5--)6--8	2--3
1.2	3	3--4(--6)	2--3(--4)
1.3	3	5--7	2--3.5
1.4	3	3--4.5(--5)	1.5--2.5
1.5	3	(5--)6--9	2--4
2	2	6--10	3
3.1	3	6--8	3--5
3.2	2	3--9	2--4
4	3	4--7	2--4
5	1	10	5--6(--7)
6	3	4--6	2--3
7	5	3--7(--9)	2--4(--5)

Where the fruit is obovate, vittae extend to roughly three quarters of the way down, as in *H. stenophylla* (3 in Figure 4.8), *H. gossweileri* (5 in Figure 4.8) and *H. involucrata* - northern forms (7b in Figure 4.8).

The two-winged mericarp of *H. papillosa* has a linear outline when viewed from the dorsal surface (2 in Figure 4.8), which is in part due to the small angle between these two wings. As in *H. arborescens* var. *montana*, the lateral wings on the other mericarp are tightly pressed against the fruit body, giving the fruit a particularly laterally compressed appearance when viewed from the stylopodium or in transverse section.

The size and shape of fruits are generally of limited taxonomic value in *Heteromorpha*, but are nevertheless diagnostic for two varieties of *H. arborescens* as well as for *H. papillosa*.

#### 4.3.2 Anatomy



The anatomy in transverse section of the fruit has been discussed elsewhere (Winter et al. 1993). The anatomy was found to be relatively uniform throughout the genus. Apart from the epidermal surface differences already discussed in the foregoing section, the only species which shows distinction in fruit anatomical characters is *H. pubescens* (Figure 4.7). Furrows between ribs and wings in all other species have solitary septate vittae, and the commissure is bivittate (Figure 4.6 B). In *H. pubescens* however, numerous vittae (c. 16) of irregular shape and length surround the seed (Figure 4.7), while additional vittae are commonly visible on the sides of the wings as well. This latter feature has been observed to occur sporadically in *H. involucrata*.

#### 4.3.3 Ontogeny

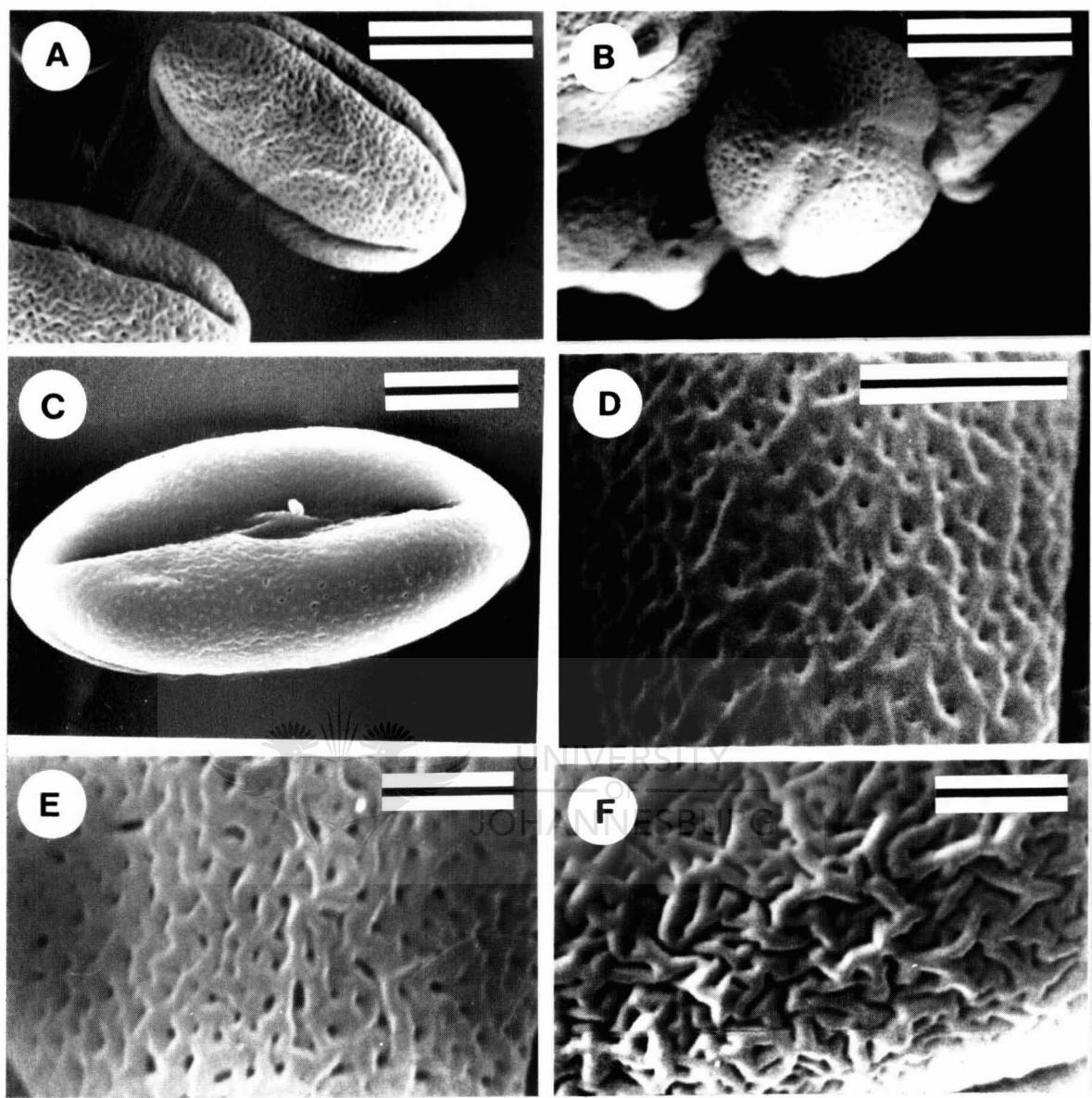
The ontogeny of the fruit wings has been used to emphasize the unique zygomorphic condition of the fruit of *Heteromorpha* (Winter et al. 1993), which is the primary generic character on which the name was based (Chamisso & Schlechtendal 1826). The zygomorphic wing configuration was shown to be present already in the flower, in contrast to the wings of the Peucedaneae, which only develop at a late stage of fruit set. The pattern in *Heteromorpha* is thus congenital rather than ontogenetically derived. The absence of this character state is enough to exclude from *Heteromorpha* the species described from Madagascar (Winter et al. 1993), and is supported by other morphological characters in these plants.



#### 4.4 Pollen morphology

Cerceau-Larrival (1962) has done extensive work on pollen of the Apiaceae. She recognized five phylogenetically serial types, based on the shape of the inner surface of the endexine. These are subrhomboidal, subcircular, oval, subrectangular and equatorial-constricted. The southern African Apioideae surveyed (Cerceau-Larrival 1974) included *Lichtensteinia* Cham. & Schlechtd., *Anginon* and *Heteromorpha*, and all had oval shapes.

The pollen grains of *Heteromorpha* species, as for the rest of the family, are tricolporate. Surface types (Figure 4.9 D--F) are slightly rugulose (Ernstman 1969) to more or less striately



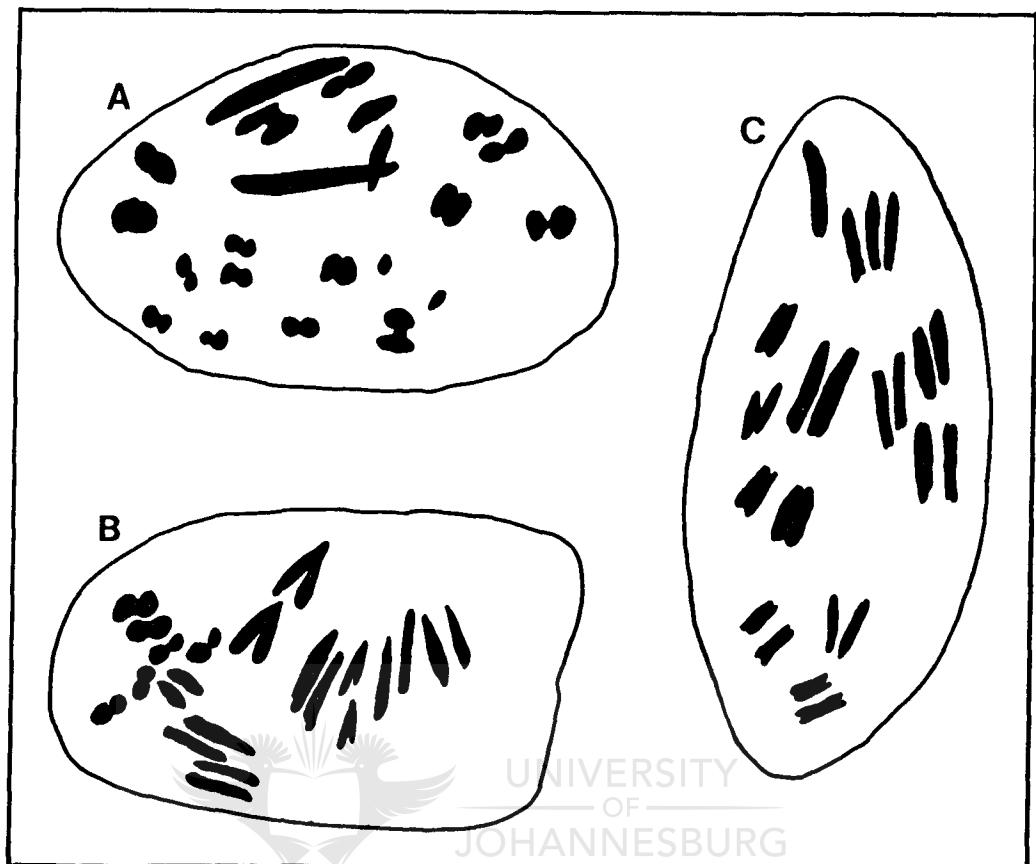
**Figure 4.9** Pollen morphology of *Heteromorpha*. A, *H. involucrata*, Torré & Paiva 11897 (PRE): equatorial mesocolpial view of a pollen grain. B, *H. involucrata*, Theron 3463 (JRAU): axial view of a pollen grain. C, *H. stenophylla* var. *transvaalensis*, Winter 54 (JRAU): equatorial colpial view of a pollen grain. D, *H. arborescens* var. *montana*, Pope & Muller 2075 (PRE): mesocolpium with foveolate surface. E, *H. gossweileri*, Milne-Redhead 3981 (PRE): mesocolpium with somewhat rugulose surface. F, *H. stenophylla* var. *stenophylla*, Schoenfelder S591 (PRE): mesocolpium with rugulose surface. Scale bars: A--C, 20 µm; D--F, 5 µm.

(Erdtman 1969) wrinkled, often somewhat foveolate. Striately wrinkled surfaces were only seen in the two varieties of *H. stenophylla* (Figure 4.9 F), suggesting a close affinity between

these taxa, but were found to grade into other types when the survey was broadened. The shape of the pollen grains (Figure 4.9 A--C) varies from oval to oblong, with length to width ratios of c. 1,8 to 2,2. Other than the distinctive but variable surface sculpturing in *H. stenophylla*, the variation found in untreated pollen of *Heteromorpha* does not correspond to any taxonomic division.

#### 4.5 Chromosome number

The chromosome base number of the genus *Heteromorpha* was established as  $n = 11$  by Constance *et al.* (1971, fig 392), based on a single count for *H. arborescens* var. *trifoliata* from Ethiopia (Meyer 7688). This was confirmed in a second study (Constance & Chuang 1982), for four more collections, one of which (Pawek 6525) is here identified as *H. involucrata*. All were reported to be diploid with  $2n = 22$ . This number is the most common one in the Apioideae (Constance & Chuang 1982). Of the other woody genera surveyed, namely *Steganotaenia*, *Glia* (L.) Sonder and *Anginon* (Constance & Chuang 1982, Moore 1971), only *Steganotaenia* differs in having a base number of  $n = 12$ , more commonly found in Araliaceae (Burtt 1991). The base number for *Annesorhiza macrocarpa* Eckl. & Zeyh. is also reported (Burtt 1991) as  $n = 12$  (Some species of *Annesorhiza* have winged fruits similar to those of *Heteromorpha*, the homology of which is currently being investigated). Chromosome numbers for *Polemannia* and *Polemanniopsis* are not available.



**Figure 4.10** Examples of drawings made of metaphase cells from root tips of *Heteromorpha* seedlings to aid the counting of chromosomes. A, *H. pubescens*, Winter 66. B, *H. arborescens* var. *frutescens*, Winter 58. C, *H. involucrata*, Winter 61. All voucher specimens in JRAU.

The reports for *Heteromorpha* (Constance et al. 1971, Constance & Chuang 1982) are confirmed in this study by chromosome counts in the following specimens (All vouchers in JRAU):

- H. arborescens* var. *trifoliata* (Winter 71)
- H. arborescens* var. *frutescens* (Winter 58)
- H. involucrata* (Winter 61, 68)
- H. pubescens* (Winter 66)

A diploid chromosome number of  $2n = 22$  (Figure 4.10) was found throughout the survey, suggesting that the genus is uniform in this character.

#### 4.6 General conclusions

Several useful characters are present in the reproductive growth phase. In the inflorescence, the length and number of rays of the main florescence are diagnostic for some taxa, while they seem to indicate apomorphic tendencies in others. Floral characters distinguish *H. stenophylla* and *H. occidentalis*, while fruit characters are useful to group *H. gossweileri*, *H. involucrata* and *H. pubescens* together phylogenetically, and to diagnose some varieties of *H. arborescens*. At the generic level fruit characters are used to exclude all Madagascar species, defining *Heteromorpha* as monophyletic. Pollen features are not very useful, but do support an affinity between the varieties of *H. stenophylla*. Chromosome numbers are uniform among species investigated and confirm previous reports for the genus.

## CHAPTER 5

### CHEMOTAXONOMIC SURVEY

As morphological characters tend to be extremely variable in many Apiaceae genera, an investigation of potential chemical characters was included in this study. Current knowledge of the occurrence of secondary metabolites in the family suggests consideration of flavonoids, phenylpropanoids, essential oils, coumarins and polyacetylenic compounds (Heywood 1971).

Villegas *et al.* (1988) isolated a phenylpropene, Sarisan (1-allyl-2-methoxy-4,5-methylenedioxybenzene) and a polyacetylenic compound, Falcarindiol (heptadeca-1,9-diene-4,6-diyne-3,8-diol), from leaves of *Heteromorpha trifoliata* from the Zomba Plateau in southern Malawi (voucher in the herbarium of the University of Malawi, Zomba). Sarisan is listed as Asaricin in the Dictionary of Natural Products (Buckingham 1994), and is an isomer of myristicin (1-allyl-3-methoxy-4,5-methylenedioxybenzene), which is known to have a common occurrence in the Apiaceae (Crowden *et al.* 1969).

Flavonoids were chosen for ease of preparation and utilization of the latest HPLC techniques (Harborne 1988), as well as the availability of the common flavonols and flavones as standards. The only chemotaxonomic investigation of flavonoids (or any other secondary metabolite for that matter) concerning *Heteromorpha* to date was done by Crowden *et al.* (1969), who

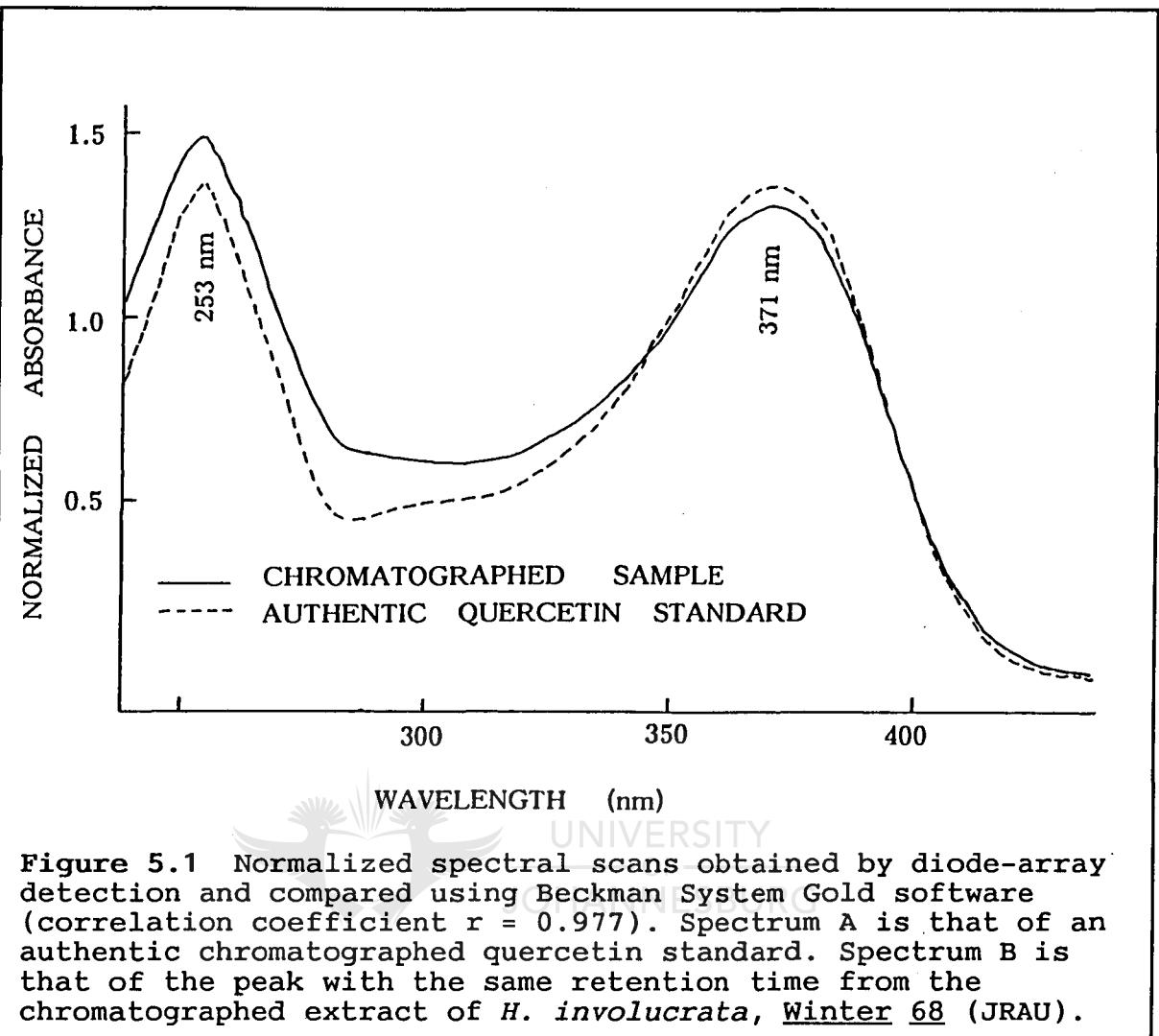
reported the presence of quercetin and kaempferol (the flavonoids present in most members of the Apiaceae) in the leaves of *Heteromorpha arborescens*.

The next class of compounds surveyed was the coumarins, of which aesculetin (6,7-dihydroxycoumarin) was detected in leaves of *Heteromorpha arborescens* (Crowden et al. 1969). Simple hydroxycoumarins such as aesculetin have a limited distribution in the Apiaceae, and are generally replaced by the more complex furanocoumarins (Murray et al. 1982).

No meaningful chemotaxonomic characters were found in the surveys for flavonoids and coumarins. The chemistry will simply be reported here as observations, as these could form the basis for further investigations into the chemistry of the Apiaceae.

### 5.1 Flavonoids

The only flavonoid detected was quercetin (Retention time = 14.4 min; spectral absorbance maxima (nm): 253, 371; spectral match with quercetin standard shown in Figure 5.1), in the leaves of *Heteromorpha involucrata*, and this was not detected in any of the other samples surveyed. The flavonoid concentration was considerably lower than that found in leaves of *Daucus carota* and fruits of *Petroselinum* (parsley). The report of quercetin and kaempferol (Crowden et al. 1969) could not be confirmed (not detected in samples) in the present survey in leaves of *Heteromorpha arborescens*.



**Figure 5.1** Normalized spectral scans obtained by diode-array detection and compared using Beckman System Gold software (correlation coefficient  $r = 0.977$ ). Spectrum A is that of an authentic chromatographed quercetin standard. Spectrum B is that of the peak with the same retention time from the chromatographed extract of *H. involucrata*, Winter 68 (JRAU).

The use of flavonoids as taxonomic characters is therefore considered to be of minimal value in this genus, at least at the species level.

## 5.2 Coumarin survey

The characteristic fluorescence of most coumarins and furanocoumarins under UV (365 nm) was used as a detection parameter. The two standards used (coumarin and dihydrocoumarin)

do not have this property however, due to the absence of oxygen at the 7-position of the molecule. In the *Heteromorpha* samples several fluorescent spots were detected on TLC plates (Table 5.1.), but after isolation these could not be identified as coumarins using mass spectrometry. Reliance on fluorescence was found to be misleading, as purity and concentration could not be assessed properly during isolation.

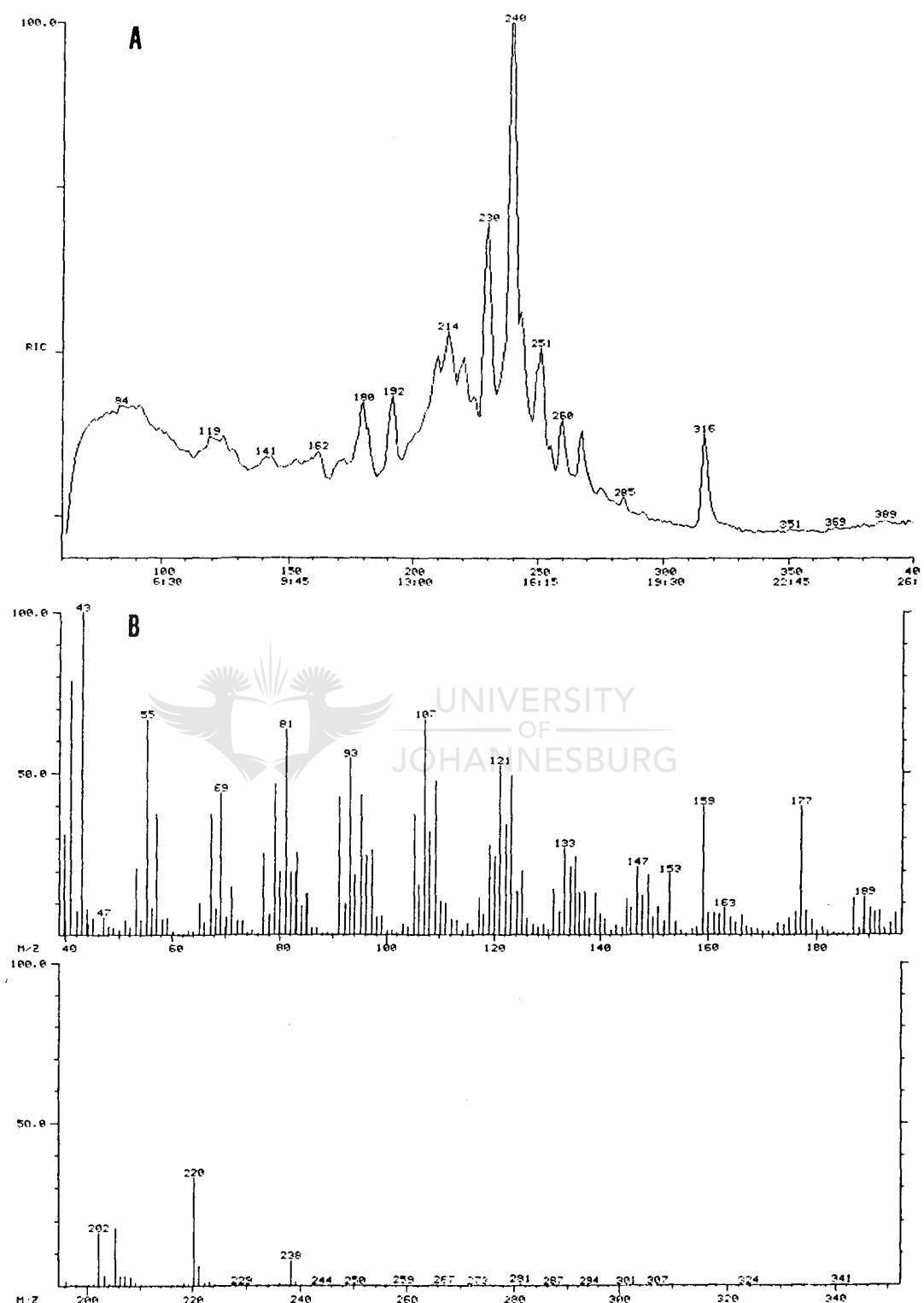
**Table 5.1** Unknown TLC "zones" from *Heteromorpha* extracts detected during a survey for coumarins.

ZONE	Rf - VALUE SOLVENT SYSTEM			SPECTRAL PROPERTIES		
	1	2	3	vis	254 nm	365 nm
X1	0.65	0.75	0.46	-	+	fluorescent with age
X2	0.50	0.10	0.02	-	+	fluorescent with age
X3	0.14	0.02	0.01	-	+	fluorescent with age
Y1	0.31	0.48	0.02	-	-	Bright Blue
Y2	0.19	0.36	0.00	-	-	Bright Blue
Y3	0.11	0.23	0.00	-	-	Bright Blue

System 1: EtOAc+Hexane (1:1)
System 2: Chloroform

System 3: Benzene

GC analysis of the isolated bands showed that these were not pure and in some cases a complex mixture was found (Figure 5.2 A) where no major constituent could be singled out. A notion that these represented polyacetylenic compounds was not supported by the GC-MS results. A typical mass spectrum for a major peak in one gas chromatogram is presented in Figure 5.2 B, and represents an unsaturated fatty acid type of compound with the formula  $C_{15}H_{26}O_2$  (Falcarindiol has the formula  $C_{17}H_{24}O_2$ ).



**Figure 5.2** Gas chromatogram (A) of a sample which corresponds to zone Y1 on TLC, isolated by column chromatography from a leaf extract of *H. arborescens* var. *frutescens*, Winter 57 (JRAU). The mass spectrum below (B) was obtained during the same GC-MS run for the major compound (peak at 240) on the chromatogram, showing the molecular ion at 238 M/Z.

The use of these compounds was found to be impractical due to the complexity of the extracts and technical difficulties in isolation. Table 5.2 shows a more or less random occurrence of the various TLC zones in the genus, and it is clear that these data do not contribute to the understanding of relationships within *Heteromorpha*. The complete absence of any of these zones in *Bupleurum mundii* Cham. & Schlechtd. suggests that they should be further investigated at the generic level.

### 5.3 General conclusions

Among those surveyed for *Heteromorpha*, there are no obvious chemical characters that could be used for chemotaxonomic purposes. A study of the essential oil components could possibly provide more evidence. Such an investigation into essential oils (characteristically abundant in most Apiaceae fruits) may prove invaluable on a higher taxonomic level in addressing questions such as the relationships of woody genera to other herbaceous genera in the Apiaceae and relationships among the woody genera themselves.

A complex mixture of unknown compounds was found in this survey, but these did not correlate with the taxonomy at all.

**Table 5.2** The occurrence of TLC zones of Table 5.1 in *Heteromorpha* and some other genera of the Apiaceae. [Chief floorescent constituents from crude (fruits and roots), and purified (leaves) ethyl acetate extracts.] Voucher specimens all in JRAU.

SAMPLE	ORGAN	YIELD (mg/g)	X1	X2	TLC ZONE X3	Y1	Y2	Y3
<b><u>H. arborescens</u> (Spreng.) Cham. &amp; Schlechtd. var. <u>arborescens</u></b>								
B-E v Wyk 3313	Lf.	10			+++			t
Vlok 2633	Fr.	137		++		++		
<b><u>H. arborescens</u> (Spreng.) Cham. &amp; Schlechtd. var. <u>trifoliata</u> (Wendl.) Sonder</b>								
Winter 71	Lf.	8			t	+++		t
	Fr.	113			t	t		
Winter 53	Lf.	8			+++	++		t
	Rt.	62	++	+++		t		t
Winter 56	Lf.	32		+++				
Schutte 795	Lf.	14			t			
Schutte 796	Lf.	7			t			
<b><u>H. arborescens</u> (Spreng.) Cham. &amp; Schlechtd. var. <u>frutescens</u> Winter var. nov.</b>								
Winter 51	Rt.	89	+	+++			t	t
	Lf.	29			+++	t	t	t
Winter 57a	Lf.	60		+++				
	Fr.	133		+				
	Rt.	59	t	+			t	
Winter 57b	Fr.	116			t			
Winter 58	Fr.	134		t				
Winter 59	Fr.	96			t			
Winter 60	Fr.	120		t				
<b><u>H. involucrata</u> Conr.</b>								
Winter 61b	Lf.	18			+++			
	Fr.	141			+++			
	Rt.	25		+		+++		
Winter 68	Lf.	69		+++				
	Fr.	179		+++				
	Rt.	65	+++	+++				

+ present

Rt.= root extract

++ strong spot

Fr.= fruit extract

+++ very strong spot

Lf.= leaf extract

t trace visible

gr.Fr.= green fruit extract

SAMPLE	ORGAN	YIELD (mg/g)	X1	X2	TLC ZONE X3	ZONE Y1	Y2	Y3
<u>H. involucrata</u> Conr. (...continued)								
Winter 67	Lf.	12		t				
	Fr.	97			+++			
Winter 69b	Lf.	22	+++	t		+		
<u>H. pubescens</u> Burtt Davy								
Winter 65	Lf.	67		+++		t	+	t
	Fr.	151		+++				
	Rt.	22	+	t				
Winter 66	Lf.	63		+++				
	Fr.	96		+++				
Winter 69a	Lf.	53		+++				
	Fr.	133		+++				
	Rt.	32	++	+++			+++	t
<u>H. stenophylla</u> Welw. ex Schinz var. <u>transvaalensis</u> (Schlechter & H. Wolff) Winter <u>comb. et stat. nov.</u>								
Winter 50	Fr.	110		t				
	Rt.	64	t	t				+
	Lf.	21			+++			
Winter 52	Rt.	73	t	t				
Winter 54	Lf.	59			+++			
Winter 55	Lf.	61			+++			
<u>Polemannia simplicior</u> Hilliard & B.L. Burtt								
B&M v Wyk 2879	gr.Fr.						+++	
	Lf.						+	
<u>Polemanniopsis marlothii</u> B.L. Burtt								
Winter 87	Fr.							
	Rt.			++				
<u>Bupleurum mundii</u> Cham. & Schlechtd.								
B&M v Wyk 2899	Lf.							
<u>Peucedanum magalismontanum</u> Sonder								
Winter 76	gr.Fr.						+++	
	Rt.				t		t	

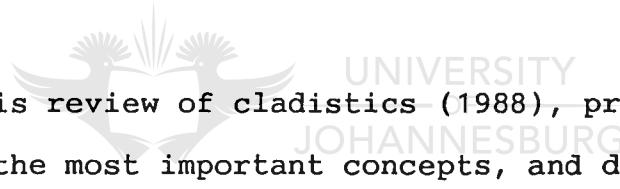
+ present  
 ++ strong spot  
 +++ very strong spot  
 t trace visible

Rt.= root extract  
 Fr.= fruit extract  
 Lf.= leaf extract  
 gr.Fr.= green fruit extract

## CHAPTER 6

**PHYLOGENY (Cladistic analysis)**

There is a noticeable lack of a phylogenetic approach to the classification of the Apiaceae in general. I have only found one case in the literature of a cladistic analysis in this family, namely that of Roux *et al.* (1977) for *Bupleurum* L., where the result was favourably compatible with a phenetic analysis done in the same study. To stimulate the application of this method in the African Apiaceae, a cladistic account is given of *Heteromorpha* Cham. & Schlechtd.



Linder, in his review of cladistics (1988), provides a broad overview of the most important concepts, and discusses the application of this technique with its limitations. This review (Linder 1988) serves as a guide to the relevant literature for getting acquainted with the method.

Apart from its use for inferring phylogeny within study groups, the value of cladistics lies not so much in its analytical accuracy as in its propensity for testability, i.e. to verify or falsify a result or to evaluate the effect of adding new data.

The premises as put forward in the original formulation by Willi Hennig in 1950 have since been deemed overly restrictive (Linder 1988). An example given is the requirement for dichotomous

speciation, not allowing for the recognition of any taxa other than those that are strictly monophyletic defined by their own autapomorphies. The relaxation of these limitations has broadened the scope of its application in resolving taxonomic problems.

The aim of using cladistics in this small study group was to evaluate the results (character transformations and phylogenetic relationships between taxa), expressed in cladistic terms, rather than to apply it primarily as an analytical tool. The method is certainly an ideal means of assessing and refining the hypothetical value of the characters employed in reaching the classification. It was also useful in drawing attention to weaknesses in the argumentation of using certain characters to circumscribe taxa, and to arrive at a natural sequence of species for the formal taxonomic treatment.

### 6.1 Choice of outgroup

The genus *Polemannia*, an endemic of the Drakensberg and Eastern Cape mountains of South Africa, was chosen for polarising character state transformation series according to the outgroup comparison method as discussed in detail by Watrous & Wheeler (1981). The characters and polarization of character states are given in Table 6.1. There is a distinct morphological resemblance between *Heteromorpha* and *Polemannia*, particularly with regard to habit, bark, and leaf division (Burtt 1988).

Mixed collections are known from areas where these genera occur sympatrically, and *Polemannia* specimens are often found erroneously filed under *Heteromorpha* in herbaria due to their superficial similarity. The synapomorphies selected to explicitly group the two genera as sister taxa are the smooth bark (Table 6.1: character 26), with layers which typically peel off in horizontal bands, and the pedately to pinnately compound foliose (Table 6.1: character 27) leaves with an entire margin (Table 6.1: character 28).

The rare wing configuration of the fruit (Figure 6.1 & 6.2: character 25) serves as a generic synapomorphy for all *Heteromorpha* species. The genus *Polemanniopsis* was initially considered as a possible outgroup on the basis of a similar wing configuration (Burtt 1988), but anatomical sections have shown a lack of homology in the fruit structure (Winter *et al.* *in prep.*).

## 6.2 Characters

All discontinuous and logically polarisable characters within *Heteromorpha* were initially selected for inclusion in the analysis. Those synapomorphies that are unique to terminal taxa (autapomorphies) were excluded and later added to the resolved cladogram. Variable characters (where the plesiomorphic and apomorphic states co-occur) were coded for the plesiomorphic state. In character 2 this led to its interpretation as an

TABLE 6.1 Characters and polarization of character states according to the outgroup method, for the genus *Heteromorpha*.

TAXA	CHARACTERS & CHARACTER STATES (? = missing data)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>POLEMANNIA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1 <i>H. arborescens</i>	0/1	0/1	0	0	1	1	0	1/2	1	0	0	0	0	0	0
2 <i>H. papillosa</i>	0	0	0	0	1?	1	0	2	1	0	0	0	0	0	0
3 <i>H. stenophylla</i>	1	0	0/1	1	1	0	0/1	0/2	0/1	0	0	0	0	0	0
4 <i>H. occidentalis</i>	1	0	1	1	1?	0	1	1/2	0	1	0	0	0	0	0
5 <i>H. gossweileri</i>	1	0/1	1	1	1?	0	0	0	0	1	1	0	0	1	0
6 <i>H. pubescens</i>	1	1	1	1	1	0	1	0/1	0	2	1	1	1	1	1
7 <i>H. involucrata</i>	1	0/1	1	1	1	0	1	1/2	0	1	0/1	1	1	1	1

1 BRANCHING (HABIT):	well branched (arborescent) = 0; third order branching uncommon = 1 (suffrutescent).
2 VESTITURE OF STEMS:	glabrous = 0; pilose = 1.
3 CORTEX:	continuous cylinder = 0; alternating strands = 1.
4 PERIDERM:	smooth, peeling = 0; granular, not normally peeling = 1.
5 CORTICAL RESIN DUCTS:	large = 0; small = 1.
6 LEAF BASE:	generally < 1/2 stem circumference = 0; generally > 2/3 stem circumference = 1.
7 PETIOLE CROSS SECTION:	not carinate = 0; carinate = 1.
8 PETIOLE CROSS SECTION:	canalicate = 0; semiterete = 1; terete = 2.
9 LEAF TRICHOME TYPE:	papillate = 0; short cylindric = 1.
10 LEAF TRICHOME TYPE:	papillate = 0; basally cushioned or tuberculate = 1; filamentous = 2.
11 LEAF VESTITURE:	margin & adaxially only = 0; at least on abaxial midrib = 1.
12 TERMINAL UMBEL RAYS:	same no. as in lateral umbels = 0; more than in lateral umbels = 1.
13 FOLIOSE INVOLUCRAL BRACKTS:	up to 2 only, simple = 0; >2, often dissected.
14 PETALINE RIBS:	unwinged = 0; half-winged = 1.
15 SECONDARY RIBS:	absent = 0; present = 1.

Autapomorphic character states (numbers in brackets refer to the relevant terminal taxa as listed in Table 6.1 )

- 16 (1) TERMINAL PINNA BASE: grading into petiole/petiolule (decurrent) = 0;  
distinct lamina and petiole/petiolule = 1.
- 17 (2) PINNA SHAPE: widely ovate to narrowly lanceolate (up to 9x longer than wide) = 0;  
linear (more than 9x longer than wide) = 1.
- 18 (2) STYLOPODUM: glabrous or sparsely hairy = 0; mostly papillose = 1.
- 19 (3) OVARY: < twice as long as the stylopodium = 0;  
> twice as long as the stylopodium = 1.
- 20 (3) LEAF VESTITURE: present = 0; absent = 1.
- 21 (4) CALYCINE VITTAE: single carinal = 0; carinal & 2 lateral = 1.
- 22 (5) PETIOLE: unwinged = 0; sometimes winged = 1.
- 23 (6) LEAF TRICHOME TYPE: papillate, cylindrical or conical = 0; filamentous = 1.
- 24 (6) VITTAE AROUND SEED: six, regular = 0; c. 16, irregular = 1.

[Character 2, after generalised coding, becomes an autapomorphy for taxon 6 with states: variably pilose = 0; invariably pilose = 1]

#### Generic synapomorphy for *Heteromorpha*

- 25 FRUIT WING CONFIGURATION: wings not limited to sepaline position = 0;  
wings limited to sepaline position = 1.

The following states were selected as synapomorphies for grouping *Polemannia* with *Heteromorpha*:

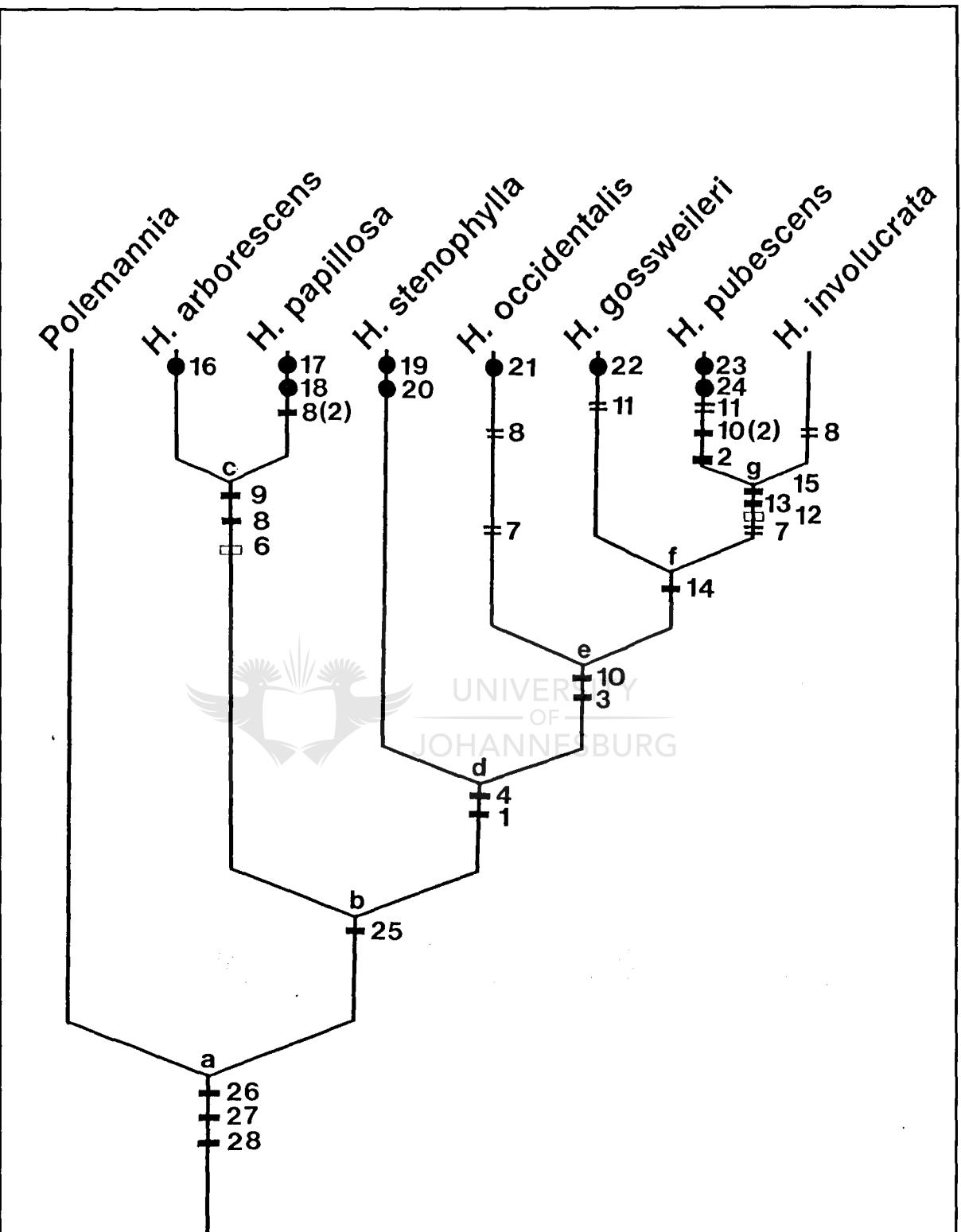
- 26 BARK: not smooth, peeling = 0; smooth, peeling = 1.
- 27 LEAF DIVISION: digitate = 0; pinnate = 1.
- 28 LEAF MARGIN: dentate = 0; entire = 1.

autapomorphy for *H. pubescens*, and it is consequently not included in the computer analysis. Character 5 is excluded due to missing data and on the basis that the initial survey showed that it was invariable within the genus. Only 13 meaningful characters were thus available for analysis. In the coding for character 8, the invariability of the state for taxon 2 compared with that in other taxa is uncertain due to a limited survey of that taxon. The value of this character is therefore questionable. Together with character 7, these are the only two characters which do not corroborate the topology which results from the combination of all other characters.

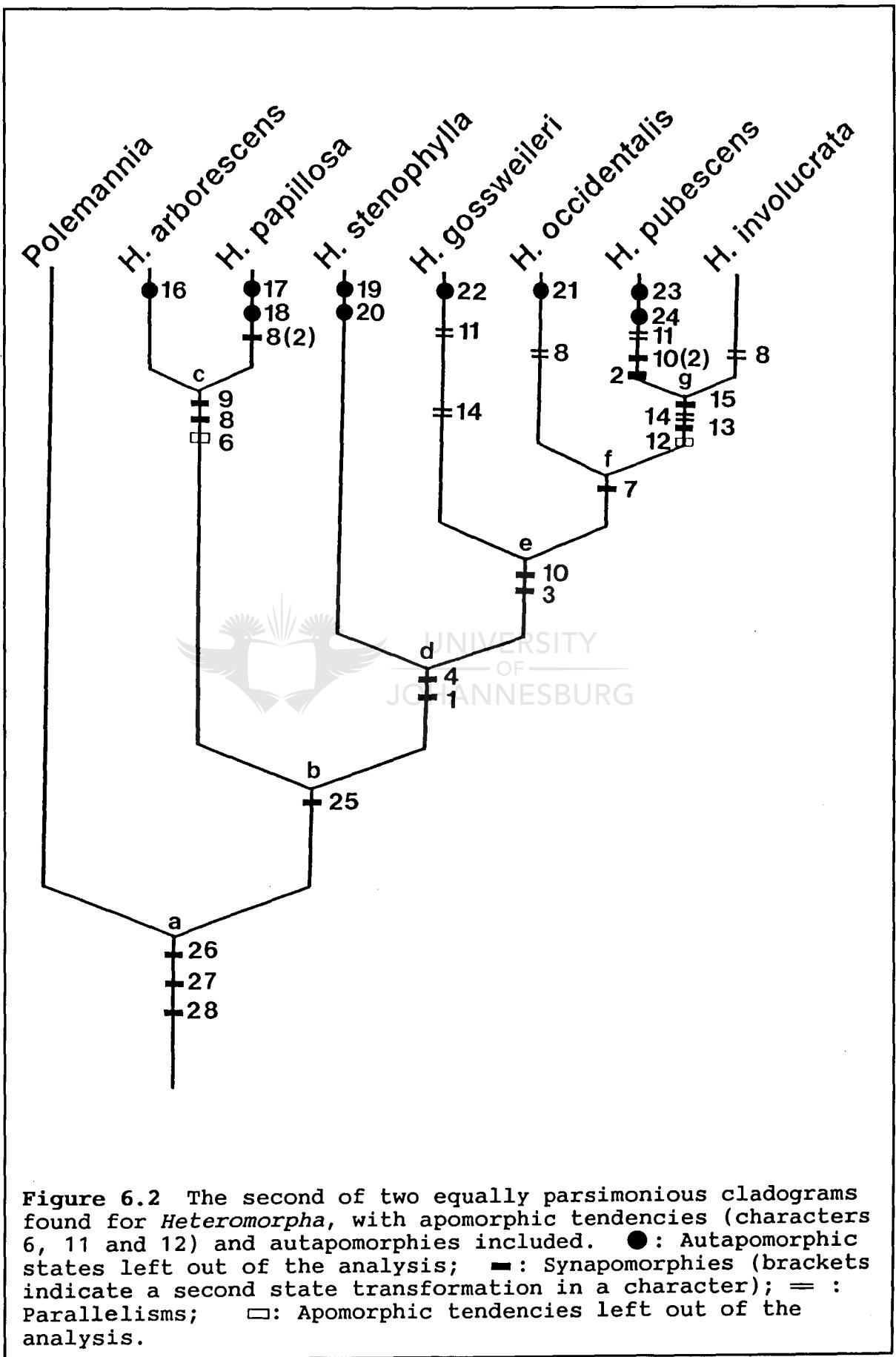
Some apomorphic tendencies have also been included in Table 6.1 (characters 6, 11, 12). These were only added after the cladogram was constructed, however.

### 6.3 Results and discussion

Two equally short trees (Figure 6.1 & 6.2) of length 15 steps and with a consistency index of 80 were found using the 'ie' command in HENNIG86. When apomorphic tendencies were added, the two topologies remained the same, the length increased to 19 steps and the consistency index was 78. The strict consensus tree was generated using the 'nelson' command, and showed that taxa 4 to 7 could not be fully resolved, although taxa 6 and 7 (*H. involucrata* & *H. pubescens*) remained grouped together. All homoplasious characters were interpreted as parallelisms rather



**Figure 6.1** The first of two equally parsimonious cladograms found for *Heteromorpha*, with apomorphic tendencies (characters 6, 11 and 12) and autapomorphies included. ●: Autapomorphic states left out of the analysis; ■: Synapomorphies (brackets indicate a second state transformation in a character); =: Parallelisms; □: Apomorphic tendencies left out of the analysis.



**Figure 6.2** The second of two equally parsimonious cladograms found for *Heteromorpha*, with apomorphic tendencies (characters 6, 11 and 12) and autapomorphies included. ●: Autapomorphic states left out of the analysis; —: Synapomorphies (brackets indicate a second state transformation in a character); =: Parallelisms; □: Apomorphic tendencies left out of the analysis.

than reversals in the analysis of each character. The lack of resolution was found to be due to a conflict between characters 7 and 14. As there is some variation in character 7 for *H. stenophylla*, character 14 is preferred as a synapomorphy for node 6 in the cladogram shown in Figure 6.2, while a homoplasy is invoked in character 7.

*H. involucrata* could be considered a so-called paraphyletic assemblage (Linder 1988), given the lack of autapomorphies. Such groups have not always been accepted in a cladistic analysis, but have been recognised by several workers eg. Linder (1984), in *Hypodiscus* Nees, by Bremer, as 'paraclades' and by Mishler & Brandon, as 'metaphyletic' taxa (Linder 1988). From an evolutionary perspective, although we can never fully understand the history of variation, it seems plausible that a species with a long history and a wide, intermittent geographical spread, should show a large amount of morphological divergence between populations. If one assumes that speciation occurs at the populational level in only one of the populations, any one speciation event for that group automatically requires that the original autapomorphy defining that species shifts down one level and becomes a synapomorphy grouping the mother and daughter species, thus leaving the mother species undefined in terms of apomorphies. For a terminal taxon to be monophyletic with an unique apomorphy, it is required that any branching event involves the dichotomous acquisition of two derived states, as well as the phasing out of the plesiomorphic

condition (Linder 1988), not only in the population concerned, but over the entire range of the species.

Alternative hypotheses were considered for the polarity of certain characters. The foremost question was whether an arborescent habit was actually inherited, or whether it could have been derived within the genus. Seen in the family as a whole, woodiness seems to be derived (section 3.2.1 – woodiness vs herbaceousness). In the Ammineae-heteroclitae, the relatively common occurrence of woodiness (in the genera *Anginon*, *Bupleurum*, *Heteromorpha*, *Polemannia* and *Polemanniopsis*) suggests that this character is plesiomorphic. The true relationships in this group are too vague, however, to draw such conclusions. When the polarity of this character is changed, it involves one extra step, but not within *Heteromorpha*. The arborescent habit is then hypothesised as a parallelism between *Polemannia* and the *H. arborescens-H. papillosa* clade. The overall topology is not disturbed. Thus if the outgroup method and parsimony criteria are followed strictly, it is concluded that woodiness is plesiomorphic in *Heteromorpha*. Changing the polarity of other characters made no improvements to the cladogram.

There is always some uncertainty (as pointed out by Stuessy & Crisci 1984) about the true relationship of the selected outgroup to the study group, i.e., whether it is attached to the base of the cladogram or from some point within. In this case monophyly of *Heteromorpha* is assumed, as the synapomorphy defining the genus is an exceptionally rare state in the family,

but the possibility remains that *Heteromorpha* may be paraphyletic and could then include *Polemannia* as a section.



## CHAPTER 7

**TAXONOMY OF *Heteromorpha* Cham. & Schlechtd.****7.1 Taxonomy of the Apiaceae**

The Apiaceae was one of the earliest groups of flowering plants to be recognized as a family (Heywood 1978). Early treatments of the family include those of De Candolle (1830) and Bentham & Hooker (1867). The most up to date account of the family as a whole is Drude's (1898) classification in Engler & Prantl's *Die natürlichen Pflanzenfamilien* (Burtt 1991). He recognizes the three subfamilies, Hydrocotyloideae, Saniculoideae and Apioideae. The two smaller subfamilies, Hydrocotyloideae and Saniculoideae, have been investigated relatively well (Burtt 1991), compared to Apioideae, where tribal classification needs serious attention (Townsend, 1989; Burtt, 1991). *Heteromorpha* is classified in the Apioideae, which is by far the largest subfamily and is subdivided into 8 tribes.

Drude (1898) recognised various subtribes in the tribe Ammineae [Apieae], and *Heteromorpha* was placed in the Carinae, recognising the two species *H. arborescens* and *H. stenophylla*. Placement in the Ammineae dates from the earliest records, ever since Thunberg's specimen was placed in *Bupleurum*, also a member of that tribe. The name Ammineae dates from 1814 and is

attributed to Koch by De Candolle (1830). Ammineae is a *nom. illeg.* as the type of the family (*Apium*) is from this tribe. The correct name, Apieae, has since been applied by recent authors.

Cerceau-larrival (1962, 1971) drew up a revised classification with new tribal and subfamily names, but a valid Latin nomenclature was never published. This work was chiefly based on evidence from palynology and the morphology of seedlings.

Burtt (1991) made a valuable contribution toward the knowledge of African Apiaceae by publishing a checklist for the southern African contingent. According to Burtt (1991), the southern African Apiaceae are interesting in that there are 19 endemic genera with very little affinity with any other genera outside the area (and limited affinities among them), indicating that they are probably relics of a much larger earlier Apiaceae representation in this area. When sub-Saharan endemics are considered, this figure increases to 24 genera, including *Heteromorpha*.

Up to 11 of the 38 southern African genera have representatives with woody habits (Burtt 1991), a feature that is uncharacteristic of the family. The study of woodiness is important in assessing the phylogeny of this family, and is suggested by Burtt (1991) as a reason for making southern Africa a focal point in the investigation of the Apiaceae.

## 7.2 Taxonomic history of *Heteromorpha* Cham. & Schlechtd.

The genus was first recognised as such by L.A. von Chamisso and D.F.L von Schlechtendal (1826), the name alluding to the peculiar fruit structure. *H. arborescens* was the only known species, based on a Thunberg specimen from South Africa. Prior to this, the species had been classified under *Bupleurum* by C.P. Thunberg (probably due to its woody habit), and segregated, along with representatives of several South African genera, by C. Sprengel (1813) under *Buprestis* Spreng, which he later called *Tenoria* (Burtt 1991). A second species was added by H. Wendland (1825), as *Bupleurum trifoliatum*. This was not recognised as distinct from *H. arborescens* by Chamisso and Schlechtendal (1826). Ecklon and Zeyher (1837) distinguished between the two, and added a third species, *H. collina*. There has been uncertainty regarding the taxonomy and correct application of names in this complex ever since.

From Ethiopia (then Abyssinia) *H. abyssinica* was described by A. Richard (1848), who added a variety, *H. abyssinica* var. *simplicifolia*. These plants have proved to be part of the variation within *H. arborescens* var. *trifoliata*, indistinct from those found in the rest of Africa.

Sonder, in Flora Capensis of Harvey and Sonder (1862), treated the three southern African taxa as varieties of *H. arborescens*. O. Kuntze (1891) changed the name to *Franchetella*, and later (1898) recognised five varieties of *F. arborescens*. Meanwhile, Engler (1892) published *H. stenophylla* Welw. ex Engl. as a *nomen*

*nudum*; this name was later validated by Schinz (1894). Hiern (1898) described (without any latin description or diagnosis) *Franchetella arborescens* var. *platyphylla* Welw. ex Hiern, from Angola, herein described as a new species, *H. occidentalis* Winter.

Conrath (1908) described a new suffrutescent species from the Transvaal which he called *H. involucrata*. Wolff, in the only revision of the genus (1910), only later incorporated *H. involucrata* as an addendum. He had till then treated *Heteromorpha* as monotypic, with *H. arborescens* as the only species, and included *H. stenophylla* Welw. ex Schinz in this broad concept. His treatment of *H. arborescens* and the resulting three varieties and two formae reflect the restriction of his study to herbarium specimens, where the full range of population variation is not evident and information regarding habit is sparse.

In a later publication, Wolff (1921) added three more suffrutescent species, namely *H. kassneri*, *H. stolzii*, and together with Schlechter, *H. transvaalensis*.

*H. pubescens* was described by Joseph Burtt-Davy (1932), who was the first author to draw up a key for *Heteromorpha* species (Transvaal and Swaziland only).

*H. gossweileri* was described by Norman (1933), who had originally (1922) described it as an *Annesorhiza*. In the same publication (1933), he described another Angolan specimen as

*Bupleurum angolense*, later (1934) correcting it to *H. angolensis*. The latter has since also been sunk under *H. gossweileri* by Townsend (1985).

The generic concept was expanded by Humbert (1956), who between 1955 and 1956 described eight woody species of Apiaceae from Madagascar as *Heteromorpha*, despite the lack of the essential fruit characters that define the genus. These plants all lack the characteristic zygomorphic wing configuration of the fruit (Winter et al. 1993), and differ in other morphological features.

A proposal to conserve the name *Heteromorpha* Cham. & Schlechtd. against the earlier homonym *Heteromorpha* Cass. (Asteraceae), was made by J.F.M. Cannon (Cannon 1968), and accepted in 1969 (Cannon 1969). *Heteromorpha* Cass. is a synonym of *Heterolepis* Cass. (Asteraceae).

Townsend (1985) described a new species, *H. papillosa*, from Namibia, and sunk *H. kassneri* H. Wolff. and *H. angolensis* (Norman) Norman, under *H. involucrata* Conr. and *H. gossweileri* respectively. He also provided a tentative key and valuable notes on the taxonomy of the genus, highlighting some problem areas.

In his checklist of southern Africa Apiaceae, Burtt (1991) took care of many of the nomenclatural and typification problems of *Heteromorpha*. He too pointed out the taxonomic difficulty of the

*H. arborescens* complex with its associated nomenclatural uncertainty.

### 7.3 Formal classification

#### 7.3.1 The genus

**Heteromorpha** Cham. & Schlechtd., Linnaea 1: 385--386; Tab.V: Fig.2. (1826), *nom. conserv.*; DC, Prod. 4: 127,134 (1830); Endl., Gen. Pl. 1: 772--773 (1839); Eckl. & Zeyh., Enum. Pl. Afr. Aust. 3: 342 (1837); A. Rich. in Tent. fl. abyss. 1: 326 (1847); Sonder in Fl. Cap. 2: 542 (1862); Benth. & Hook. f., Gen. Plant. I. 3: 887 (1867); Hiern in Oliv., Fl. Trop. Afr. 3: 10 (1877); Engl. Hochgebirgsfl. Tr. Afr: 317--318 (1892); Briquet in Bull. Herb. Boiss. 5: 438 (1897); Drude in Engl., Nat. Pflanzenfam. III. 8: 176, 179--180 (1898); H. Wolff in Engl., Pflanzenr. Heft 43: 32--36 (1910); Burtt Davy, Man. Fl. Pl. & Ferns Transvaal II: 519--520 (1932); Phill., Gen. S. Afr. Fl. Pl.: 551 (1951); Humb. in Not. Syst., Paris XV (1956); Neusser & Schreiber in Merxmüller, Prod. Fl. S.W. Afr: 5--6 (1967); Cannon in Taxon 18(4): 478 (1969); Jac.-Fel. in Fl. Cameroun 10: 74 (1970); Dyer, Gen. S. Afr. Fl. Pl. 1: 420 (1975); Compton, Fl. Swaziland: 407 (1976); Cannon in Fl. Zambesiaca: 578 (1978); Cannon & Sampaio Martins in Fl. Mocambique: 26--27 (1981); C.C. Townsend in Kew Bull. 40: 843--850 (1985); C.C. Townsend in Fl. Trop. E. Afr: 37--41 (1989);

B.L. Burtt in Edinb. J. Bot. 48: 213--215 (1991). Type species:  
*H. arborescens* (Spreng.) Cham. & Schlechtd.

*Franchetella* Kuntze, Revisio Generum Plantarum 1: 267  
(1891) - *non* Pierre (1890); Hiern, Cat. Afr. Pl. Welwitsch I. 2:  
424 (1898); Kuntze, Rev. Gen. III. 2: 112 (1898). Type as above.

The generic concept was expanded by Humbert (1956) to include eight species (Humbert 1955, 1956) from Madagascar, herein listed under excluded species.

#### Description

Suffrutices, shrubs or trees, up to 20 m high, rarely facultative climbers. *Stems* simple, arising from woody subterranean base, or repeatedly branching above ground, terete, smooth to longitudinally grooved, glabrous to somewhat hairy, pith variable in thickness. *Bark* virtually absent or well developed, then somewhat waxy, layers peeling in horizontal bands. Newly exposed bark smooth and shiny, reddish or yellowish brown, translucent for several years, becoming dull black or grey with age. *Roots* initially contractile, solitary, or simply branched, tuberous, 25--40 mm in diameter, or well branched from woody caudex. *Leaves* 10--320 mm long, 5--200 mm wide, simple or trisect to pinnately and/or pedately compound, glabrous to variably pilose, distinctly petiolate to subsessile; bases non-amplexicaul, semi-amplexicaul, or amplexicaul, often ciliate, *petioles* (3--)5--80(--110) mm long, shallowly semiterete to terete or V-shaped in transverse section, widely to narrowly

grooved, with collenchyma ridges at least along edges of groove, sometimes carinate. Incision variable, often decursive. *Pinnae* very narrowly to widely elliptic, ovate or lanceolate to obovate or oblanceolate, sometimes outwardly curved; apices acute to emarginate, mucronulate to apiculate; margins entire to markedly crenulate, sometimes thickened, undulate or ciliate; bases truncate to narrowly cuneate or attenuate; 10--160 mm long, 5--45 mm wide. *Inflorescence* a panicle of few to over 40 compound umbels, sometimes with lateral umbels suppressed so that only the main florescence remains, bracts trifoliolate or mostly simple, sometimes reduced in size, usually at least one pair of opposite simple bracts in each paraclade; main florescence of (4--)10--25(--68) rays, (11--)15--40(--80) mm long, and (4--)11--21(--30) raylets, (1--)2--7(--10) mm long, sometimes with an additional simple umbel directly below terminal compound umbel. Main florescence developing in advance of coflorescences. Simple flowers occasionally found among secondary umbels in a compound umbel. *Involucro* present, involucral bracts small to broad and conspicuous, somewhat caducous, equal or unequal. *Involucel* of small, lanceolate bracteoles. *Flowers* bisexual, occasionally andromonoecious. *Calyx lobes* distinct, acute, persistent in fruit, with a single vitta along the keel (carinal vitta) often decurrent along wings on fruit walls, or with two additional smaller lateral vittae. *Petals* cream-coloured to greenish yellow, glabrous, papillose or hairy, emarginate above with an inflexed lobule, keeled on inner face. *Stamens* as long or up to twice as long as petals, inflexed; anthers divided above. *Stylopodia* conical, somewhat crenulately margined, with short, rather rigidly divergent to recurved styles. *Fruit* slightly

laterally compressed, elliptic, broadly or narrowly obovoid or obpyriform, with a broad commissure, glabrous or more rarely pilose or papillose; mericarps dissimilar, one with the two intermediate primary (sepaline) ribs expanded into wings and the dorsal and marginal (petaline) ribs much smaller, the other with the two marginal ribs and one dorsal (sepaline) rib winged and the intermediate (petaline) ribs much smaller so that the fruit appears somewhat trigonous when viewed from above; vittae solitary and conspicuous in the valleculae, two on the commissure, or up to 16 irregular vittae around each seed; occasional small vittae occurring in the tips of the ribs or part way along them; carpophore bifid to the base; endosperm pentagonal to broadly reniform or almost round in transverse section. *Chromosome number:*  $2n=22$ .



*Diagnostic characters.* *Heteromorpha* is similar to *Polemannia*, but lacks the intramarginal vein in the leaf, and has wings associated with the sepaline bundles in the fruit (*Polemannia* has only slight commissural extensions and no sepaline or petaline wings). The fruit differs from that of *Polemanniopsis* by the presence of conspicuous petaline ribs and many other anatomical details (Winter *et al.* in prep.).

*Distribution and ecology.* *Heteromorpha* is essentially restricted to the African continent south of the Sahara, its range just extending into the middle-east as far as the Yemen Arab Republic (Figures 7.1, 7.9, 7.14 & 7.22). The most obvious discontinuities correspond to the equatorial rainforests and arid regions. The occurrence of fire and periodic drought in the

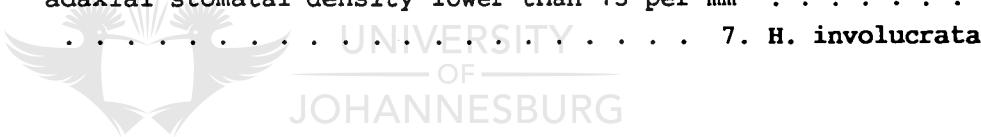
Afromontane and Savannah vegetation types typical of the distribution range seem to have been important factors in the evolution of the genus.

*Flowering time is in summer, and fruit reaches maturity in autumn, but at low latitudes, flowering and fruiting occur throughout the year. Fruiting on the main florescence and flowering on paraclades often coincide.*

#### 7.3.2 Key to the species of *Heteromorpha* Cham. & Schlechtd.

- 1a Trichomes very long and slender (filamentous), present over all aerial parts, up to the corolla; suffrutices or weakly branched shrubs; vittae many (c. 16), irregular, surrounding the seed; secondary ribs present on the fruit surface . . . . . 6. *H. pubescens*
- 1b Trichomes, if present, papillate to cylindric, never filamentous or not on all aerial parts; suffrutices, shrubs or trees; vittae six, four in valleculae, two on commissural face; secondary ribs rare on the fruit surface.
- 2a Trees or shrubs (rarely facultative climbers), vegetative stems ramos; leaf trichomes not set on cushions or tubercles.
- 3a Pinnae narrowly lanceolate to very narrowly elliptic; more than four times longer than wide; papillose trichomes often occurring on stylopodium; adaxial stomatal density up to 43 per mm<sup>2</sup>; vicariant distribution in Windhoek area of Namibia . . . . . 2. *H. papillosa*
- 3b Pinna shape variable; rarely more than four times longer than wide; stylopodium glabrous, or sparsely pilose at rim or bases of styles; adaxial stomatal density lower than 10 per mm<sup>2</sup>; not in Windhoek area of Namibia, but widely distributed in Africa . . . 1. *H. arborescens*
- 2b Suffrutices, stems simple (unbranched), normally only branching in the reproductive phase, or weakly branched shrub; leaf trichomes sometimes set on cushions or tubercles.

- 4a Calyx lobes with carinal vitta and two additional lateral vittae . . . . . 4. *H. occidentalis*
- 4b Calyx lobes with carinal vittae only.
- 5a Plants mostly glabrous; ovary more than twice as long as the stylopodium . . . . . 3. *H. stenophylla*
- 5b Leaves, sometimes stems, at least with some papillae or trichomes; ovary less than twice as long as the stylopodium.
- 6a Terminal umbel rays thin, not more than 16; involucre with few, slender, bracteose bracts; leaves sub-sessile, simple or with short petioles, trifoliolate; lateral pinnae never further dissected; stems thin, weak; adaxial stomatal density higher than 40 per mm<sup>2</sup> . . . . . 5. *H. gossweileri*
- 6b Terminal umbel rays stout, normally more than 25; involucre with many foliaceous bracts; leaves with short or long petioles, trifoliolate, decursively pinnate or pedate; lateral pinnae sometimes further pinnatisect; stems robust; adaxial stomatal density lower than 15 per mm<sup>2</sup> . . . . . 7. *H. involucrata*



### 7.3.3 The species of *Heteromorpha* Cham. & Schlechtd.

1. *H. arborescens* (Spreng.) Cham. & Schlechtd. in Linnaea 1: 385 (1826); DC, Prod. 4: 134 (1830); Eckl. & Zeyh., Enum. Pl. Afr. Aust. 3: 342--343 (1837); Sonder in Fl. Cap. 2: 542 (1862); Benth. & Hook. f., Gen. Plant. I. 2: 887 (1867); Hiern in Oliv., Fl. Trop. Afr. 3: 10--11 (1877); Engl. Hochgebirgsfl. Tr. Afr: 317--318 (1892); Briquet in Bull. Herb. Boiss. 5: 438 (1897); Drude in Engl., Nat. Pflanzenfam. III. 8: 179 (1898); H. Wolff in Engl., Pflanzenr. Heft 43: 33--35 (1910); Engl., Pflanzenw. Afrikas III. 2: 805 (1921); C.C. Townsend in Kew Bull. 40: 843--850 (1985); B.L. Burtt in Edinb. J. Bot. 48: 213 (1991). Type:

Cape, "In regionibus occidentalibus Promontorii bonae spei ad Gamka et Cango fluvios Aprili mense et in terra Auteniquarum Januario mense legerunt Mundt et Maire.", Thunb. s.n sub Thunb-UPS 6751 (UPS, lecto., designated by Burtt (1991); PRE, microfiche!).

### Description

Well branched woody shrub or tree (1,5--)3--9(--15) m high, rarely a facultative climber. Trunk diameter 50--250 mm. *Stems* well branched (branching limited in var. *frutescens*), terete, smooth, glabrous to pilose. Pith variable in thickness. Bark well developed, peeling in horizontal bands, translucent for several years, somewhat waxy. Newly exposed bark smooth and shiny, reddish or yellowish brown, becoming dull black or grey with age. Leaves with a maximum length of 10--180(--202) mm, with a short to long petiole (3--)5--50(--80) mm, semiterete, sometimes terete, glabrous to pilose, then more so in groove, base amplexicaul, rarely non-amplexicaul; outline variable, even on a single stem, simple or trisect to pinnately and/or pedately compound, or bipinnatifid (typically pinnate with 5 pinnae). Incision sometimes decursive, terminal leaflet often distinctly petiolulate. *Pinnae* narrowly to widely elliptic, lanceolate, ovate, obovate or trullate, sometimes falcate; apex emarginate to acuminate, mucronate to apiculate; margins entire or somewhat crenulate, sometimes ciliolate; base acuminate or attenuate to rounded or obtuse; with a maximum length of 10--79 mm, 5--29 mm wide; adaxial midrib with short, unicellular, cylindrical trichomes, rarely glabrous. *Inflorescence* a single compound

umbel or a panicle of few to more than 40 compound umbels, rarely reduced in size (in var. *frutescens*); main florescence of (4--)10--23(--32) rays, 11--24(--37) mm long, (4--)11--21(--28) raylets, 1,5--3,5(--8) mm long. *Involucral bracts* mostly small, lanceolate, interspersed with up to 2 larger foliose, elliptic bracts. *Petals* cream-coloured to greenish yellow, higher than, or as high as broad. *Stylopodium* sometimes sparsely pilose at the rim, or at the bases of styles. *Fruit* glabrous or pilose, elliptic to ovoid or obpyriform, 3--9 mm long, 1.5--4 mm wide; vittae solitary [and conspicuous] in the valleculae, two on the commissure. *Chromosome number:* 2n=22.

*Diagnostic characters.* *H. arborescens* is distinguished from most other species by its habit (woody tree or shrub, usually well branched from one or several trunks, or a facultative climber), the vestiture of leaves generally confined to adaxial midrib and margin, and trichomes that are short, cylindrical, not raised on tuberculae. It is closest to *H. papillosa*, but the pinnae are rarely more than four times longer than wide as in that species.

*Distribution and ecology.* *H. arborescens* appears to be restricted to the eastern part of the African continent (Figure 7.1), and is associated with Afromontane vegetational elements or relicts thereof.

*Infraspecific variation.* Various regional forms have been recognised as distinct taxa in the past, and have been accorded status either as species (Ecklon & Zeyher 1837), varieties (Sonder, Kuntze, Wolff, Hiern), or formae (Wolff 1910). As

intermediates have been found for all these forms, they are not considered as species in this treatment. Nevertheless, *H. arborescens* is so polymorphic and taxonomically unwieldy, that the traditional infraspecific rank of variety is quite useful to describe the observed general patterns of morphological and geographical variation, while maintaining nomenclatural stability (only two of the varietal names applied here are new). The application of the rank of variety as infraspecific category corresponds to the recommendations given by Stuessy (1990). According to Stuessy, the characteristics of the rank of variety are: One to few conspicuous morphological differences, cohesive geographical distributions, largely allopatric with some overlap, probable natural hybridization in overlap region, and reduced fertility of hybrids (Stuessy 1990: Table 12.1). As it is not possible in this revision to determine the ultimate biological nature of each unit, the last criterion was not considered. Burtt (1991) emphasized the need, at least in southern Africa, to afford the various forms different names.

#### **Key to the varieties of *H. arborescens***

- 1a Mature leaves unifoliolate (coppice leaves may be trifoliolate); petioles short, with a maximum length of 3--27 mm.
- 2a Leaves typically more than 30 mm long, not obovate; leaf apex acuminate to rounded; mature fruits (excluding stylopodia) up to 8 mm long, with an oblanceolate to narrowly obpyriform outline in dorsal view; typically a tree, 2--15 m high . . . . . 1.1. var. *arborescens*
- 2b Leaves typically less than 30 mm long, obovate; leaf apex rounded, more often truncate to emarginate; mature fruits (excluding stylopodia) typically shorter than 5 mm, up to 6 mm long, with an elliptic outline in dorsal view; typically a shrub, 0,4--2(--3) m high, rarely a facultative climber . . . . . 1.2. var. *collina*

- 1b Mature leaves trifoliolate, pinnately or pedately compound; petioles long, with a maximum length of 24--70(--80) mm.
- 3a Shrubby habit; trunk not more than 50 mm in diameter; bark not readily peeling; regeneration mostly from caudex after reproductive phase; pinnules, when present, opposite or sub-opposite along rachilla; synflorescence lax, borne clear of vegetative leaves, with bracts reduced, fruit wings well-developed . . . . . 1.4. var. *frutescens*
- 3b Typically a tree, 2-15 m high; trunk 50--200 mm in diameter; bark peels readily in horizontal bands, revealing smooth underbark or remaining as laminated flakes; innovation buds active throughout aerial vegetative system.
- 4a Mature fruits (excluding stylopodia) up to 5 mm long; leaves trifoliolate, more often pinnately decomound, with strongly decursive lateral pinnae along rachis, lateral pinnules often decursive along upper side of rachilla only; pinnae narrow, gradually tapering toward acuminate apex, often falcate; restricted to central African mountainous habitats . . . . 1.5. var. *montana*
- 4b Mature fruits (excluding stylopodia) more than 5 mm long; leaves trifoliolate, pinnately or pedately compound, sometimes with weakly decursive lateral pinnae along rachis, lateral pinnules not unilaterally decursive along rachilla; pinnae not narrow or gradually tapering toward acuminate apex or falcate; not restricted to central African mountainous habitats . . . 1.3. var. *trifoliata*

### 1.1. var. *arborescens*

*Buprestis arborescens* Spreng. in Mag. Ges. Naturforsch. Fr. Berlin 6: 255--261 (1813). Type as above.

*Bupleurum arborescens* auct. non Jacq.: Thunb., Prod. Pl. Cap. I: 50 (1794) nom. illegit.; Willd., Spec. Plant. I. 2: 1376 (1798); Thunb. Fl. Cap. 1. II. 182 (sec Sprengel), ed. 2 (Schultes): 247 (1823). Type as above.

This is an illegitimate later homonym of *B. arborescens* Jacq., so that for purposes of priority the basionym is therefore dated from 1813 - see notes 5 & 9 on pp. 259--261, 269 in Burtt (1991).

In several of the following citations, the author of the basionym was not cited (or cited erroneously), and these have been corrected below.

*Tenoria arborescens* (Spreng.) Spreng. in Pl. Umb. den. desp. prod. p 32 (1813); Spreng. in Roem. & Schult., Syst. Veg. 6: 375 (1820); Spreng. in Syst. Veg. ed. 16, 1 (1825). Type as above.

*Franchetella arborescens* (Spreng.) Kuntze, Rev. gen. 1: 267 (1891); Kuntze, Rev. gen. pl. 3. 2: 112 (1898) [basionym incorrectly attributed to L.]; Hiern in Cat. Afr. pl. Welwitsch I. 2: 424 (1898). Type as above.

*Heteromorpha arborescens* (Spreng.) Cham. & Schlechtd. var. *integrifolia* Sonder in Fl. Cap. 2: 542 (1862), *nom. illeg.= var. arborescens*. Type as above.

*Heteromorpha arborescens* (Spreng.) Cham. & Schlectd. var. *platyphyllum* Welw. *sensu* H. Wolff in Engl., Pflanzenr. Heft 43: 35 (1910), *p.p.*, *nom. superfl.* Type as above.

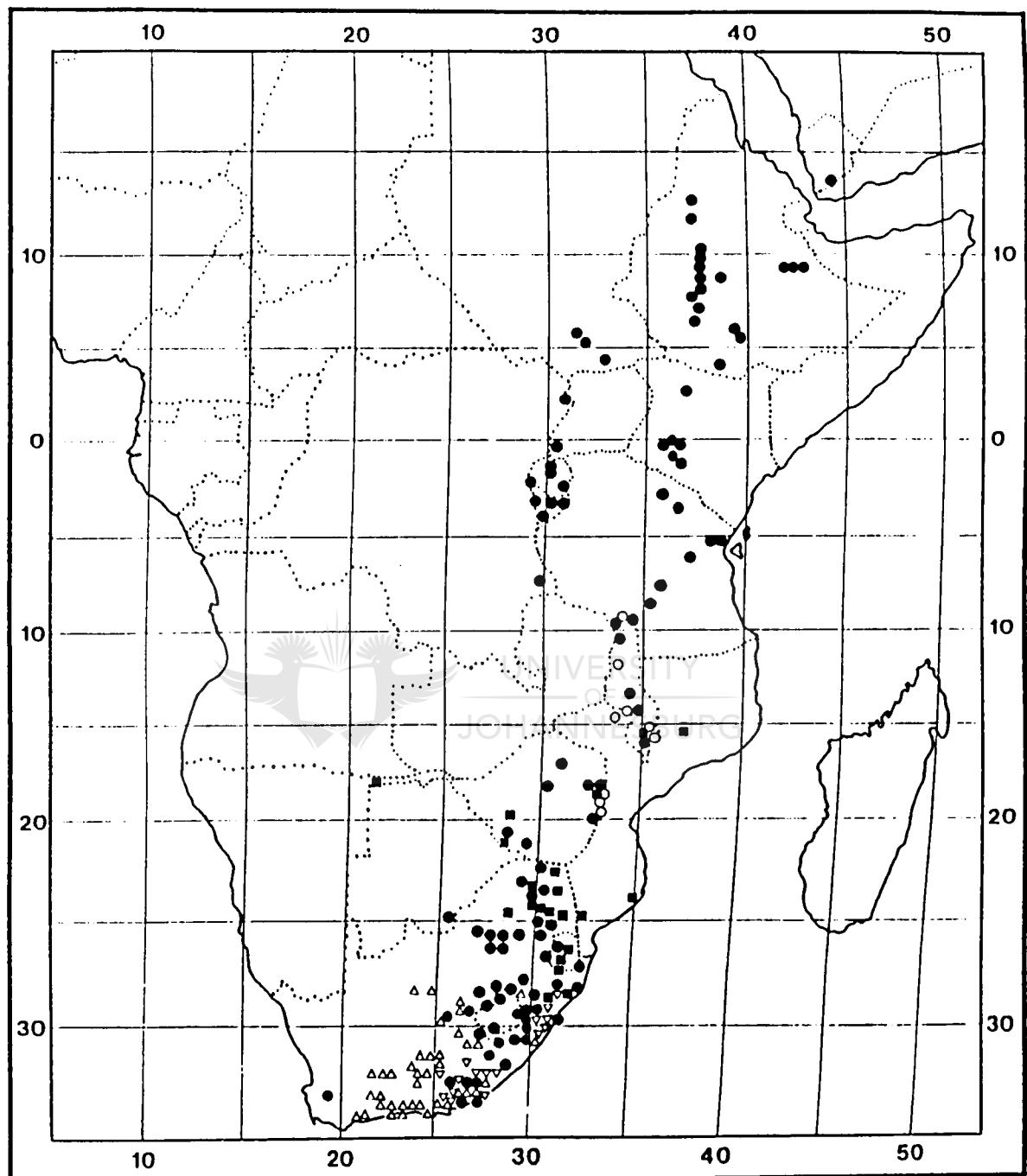
*Diagnostic characters.* Tree, or shrub, similar to *H. arborescens* var. *trifoliata*, up to 15 m high. Distinguished by simple mature

leaves (Figure 3.16) with shorter petioles with a maximum length of 6--27 mm.

*Distribution and ecology.* *H. arborescens* var. *arborescens* is found in South Africa in wooded areas of the Cape province and in drier parts of the Orange Free State (Figure 7.1).

### Specimens examined

- SOUTH AFRICA (with included territories)---2823 (Griekwastad): Daniel's Kuil (-BA), Lewis sub SAM 53935 (SAM); Klipvlei (-BA), Esterhuizen 777 (BOL).  
 ---2824 (Kimberley): Bastkop (-BD), Acocks H 1272 (PRE, 2 sheets).  
 ---2826 (Brandfort): Krugersdriftdam nature reserve, Deelkop (-CC), Muller 1771 (PRE).  
 ---2829 (Harrismith): Harrismith (-AC), Rycroft 2734 (NBG).  
 ---2925 (Jagersfontein): Farm Groenvlei (-CB), Gill 22 (BOL).  
 ---2926 (Bloemfontein): Bayswater (-AA?), Beck sub Marloth 13533 (PRE, STE); Bloemfontein Botanical Garden (-AB), Muller 16 (NBG).  
 ---3026 (Aliwal North): Tussen die riviere Nature Reserve (-AC), Roberts 5471 (PRE); Eland's Hoek (-DC), Acocks 12514 (PRE); Bolus 74 (BOL, GRA).  
 ---3027 (Lady Grey): Kraai River on Lady Grey to Jamestown road (-CC), Welman 762 (PRE).  
 ---3030 (Port Shepstone): Umtamvuna, Junction margin (-CC), Abbott 2328 (NH).  
 ---3123 (Victoria West): River near Murraysburg (-DD), Tyson 381 (NH).  
 ---3124 (Hanover): Grootfontein, Aloe valley (-AC), Verdoorn 1552 (BOL, PRE); Wildfontein (-BB), Acocks 8697 (PRE); Gryskop, Grootfontein (-BD), Archibald 3145 (GRA).  
 ---3125 (Steynsburg): Middelburg, 4 miles on Rietpoort road (-AC), Comins 728 (PRE); Groote Vis River NE of Graaff-Reinet (-CB), Brenan 14077 (NBG).  
 ---3221 (Merweville): Layton (-BB), Shearing 73 (PRE).  
 ---3222 (Beaufort West): Karoo National Park, Doornhoek (-AD), Stuart 3 (PRE); Klipbank (-AD), Pillans 16455 (BOL); Courland's Kloof (-BB), Pearson 1472 (SAM); Beaufort West (-BC), Jack 1 (NBG).  
 ---3224 (Graaff-Reinet): Valley of desolation (-AD), Wisura 3374 (NBG); Graaff-Reinet (-BC), Rattray 97 (GRA); sub BOL 87 (BOL); Bayliss 1950 (NBG); Valley of desolation (-CB), Levyns 9587 (BOL).  
 ---3225 (Somerset East): Mountain Zebra National Park (-AB), Brynard 29 (PRE).  
 ---3226 (Fort Beaufort): Farm Leeuwdrift (-CB), Dugmore 9, 22 (GRA); University of Fort Hare Farm, Honeydale section (-DD), Gibbs-Russel 3718 (BOL, GRA, NU, PRE); 10 km E of Alice, Good Hope farm (-DD), Gibbs-Russel



**Figure 7.1** The known geographical distribution of the five varieties of *Heteromorpha arborescens*: var. *arborescens* ( $\Delta$ ), var. *collina* ( $\nabla$ ), var. *trifoliata* ( $\bullet$ ), var. *montana* ( $\circ$ ), and var. *frutescens* ( $\blacksquare$ ).

3977 (GRA, PRE); Sandile's Kop (-DD), *Giffen s.n. sub FH 2280A* (PRE); Alice, Goga river bridge (-DD), *Giffen s.n.* (GRA); Alice, Tyume river, bridge to King William's Town (-DD), *Phillipson 226* (PRE).

---3227 (Stutterheim): Dohne hill (-CB), *Sim 1152, 2102* (NU); Komgha, Woods (-DB), *Flanagan 492 pro parte* [duplicate in NU is var. *collina*] (PRE); Berlin (-DC), *Compton 19816* (NBG); East London (-DD), *Thode [1888? = NH17131] pro parte* (NH, 2 out of 4 sheets).

---3321 (Ladismith): Gamkaskloof (-BC), *Geldenhuys 449* (PRE); Die Hel (-BC), *Linder 3218* (BOL).

---3322 (Oudtshoorn): Boomplaas, Cango valley, Grobbelaars river (-AC), *Moffet 52* (STE); Oudtshoorn (-CA), *Britten 32* (GRA); 1 km from turnoff to Cango Caves toward Swartberg Pass, Grobbelaars river (-CA), *B-E. v. Wyk 3313* (JRAU); Cango valley (-CB), *Compton 10651* (NBG); De Rust, Doornkraal (-DA), *Dahlstrand 2362* (PRE, STE); Kamanassieberg, Vermaaksrivier (-DA), *Vlok 2633* (JRAU); Wilderness (-DC), *Marloth 12711* (PRE [mixed], STE); Lange Vlei (-DC), *Fourcade 6377* (BOL, STE); George, Montagu Pass (-DD), *Bayliss 7325* (GRA); Knysna, Portland (-DD), *Duthie 859* (GRA); *Duthie 927* (STE); Kaimansrivier (-DD), *Schlechter 2379* (GRA); Swartvlei, Sedgefield (-DD), *Stannard sub GRA A1206* (GRA).

---3323 (Willowmore): Keurboom's River, Stinkwood Kloof junction (-CD), *Fourcade 219* (BOL, GRA); Uniondale, foot of Kamanassie mountains (-DA), *Esterhuysen 4701* (BOL).

---3324 (Steytlerville): Loerierivier, *Ecklon & Zeyher 2203* (GRA); Drinkwaterskloof (-CB), *Schönland s.n. sub GRA A7591* (GRA); Kareedouw Pass (-CD), *Esterhuysen 27187* (BOL).

---3325 (Port Elizabeth): Uitenhage, Zwartkop River (-CB), *Ecklon & Zeyher 58i* (BOL, GRA, SAM), *2203* (GRA, SAM), *sub GRA A7590* (GRA); *Tyson 381* (BOL [mounted with E & Z 58i]); *Zeyher 581* (STE); Berg River (-CC), *Dix 197* (GRA); Van Staden's River (-CC), *Drége 45041* (NBG, SAM [mounted with E & Z 2203]); Baaken's River valley (-DC), *I.L. Drége 563* (GRA).

---3326 (Grahamstown): Grahamstown (-AA), *Brink 597* (GRA); Seven Fountains (-AD), *Bayliss 8415* (GRA), *8815* (PRE); Salem (-AD), *Britten 2524* (GRA); Coldsprings (-AD), *Wells 3871* (GRA); Grahamstown, Potteries (-BC), *Noel 6966* (RUH); Grahamstown (-BC), *Noel 364* (GRA); *Ad ripas rivulorum pr. Grahamstown* (-BC), *MacOwan 193* (NH); "In silvis ad latera (montuum?) prope Grahamstown" (-BC), *MacOwan 1877* (SAM) [mixed sheet with three twigs of var. *collina*].

---3327 (Peddie): Paradise Kloof (-AA), *Compton 17832* (NBG), *17837* (BOL).

---3420 (Bredasdorp): Zuurbraak (-AB), *Thode A2331* (PRE); Langeberg, between Swellendam and Zuurbraak (-BA), *Taylor 7623* (STE).

---3421 (Riversdale): Korente River dam (-AA), *Bohnen 7590* (PRE, STE); Riversdale (-AB), *Marloth 4999* (PRE); Soetmelksrivier (-AB), *Bohnen 7823* (PRE, STE).

---3422 (Mosselbay): Wilderness, Eilandsvlei (-BA), *Jacot Guillarmod 8192* (GRA).

---3423 (Knysna): Plettenbergbay, Wittedrift (-AB), *Zeyher sub SAM 15976* (SAM); Keurboomstrand, Bridge (-AB), *Taylor 1979* (NBG).

---3424 (Humansdorp): Humansdorp (-BB), *Wagener 17123* (STE).

Precise locality unknown: Kimberley, Kraanvogelvallei, Acocks 1682 (BOL, PRE); East London, Thode 9225 (STE); East London, Rattray 296 (GRA); Schimper 37109 (NBG); Cole 637 (BOL); Burchell 2788 (GRA [mixed with var. *collina*]).

1.2. var. *collina* (Eckl. & Zeyh.) Sonder in *Flora Capensis* 2: 542 (1862). Type (Figure 7.2): Uitenhage, "Adow" [Addo] and "Olifantshoek", Ecklon & Zeyher 2205 (S, specimen on left, lecto!, here designated; GRA!, SAM!, Z!).

The specimen in Stockholm is selected as lectotype since most of Ecklon & Zeyher's material was sent there and eventually ended up in Sonder's herbarium after the records had been incorporated in the *Enumeratio*.

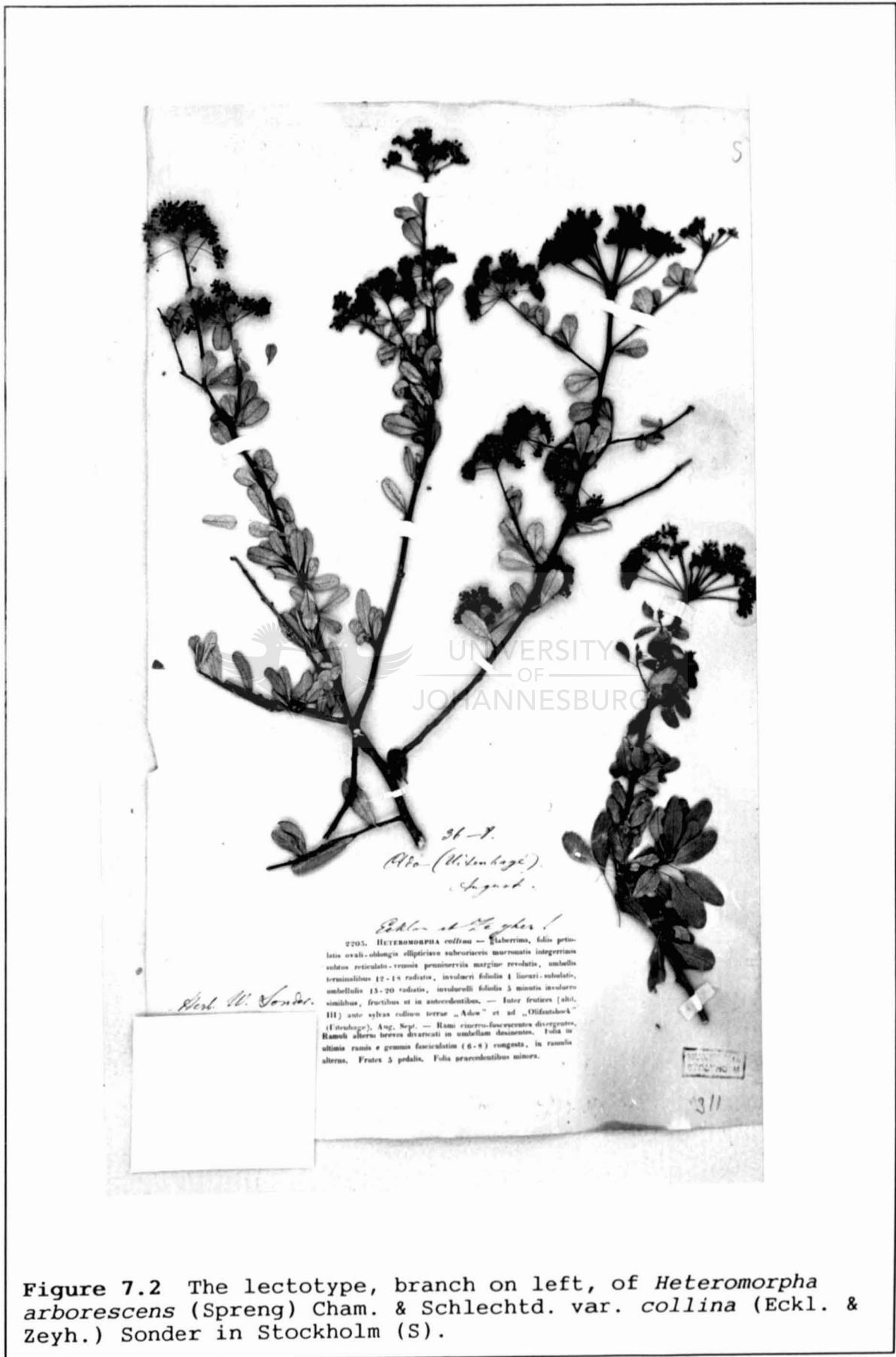


*Heteromorpha collina* Eckl. & Zeyh., *Enum.* Pl. 3: 342--343 (1837). Type as above.

*Bupleurum collinum* (Eckl. & Zeyh.) D. Dietr., *Syn. Pl.* 2: 951 (1840). Type as above.

*Franchetella arborescens* (Spreng.) Kuntze var. *collina* (Eckl. & Zeyh.) Kuntze, *Rev. gen. III.* 2: 112 (1898). Type as above.

*Heteromorpha arborescens* (Spreng.) Cham. & Schlectd. var. *collina* (Eckl. & Zeyh.) Sonder f.l. *normalis* H. Wolff in Engl., *Pflanzenr. Heft 43:* 36 (1910).



**Figure 7.2** The lectotype, branch on left, of *Heteromorpha arborescens* (Spreng) Cham. & Schlechtd. var. *collina* (Eckl. & Zeyh.) Sonder in Stockholm (S).

The lectotype is to be selected, according to Wolff's (1910) description, from his joint list of specimens under *H. a.* var. *collina*.

*Heteromorpha arborescens* (Spreng.) Cham. & Schlectd. var. *collina* (Eckl. & Zeyh.) Sonder f.2. *anomala* H. Wolff in Engl. Pflanzenr. Heft 43: 36 (1910).

The lectotype is to be selected, according to Wolff's (1910) description, from his joint list of specimens under *H. a.* var. *collina*.

*Diagnostic characters.* Shrub similar to *H. arborescens* var. *arborescens*, but differs in the smaller habit, 0,4--2(--3) m high (rarely a facultative climber); leaves mostly less than 30 mm long, obovate (Figure 3.16), margin often thickened, apex obtuse to emarginate, petiole with a maximum length of 3--9 mm and fruit typically shorter than 5 mm, up to 6 mm long, with an elliptic dorsal outline.

*Variation.* Specimens from Aliwal North, Farm Elandshoek (3026-CC), Bolus 74 (GRA), Bergsig (3126-DD), Green 717 (NH), and Kamanassi Berg (3323-CA), Compton 10545 (NBG), have leaves intermediate in character between var. *arborescens* and var. *collina*. A collection from Hel Poort (3326-AA), Burrows 2702 (GRA) has trifoliolate leaves. The climbing habit found for var. *trifoliata* along the Transkei and Natal coastline and near Barberton, Transvaal, is also present in var. *collina* in Strey 11183 (NH, NU, PRE) from Quora mouth in the Butterworth district.

*Distribution and ecology.* *H. arborescens* var. *collina* is found in the eastern Cape province, Transkei and the Natal midlands and lowlands (Figure 7.1), associated with forest fringes, in open scrub invading mixed grassland, and in grassy fynbos. From these habitat descriptions taken from herbarium labels (also: "in grass on edge of bush"; "margins of woods"), it seems that this is an "ecospecies", associated more with grassland than with forest.

### Specimens examined

- SOUTH AFRICA (with included territories)---2830 (Dundee): Entumeni [Ntunyeni (-CB) ?], *Wylie sub Medley Wood* 8746 (NH).
- 2831 (Nkandla): Eshowe, Impusheni Falls (-CD), *Lawn* 1984 (NH); Eshowe (-CD), *Lawn* 598, 774 (NH).
- 2930 (Pietermaritzburg): Albert Falls (-BD), *Comins* 532a (NU); *Demont* 59 (NU); Hela-Hela Nature Reserve (-CC), *Edwards* 811 (NU); "Tala", 5 miles on Thornville to Eston road (-DC), *Moll & Morris* 623 (NU, PRE); *Moll* 3053 (NH, NU); Sarnia Beacon Hill (-DD), *Ward* 7538 (NU, PRE).
- 3030 (Port Shepstone): Ellesmere, Umgaye [Umgai farm] (-BC), *Rudatis* 1069 (STE); Umtamvuna Nature Reserve, Smedmore Ridge (-CC), *Abbott* 1637 (NH); Umtamvuna Nature Reserve, Aerodrome (-CC), *Abbott* 2309 (NH); Umtamvuna, Gonioma Heights (-CC), *Abbott* 3451 (NH).
- 3126 (Queenstown): Lesseyton Mountain (-DD), *Galpin* 1968 (PRE); Queenstown (-DD), *Page* 16443 (BOL).
- 3225 (Somerset East): Mountain Zebra National Park, Bakenkop (-AD), *B.-E. v. Wyk* 1324 (JRAU).
- 3227 (Stutterheim): Kabaku hills (-CB), *Acocks* 9653 (PRE); Dohne hill (-CB), *Sim* 2101 (NU [mixed with var. *trifoliata*])); Komgha, Woods (-DB), *Flanagan* 492 (NU); Prospect farm (-DB), *Flanagan* 493 (SAM).
- 3228 (Butterworth): Kentani (-AD), *Pegler* 10 (BOL, GRA); Quora Mouth (-BC), *Strey* 11183 (NH, NU, PRE).
- 3325 (Port Elizabeth): Zuurberg National Park, Lot 16 (-BC), *B.-E. & M. v. Wyk* 24, 2204 (JRAU); Zuurberg (-BC), *Holland* 77, 80 (GRA); "Ado (Uitenhage)" [Addo] (-DA), *Ecklon & Zeyher* 2205 (S, SAM); *Zeyher* 2205 (PRE).
- 3326 (Grahamstown): Riebeeck Oos, Hel Poort (-AA), *Burrows* 2702A (GRA); "In silvis ad latera (montuum ?) prope Grahamstown" (-BC), *MacOwan* 1877 (SAM); Alexandria, Kolsrand (-CA), *Archibald* 4501 (GRA); Port Elizabeth road, "Slagboom" (-CD), *Britten* 5806 (GRA).

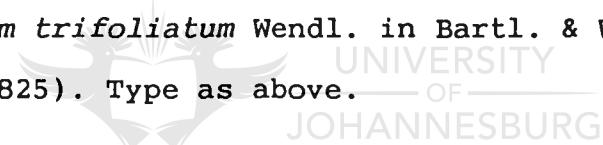
---3327 (Peddie): East London (-DD), Thode [1888? = NH17131] pro parte (NH), 2 out of 4 sheets.

Precise locality unknown: Burchell 2788 (GRA) [mixed with var. *arborescens*]; Victoria College Herbarium s.n. (STE); "Intaba Magwele altus, d'tam", Galpin 1968 (GRA).

1.3. var. *trifoliata* (Wendl.) Sonder in Flora Capensis 2: 542 (1862), Type (Figure 7.3): South Africa, "Caput bonae spei", Hesse s.n. (GOET, holo., photo!).

The specimen in GOET is specifically selected by Wendland by the inscription "*Bupleurum trifoliatum mihi*" on the herbarium sheet.

*Bupleurum trifoliatum* Wendl. in Bartl. & Wendl., Beitr. Bot. 2: 13 (1825). Type as above.



*Heteromorpha trifoliata* (Wendl.) Eckl. & Zeyh., Enum. Pl. Afr. Aust. 3: 342 (1837); Burtt Davy, Man. Fl. Pl. & Ferns Transvaal II: 519--520 (1932); Cufodontis, in Bull. Jard. Bot. Bruxelles 29. 3: 641 (1959); Jac.-Fel. in Fl. Cameroun 10: 74 (1970); Compton, Fl. Swaziland: 407 (1976); Cannon in Fl. Zambesiaca: 578 (1978); Cannon & Sampaio Martins in Fl. Mocambique: 26--27 (1981); C.C. Townsend in Kew Bull. 40: 843--850 (1985); C.C. Townsend in Fl. Trop. E. Afr. (1989); B.L. Burtt in Edinb. J. Bot. 48: 213 (1991). Type as above.

*Franchetella arborescens* (Spreng.) Kuntze var. *acuminata* Kuntze, Rev. Gen. III. 2: 112 (1898). Types: E. Cape, Cathcart, 25 February 1894, Kuntze s.n. (NY, specimen on the left,

HERBARIUM GOTTINGEN

Aus dem Herbar der ehem. Königl. Gärten  
zu Herrenhausen b. Hannover  
Geschenkt durch Prinz Ernst August  
von Hannover im Dezember 1969



Bryonia trifoliata  
var. trifoliata

Bryonia trifoliata  
var. trifoliata

**Figure 7.3** The holotype of *Heteromorpha arborescens* (Spreng) Cham. & Schlechtd. var. *trifoliata* (Wendl.) Sonder in Göttingen (GOET).

lecto.!, here designated); Natal, Van Reenen's Pass, 17--1900 m., 19 March 1894, *Kuntze s.n.* (NY!), *Kuntze s.n.* sub Z 21793 (Z!); Krantzkloof, 12 January 1894, *Kuntze s.n.* (NY!).

Since the Cathcart specimen is the one which clearly shows the acuminate leaves and is part of Kuntze's personal herbarium which was acquired by NY (Stafleu & Cowan 1979), it is selected as lectotype.

*Franchetella arborescens* (Spreng.) Kuntze var. *normalis* Kuntze, Rev. Gen. III. 2: 112 (1898). Type: E. Cape, Cathcart, 25 February 1894, *Kuntze s.n.* (NY, lecto.!, here designated).

There is only one specimen under this varietal name in Kuntze's personal collection.



*Franchetella arborescens* (Spreng.) Kuntze var. *sylvatica* Kuntze, Rev. Gen. III. 2: 112 (1898). Type: E. Cape, Perie forest, 2 March 1894, *Kuntze s.n.* (NY, larger, central specimen, lecto.!, here designated).

There is only one specimen under this varietal name in Kuntze's personal collection.

*Annesorhiza abyssinica* A. Braun in Flora (Bot. Zeit.) 24.1: 337 (1841) nom. nud. [as *Anesorhiza abyssinica*]; A. Rich. in Tent. fl. abyss. 1: 326 (1848).

*Heteromorpha abyssinica* Hochst., in Intell. bl. (zur Flora) 2: 28. (1841) nom. nud. [Catalogue listing as "*Heteromorpha abyssinica* Hochst., Sine Nro."]

*Heteromorpha abyssinica* Hochst. ex A. Rich., Tent. fl. abyss. 1: 325 (1848). Type: Ethiopia, "Crescit in monte Selleuda [Mt. Scholoda], et inter Maye-Gouagoua et Debra-Sina, in provincia Tigré (Quartin Dillon et Schimper)", *Schimper* 1816 (not found); Ethiopia, "In monte Scholoda...1844", *Schimper* s.n. (Z, specimen on the left, lecto!, here designated, Figure 7.4; BM; K, Herb. Benth.; K, Herb. Hook.; P, 3x).

Since no vegetative (trifoliolate) leaves are present on the Paris specimen, I prefer to select the isotype in Zürich Herbarium as lectotype, to avoid confusion with var. *simplicifolia*.

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*Franchetella arborescens* (Spreng.) Kuntze var. *abyssinica* (A. Rich.) Kuntze [as var. *abyssinica* (Hochst.) Kuntze], Rev. Gen. Pl. III. 2: 112 (1898). Type as above.

*Heteromorpha arborescens* (Spreng.) Cham. & Schlectd. var. *abyssinica* (A. Rich.) H. Wolff [as var. *abyssinica* (Hochst.) Kuntze], Engl., Pflanzenr. Heft 43: 35--36 (1910), *pro parte*. Type as above.

Wolff included various taxa in his broad concept of *H. arborescens* var. *abyssinica*. These include *H. stenophylla*, *H. involucrata* and probably *H. papillosa*.



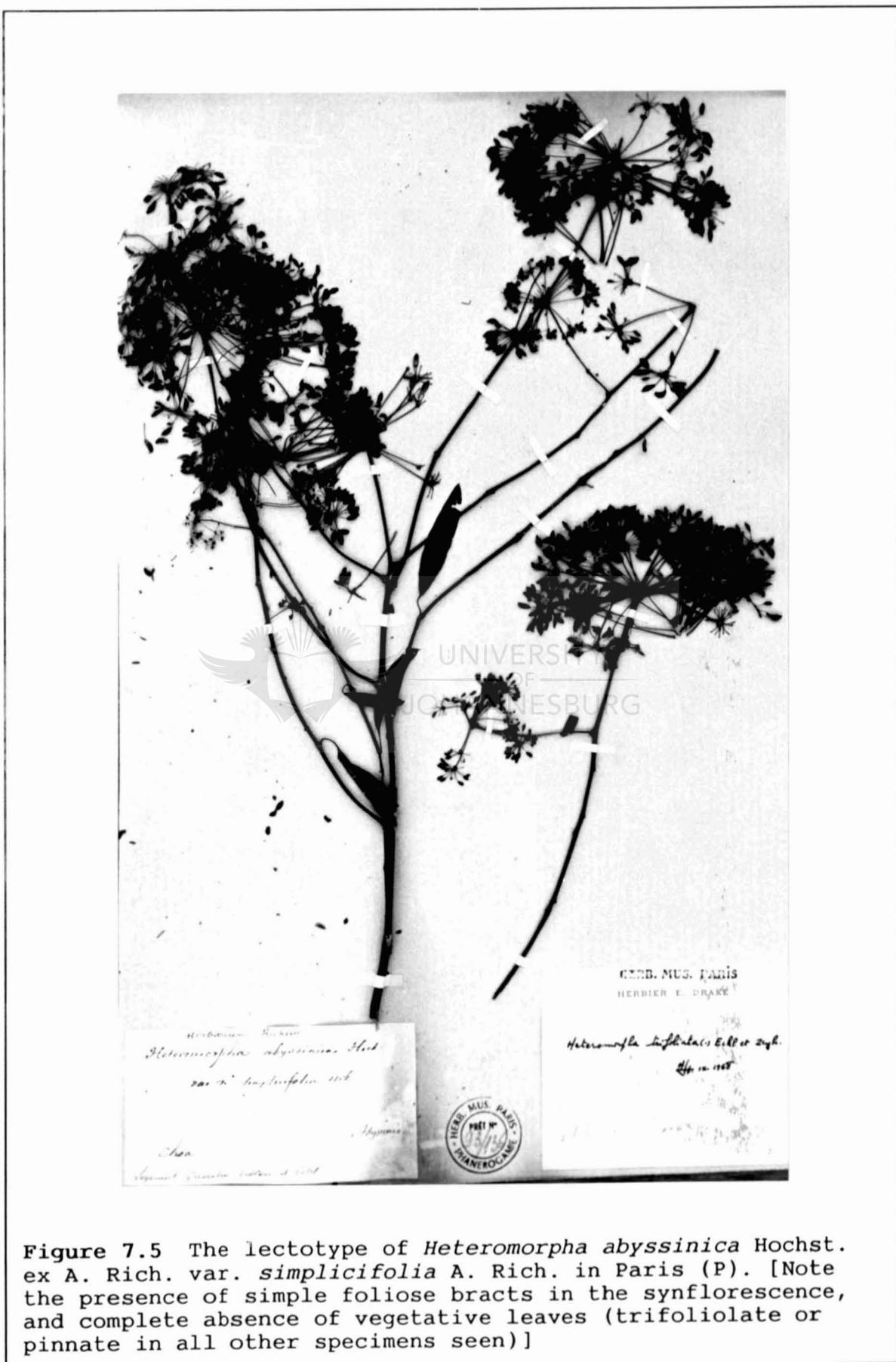
**Figure 7.4** The lectotype, branch on left, of *Heteromorpha abyssinica* Hochst. ex A. Rich. in Zürich herbarium (Z).

*Heteromorpha abyssinica* Hochst. ex A. Rich. var.  
*simplicifolia* A. Rich. in Tent. fl. abyss. 1: 325 (1848). Type  
 (Figure 7.5): Ethiopia, "in provincia Choa [Shoa]", Ant. Petit  
 (P, lecto.!, here designated; K, photo!; Z!).

The specimen in Paris is labelled: Legerunt Quartin Dillon et  
 Petit. It was chosen as lectotype because it was annotated by A.  
 Richard himself and bears the type locality "choa". The same  
 specimen was referred to as the holotype by Townsend (1989).  
 Since all material seen from Ethiopia has trifoliolate  
 vegetative leaves and unifoliolate bracts on the branches of the  
 synflorescence, there is no doubt that the description was based  
 on a specimen without vegetative leaves. Richard must have been  
 unaware of the difference between vegetative leaves and those  
 leaf-like bracts, hence his misinterpretation.

[*Heteromorpha multifoliata* C.E. Moss, ined.; Watt & Breyer-  
 Brandwijk, Med. & Poisonous Pl. S & E Africa ed. 2, 1039 (1962)  
 nom. nud. Based on: Transvaal, Roodepoort, Witpoortjie Kloof,  
 Moss 4492 (J).]

*Diagnostic characters.* Tree or shrub similar to var. *arborescens*  
 (rarely a facultative climber). Mature leaves trifoliolate to  
 pinnately or pedately compound (Figure 3.16), incision rarely  
 decursive. Petioles with a maximum length of 24--70(--80) mm.  
 Terminal pinna in compound leaf usually distinctly petiolulate  
 with rounded or obtuse base (Figure 3.16). Adaxial midrib of  
 pinnae and sometimes margins typically pilose.



The leaf outline is extremely variable in this variety, even at the level of the individual, so that some leaves may have five segments and some up to 13 segments on the same stem.

*Distribution and ecology.* *H. arborescens* var. *trifoliata* is the most common taxon in the genus and has the widest distribution range (Figure 7.1). It is found from the western (rare) and eastern Cape province (where forms intermediate with both var. *arborescens* and var. *collina* occur), all the way up through tropical east Africa to Ethiopia and the Arabian Peninsula. It occurs in open or closed woodland, mostly on lower slopes (Witwatersrand Botanical Gardens, Roodepoort; Melville) or along watercourses (Florida Hills; Pilgrims' Rest; Melville), occasionally on rocky ridges, but then in sheltered positions (Windsor East; Quellerina/Northcliff boundary). In Natal, this is the only variety in the highlands. Both here and in the eastern Cape kloof forests, it attains great dimensions, with unconfirmed reports of up to 20 m high.

This taxon has been reported from Angola by Norman (1929) and Cannon (1970), and in Cameroun by Jacques-Félix (1970). All specimens I have seen from these regions can however be accommodated in either *H. stenophylla* or *H. occidentalis*, so that the occurrence of *H. arborescens* in this region is doubtful. Schreiber records specimens of *H. papillosa* and *H. stenophylla* from Namibia as *H. trifoliata*, and refers to a form with hairy rays from the Okavango-Caprivi region which is better matched with *H. arborescens* var. *frutescens*. A re-evaluation of

specimens named *H. trifoliata* not cited in this treatment, especially from Angola, is called for to confirm the apparent absence (Figure 7.1) of this taxon from West Africa.

*Forms* with a climbing or scandent habit (which has also been observed in var. *collina* from Quora mouth in the Butterworth district) have been recorded at several localities from Ciskei to the Barberton district of Transvaal, particularly in southern Natal. These are:

- 2531 (Komatipoort): Barberton, Target valley (-CC), Clarke 54 (PRE).
- 2831 (Nkandla): Umhlatuzi valley, Nogeya [Ngoye ?] (-DD), Venter 3693 (PRE).
- 3029 (Kokstad): Umtamvuna valley, Pondo memorial road (-DD), Abbott 4914 (NH).
- 3030 (Port Shepstone): Amanzimtoti (-BB), Ward 6187 (NH, NU, PRE); Uvongo, Voigts farm (-CD), Strey 9601 (NH).
- 3130 (Port Edward): Umtamvuna N.R., Dog's leg, River (-AA), Abbott 3964 (NH).
- 3227 (Stutterheim): Prospect farm (-DB), Flanagan 559 (SAM).
- 3228 (Butterworth): Willowvale, Ngqaqini admin. district (-AD), Van Eeden B450 (PRE).

One collection from Oribi Gorge Nature Reserve (3030-CB), Nicholson 1922 (PRE), has all the leaves simple as in var. *arborescens*. These are probably bracts, however, since no definite vegetative leaves are present, so that it cannot be classified as such.

A few specimens from Tanzania (*Stolz 1246, Stolz 1940, Stolz 24699*) are atypical and deserve closer examination (*in situ*) for phenotypic plasticity. The plant has very slender stems, and long-petiolate, parchment-like pinnate leaves with a pilose abaxial midrib. Rays are also exceptionally thin.

### Specimens examined

- YEMEN ARAB REPUBLIC---1344:** Ibb to Udayn pass (-AA), *Hepper & Wood* 5970 (K); 3 miles W of Ibb (-AA), *Spellenberg* 7305 (K).
- ETHIOPIA---1237:** Bacino del Lago Tana, Pendici orient. di M.Guranghe (Nord di Gondar) (-AD), *Pichi-Sermoli* 700 (MO).
- 1137: Godjam, 17 km from Bahar-Dar to Blue Nile Falls (-AD), *J. de Wilde* 5791 (MO).
- 1037: Gojjam, Choké mountains, Ejubi, S of Debra Marcos (-DB), *Hillier* 954 (K).
- 0937: Wallega, Fincha airport (-BD), *M.G. & S.B. Gilbert* 1984 (K); 6 km NW of Ambo, Hagere Hiwot, Tributary of Güder river (-DD), *W. de Wilde c.s.* 10475 (MO).
- 0941: 1 km NW of crossing of Harrar to Dire Dawa road with Addis Ababa via Kalube & Asbe Tafari road (-DB), *J. de Wilde* 4086 (MO).
- 0942: 5 km N of Harar (-CC), *W. de Wilde c.s.* 9853 (MO), 9855 (PRE); road SW of Whates to Gara Mullata (-DB), *Burger* 2404 (K); 8--11 km ENE of Jijiga (-DA), *Le Houérou* 08-10 (MO); 90 km from Harar to Jijiga (-DA), *J. de Wilde* 5117 (MO).
- 0837: Shoa, 12 km W of Ambo (-BB), *Meyer* 7688 (MO); Ghion, 114 km SW of Addis Ababa on Jimma road (-DA), *Ash* 671 (K, MO).
- 0838: 80 km S of Addis Ababa on Gogeti road (-BD), *Ash* 632 (MO).
- 0737: c. 245 km from Addis Abeba on Jimma road (-AA), *Jaddesse Ebbe* 577 (K); Sidamo, Omo river valley c. 53 km W of Soddo (-DC), *J. de Wilde* 5624 (MO).
- 0637: Gamo Gofa region: Gamo Awraja 11--12 km on Chencha to Arba Minch road (-CB), *Tadesse* 6961 (MO).
- 0539: Sidamo, 68 km NW of Neghelli, Kebre Mengist road (-AB), *De Wilde* 6041 (MO); Sidamo, 2 km SE of Neghelle (-DA), *Friis, Gilbert, Rasmussen & Vollesen s.n.* (K); Sidamo, Neghelli, 4900 ft (-DA), *Mooney* 7356 (K).
- 0438: Mega, Mountain up to 2000 m (-DC), *Gillet* 14223 (K).
- SUDAN---0531:** Equatoria province, Luka hill near Juba (-DC), *Andrews* 1048 (K); Imatong mountains near Agoro (-AA), *Eggeling* 823 (K).  
[Grid reference not found: Equatoria province, Lomaru, Imatong mountains 6300 ft (c. 0432DD), *A.S.Th.* 1769 (K)]
- ZAIRE---02N30:** E province, Mahagi, Mont Llelo (-DD), *Froment* 638 (MO).
- 07S29: Katanga province, Pepa to Badouinville road, Mont Lusala (-BD), *Devred* 3712 (MO).
- UGANDA---00S30:** Ankole, Rugongo (-AD), *Rwaburindore* 153 (MO); Ankole, Nyabirerema (-AD), *Rwaburindore* 1611 (MO).
- KENYA---02N36:** Mount Kulal (-BD), *Otelle* 126 (MO).
- 00S35: Nakuru, Londioni (-BC), *Perdue & Kibuwa* 9071 (PRE); Eastern Mau Forest Reserve, Naishi river area (-BD), *Maas Geesteranus* 6198 (MO).
- 00S36: Nakuru, Menengai forest (-AA), *Mwanangangi* 188 (MO); Mount Aberdare (-BC), *R & T Fries* 437 (MO); Narok, Nasampolai valley (-CC), *Greenway &*

*Kanuri* 14567 (MO); *Naivasha*, Mount Longonot (-CD), *Polhill* 50 (MO); *Naivasha*, *Sussex farm*, *Kinangop* (-DA), *Taylor* 1529 (MO).

---01S36: *Kiambu*, *Mugaga relict forest* (-BA), *Robertson* 1554 (MO); *Ngong escarpment*, road to *Magadi* (-BC), *Lavrano*s 12434 (MO); *Nairobi*, *Langata forest edge* (-BD), *Bogdan* 307 (MO); *Nairobi*, *Thompson's estate* (-BD), *Napier* 2652 (MO); *Nairobi*, *Ngong road* (-BD), *Perdue & Kibuwa* 8137 (MO).

**RWANDA**---0130: *Biumba territory*, *region de Mutara*, *plaine Gikandura* (-AC), *Troupin* 6056 (MO); *Biumba territory*, *region de Mutara*, *environ de Mimuli*, *réserve IRSAC colline Bibare* (-CA), *Troupin II.684* (MO).

---0229: *Lake Kivu*, 72 km on *Kibuye road* from *Nyamasheke* (-AB), *Bouxin* 1551 (K).

---0230: *Rusumo* (préf. *Kibungo*), *vallée de l'Akagera* (-BD), *Raynal* 20682 (K).

**BURUNDI**---0329: *Bubanza*, *Musigati* (-AB), *Reekmans* 476 (MO); *Muramvya*, *Lieu Bukeye*, *Mont Teza* (-BA), *Lewalle* 6030 (K, MO); *Bujumbura*, 8 km on *Bugarama road* (-AD), *Reekmans* 5172 (MO); *Buturi*, *Butare (Mosso)* (-DD), *Reekmans* 10.274 (K, MO).

---0330: *Ruyigi*, *Musongati* (-AD), *Reekmans* 3382 (MO); *Ruyigi*, *Gitwenge*, *colline Nyabitangu* (-BA), *Reekmans* 9049 (MO); *Ruyigi*, 4 km on *Gitwenge* to *Cendajuru* (-BA), *Reekmans* 7609 (MO); *Rusengo - Mosso - Urundi* (-BC), *Michel* 4431 (MO).

[Grid reference not found: *Congo Belge*, *Kininya - Mosso - Urundi*, *Michel* 2390 (MO)]

---0429: *Bururi*, *Butare*, 10 km on *Dunga road* (-BB), *Reekmans* 6306 (MO).

---0430: *Bururi*, *Bukemba (Mosso)* (-AA), *Reekmans* 9793 (MO).

**TANZANIA**---0235: *Arusha*, *Ngorongoro Conservation area*, *Empakaai crater* (-DD), *Frame* 901 (MO).

---0336: *Arusha*, *Suye hill*, c. 2 km E of city center (-BC), *Gereau & Mziray* 1683 (MO).

---0538: *Lushoto*, *Kitiwu* (-AB), *Peter* 56360 (MO); *Tanga district*, *Ngua Forest* (-BA), *Semsei* 4122 (PRE); *Muheza*, E *Usambara mountains*, *Mlinga peak* (-BB), *Borhidi*, *Iversen*, *Ruffro & Steiner* 86479 (MO).

---0637: *Morogoro*, *Nguru mountains*, *Mimanga mountain* near *Maskati mission* (-AB), *Thulin & Mhoro* 3159 (MO).

---0735: *Iringa*, cultivated area (-DC), *Muumba DSM3030* (MO); *Iringa* E of *College of National Education* (-DC), *Pederson* 1049 (MO).

---0835: *Iringa*, *Mufindi*, *Ngwazi village* (-CA), *Lovett & Lovett* 703 (MO); *Mufindi*, *Echidina* (-CB), *Paget-Wilkes M24(394)* (MO); *Iringa*, *Mufindi*, *Lake Nkwazi* (-CB), *Shabani* 1024 (MO).

---0933: *Nyassa Hochland*, *Station Kyimbila*, 1800 m (-BB), *Stolz* 2086 (BM); *Nyassa Hochland*, *Station Kyimbila*, 1200 m, *Stolz* 1246 (MO, SAM, Z), 1940 (Z); *Nyassa*, 1200 m, *Stolz* 24699 [cf. *Stolz* 1246] (PRE).

---0934: *Iringa*, *Livingstone mountains*, *Ligala mountain*, near *Madunda* (-CD), *Gereau & Kayombo* 4067 (MO).

[Grid reference not found: *Tanganyika*, *Southern Highlands between St. Michael's & St. George's*, *Mathias & Taylor sub LA*: A157 (MO)]

**MALAWI**---0933: N province, Chitipa district, Misuku hills, Mughesse (-CB), Pawek 7034 (MO).

---1033: N province, Nyika Plateau, Chowo, Forest edge, 7400 ft, Phillips 1720 (MO).

---1434: Dedza, Ciwau & Nchenchere hills (-AD), Chapman 1148 (MO).

---1535: Zomba district, Ulumba Hill, Kagaso village, T.A. Chikowi (-BC), Kwatha & Nachamba 146 (BOL); Zomba, Chingwe's hole, Zomba Plateau (-BC), Salubeni 3166 (MO); Blantyre, Michura mountain (-CC), Morgan 0002 (RUH); Blantyre, N'dirandi mountains (-CC), Benson 534 (GRA); Mlanje mountain, Lichenya plateau (-CD), J & E Chapman 7223 (MO); Mount Mulanje, Madzeka, Sombani path (-DC), J & E Chapman 8368 (MO).

**MOZAMBIQUE**---1834: Gogogo mountains, Gorongoza S sector (-AC), Schelpe 469 (BOL).

**ZIMBABWE**---1830 (Hartley [Chegutu]): Hartley [Chegutu] district, Poole farm, Hornby 3275 (MO).

---1832 (Umtali [Mutare]): Makoni, c. 20 km a Rusapi [Rusape] ad viam versus Inyanga (-AD), Fries, Nordlindh & Weimarck 3422 (BOL, MO, NBG); Inyanga, in walls of old fort (-BA) Fischer 1447 (NU); 7 km from Inyanga (-BB), Bamps, Symons, Van den Berghen 293 (MO); Umtali [Mutare] commonage (-DC), Chase s.n. (NU); Mutare, 3500 ft, Christmas Pass (-DC), Davies 2704 (MO).

---1932 (Melsetter [Chimanimani]): Umtali [Mutare] heights (-BB), Meara 80 (MO); Melsetter [Chimanimani], Foot of mountain (-BD), Rutherford-Smith 175 (MO); Melsetter [Chimanimani], 5000 ft, Mwenje farm (-DC?), Chase 4846 (MO).

---2028 (Bulawayo): Matopo Hills, Outspan for the World's view (-CB), Rogers 5166 (GRA).

---2128 (Bobonong): Simukwe River, c. 8 km downstream from mount Jim (AC?), Ngoni 369 (MO).

---2129 (West Nicholson): Gwanda, Doddiburn Ranch, Msilikwe river near confluence with Umzingwane river (-AD), Pope 654 (PRE).

**BOTSWANA**---2425 (Gaborone): 6 km W of Kanye (-CD), Hansen 3407 (PRE).

**SWAZILAND**---2631 (Mbabane): Black Mbuluzi valley, Boulder forest (-AA), Compton 25923 (NBG); Duiker Bush (-AA), Compton 25526 (NBG), 25604 (NH); Palwane valley c. 4000 ft (-AC), Compton 25877 (NBG, BOL, NH); Gobolo, 3500 ft (-AC), Dhlamini s.n. (NBG, NH 48125); Manzini, Tulwane (-AD), Compton 29015 (NBG).

**LESOTHO**---2828 (Bethlehem): Leribe (-CC), Dieterlen 4 (STE); *ibid.*, 5-600 ft, Dieterlen 661 (PRE [mixed with *Polemannia simplicior* Hilliard & Burtt]).

---2927 (Maseru): Sabalabala near Mamathes (-BB), Lawson 912 (NH); Berea dist., Colony (-BC), Jacot Guillarmod 1443 (RUH).

**SOUTH AFRICA** (with included territories)---2230 (Messina): Zoutpansberg (-AC), Rogers 20857 (PRE).

---2329 (Pietersburg): Blaauberg Kloof (-AA), Strey & Schlieben 8589 (PRE); 49 km on Pietersburg to Tzaneen road (-DD), Winter 53 (JRAU).

---2330 (Tzaneen): Giyani, Middle Letaba Dam (-AD), Venter 12935 (NU); Duiwelskloof, Westfalia Estate (-CA), Bos 1329 (PRE); Woodbush (-CC), Wager 23018 (NU); Tzaneen, 12.6 km up Magoebaskloof pass (-CC), Winter 56 (JRAU).

- 2428 (Nylstroom): Naboomspruit, Waterberg, Mosdene (-DA), *Galpin 14849* (PRE, BOL).
- 2429 (Zebediela): Percy Fyfe Nature Reserve (-AA), *Huntley 1979* (PRE).
- 2430 (Pilgrim's Rest): Mariepskop, Bedford trail (-DB), *Van der Schijff 4965* (PRE); 1.2 km E of Pilgrim's Rest (-DD), *Winter 64* (JRAU); Graskop, Base of Kowyn's Pass (-DD), *Galpin s.n.* (BOL).
- 2527 (Rustenburg): Pilanesberg (-AC), *Selaledi & Sekhaolelo 87* (PRE); Rustenburg, 4500 ft (-CA), *Nation 54*; F. McGregor's farm "Rainhill", 4500 ft (-CA?), *Codd 1069* (PRE); Uitkomst 499 JQ, W of Skeerpoortrivier (-DD), *Coetzee 446* (PRE).
- 2528 (Pretoria): Pretoria, Kopjes (-CA), *Leenderts 23* (GRA); Ashbury dolomites (-CA), *Mogg 12313* (PRE); Groenkloof (-CA), *Pole-evans 328* (PRE); Irene (-CC), *sub PRE 14654* (PRE); Irene, Doornkloof (-CC), *Smuts s.n.* (STE); Faerie Glen (CD) *SAAB 3/44* (PRE).
- 2529 (Witbank): Middelburg, Farm Welverdiend (W. Meyer) (-CD), *Hilliard & Burtt 14421* (NU).
- 2530 (Lydenburg): Sterkspruit (-AB), *Galpin s.n.* (BOL); Lydenburg, 4 miles up kloof toward Sabie (-BA), *Smuts & Gillet 2500* (STE); Sabie valley (-BB), *Galpin 1391* (PRE, BOL); Waterval Onder, 4100 ft (-CB), *Rogers 314* (GRA); Kaapsche hoop, 5 miles SW of Hotel (-DB), *Nel 220* (PRE, NBG).
- 2531 (Komatipoort): Krokodilpoort, 28 km from Nelspruit toward Kaap Muiden, N slope (-CB), *Van Jaarsveld 1131* (NBG, PRE); Kangwane, Somgimvelo Game Reserve, Diepgeset farm (-CC), *Germishuysen 5746* (PRE); Barberton (-CC), *Thornicroft s.n.* (NBG); *ibid.*, *Thornicroft 7* (GRA).
- 2627 (Potchefstroom): Krugersdorp (-BB), *Jenkins 9257* (PRE); Witpoortjie falls, Roodekrantz 83 [Witwatersrand Botanic Garden] (-BB), *Mogg 21367* (BOL); Roodepoort, Tvl. [Witwatersrand] Botanic Garden (-BB), (NBG); Farm Gladysdale (-BB), *Rodin 3887* (PRE); Johannesburg, Western Melville ridge (-BB), *Winter 71* (JRAU).
- 2628 (Johannesburg): Heidelberg Kloof, 5500 -- 5800 ft (-AD), *Mogg 20427* (BOL).
- 2630 (Carolina): Lothair, Farm Busby IT222, Umpuluzi river, weir (-DC), *Winter 83* (JRAU).
- 2729 (Volksrust): N Drakensberg, Ncandu State Forest (-DC), *Nicholas & Button 1954* (MO, NH).
- 2731 (Louwsburg): Ngotshe, Itala Nature Reserve (-AB), *Hilliard & Burtt 10065* (NU); Road to main entrance of Itala Nature Reserve (-CB), *Jordaan 2090* (NH); Ngome Forest Station, Ntendeka Wilderness Area (-CD), *Jordaan 535* (NH).
- 2732 (Ubombo): Lebombo mountains, Ingwavuma region (-AA), *Strey 4695* (NH); Ingwavuma hill (-AA), *Strey 8174* (NH, NU); Gwalaweni forest (-AC), *Moll 4487* (NH).
- 2827 (Senekal): Winburg, Willem Pretorius Game Reserve, below rest camp (-AC), *Leistner 2967* (PRE); c. 15 km E of Marquard, Farm De Hoek (-DA), *Munro sub PRE 48117* (PRE); Waterkloof trail near Holkranz (-DD), *Schutte 795, 796, 797* (JRAU).

- 2828 (Bethlehem): Bethlehem, cliff face near village (-AB), *Phillips* 3183 (GRA, PRE); Farm Welgevonden 246, NE of Leeuwkop summit (-AB), *Scheepers* 1757 (PRE); Bethlehem, Woodfort Koppie (-AB?), *Gillet* 1136 (BOL, NH); Clarens municipal area, Kloof (-CB), *Ferreira* 226 (PRE); Golden Gate Nature Reserve (-DD), *Compton* 22466 (NBG); Royal Natal National Park, Forest (-DD), *Moll* 5427 (NH).
- 2829 (Harrismith): Harrismith commonage (-AC), *Rycroft* 2734 (NBG), *Thompson* 2734 (STE); Van Reenen, Kloof (-AD), *Franks* in NH 14209 (NH); Van Reenen, Bush (-AD), *Bews* 2092, 2098 (NU); Mount Aux Sources district, Tugela valley (-BB?), *Bayer & McLean* 31 (GRA, NU); Cathedral Peak catchment 10 (-CC), *Scott* 105 (NH); Cathkin Peak, Ndema Forest (-CD), *Galpin s.n.* (BOL); Cathedral Peak area, Umhlanibonja river (-CD), *Schelpe* 258 (NU); Mielietuin station, Hillside (-DD), *Strey* 9495 (NH, NU); 5 km NE of Estcourt, Rensburg spruit near Rensburg koppie (-DD), *Jordaan* 1136 (NH).
- 2830 (Dundee): Msinga, Pomeroy (-CB), *Ram s.n.* (NU).
- 2831 (Nkandla): Vryheid, Nhlazatshe mountain (-AA), *Gandar* 004 (NU); Port Durnford (-DD), *Gerstner* 2963 (NU).
- 2832 (Mtubatuba); Hlabisa, Hluhluwe state dam (-AA), *Ward* 5612 (NH, NU).
- 2925 (Jagersfontein): Fauresmith Botanical Reserve (-CB), *Smith* 5214 (PRE).
- 2926 (Bloemfontein): OFS Botanical Garden (-AA), *Müller* 16 (NBG).
- 2929 (Underberg): Drakensberg, near Old Caves (-AB), *Evans* 167 (NH); Mpendhle, Upper Loteni valley, vicinity of Ash Cave (-AD), *Hilliard & Burtt* 18173 (NU); Giant's Castle Game Reserve, Farm Arbourfield, Injasuti Outpost (-AD), *Willcox s.n.* (NU); Estcourt Research Station, Kloof below lab (-BA), *West* 532 (NH); Kamberg, Gam Pass farm, N of Mooi River (-BC), *Williams* 777 (NH); 17 km E of Mooi River on Hlatikulu road, Farm Lanner Veane (-BC), *Balkwill & Manning* 499 (NU); Kamberg (-BC), *Wright* 1733 (NU); Nottingham road (-BD), *McClean* 908 (NH); Cobham forest station, Ndlovini, (Troutbeek?) (-CB), *Hilliard & Burtt* 13300 (NU); Bamboo mountain (-CB), *McClean* 714 (NH); Polela, Sunset, Krantz above Pevlos kraal (-CB/DC?), *Rennie* 827 (NU); Polela, E of Hlabeni on Creighton to Bulwer road (-D?).
- 2930 (Pietermaritzburg): Estcourt, Giant's Castle Game Reserve (-AA), *Morris* 423 (NU); Lidgetton waterfall, Nottingham Road to Howick road (-AC), *Schrire* 2247 (NH); Lions River, Ehlatini farm, Karkloof (-AC), *Moll* 3496 (NH, NU); Karkloof, Mistbelt forest (-AC), *Moll* 1674 (NH); Table Mountain (-BA), *Killick* 346 (NU); Umvoti, Seven Oaks, "Ezinyosini" (-BA), *Guy* 53 (NU); New Hanover (-BC), *Wells* 1895 (NU); Karkloof forest, "Benvie", roadside (-BD), *Wirminghaus* 1156 (NU); Lions River, Mount Ashley (-CA), *Moll* 1303 (NU); Cedara state forest, Forestry dam (-CB), *Mac Devette* 623 (NH); Town Hill (-CB), *Moll* 55 (NU); Keerom (-CC), *Strey* 10843 (NH); Krantzkloof (-DD), *Haygarth* 126 (NH, STE); Marianhill (-DD), *Gerstner* 39 (NU); Field's Hill (-DD), *Wood* 2503 (NH).
- 2931 (Stanger): Red Hill (-CC?), *Watt & Brandwijk* 1253 (PRE).
- 3028 (Matatiele): Maclear, Mondi Purchase area (-CC), *Palmer* 3034 (GRA); Maclear, Woodcliffs farm, Kloof (-CC), *Bester* 7 (PRU).

- 3029 (Kokstad): 10 miles from Ixopo on Donnybrook road, Farm "Lynn Avis" (-BB), Crewe 38 (NH, NU); Alfred, Zuurberg (-BC), Hilliard & Burtt 10191 (NU); Westlands farm, Nolengeni mountain (-CB), Rourke 1546 (NBG); Mount Frere, Cedarville, Cattle dip (-CC), Strey 10796 (GRA, NH); Weza forest reserve, ridge 3818 (-DA), Stutz 17 (NU); Ngele mountain, 3 km N of Eagle's Nest (-DA), Abbott 5507 (NH); Harding, Rooivaal (-DB), Taylor 5364 (NBG).
- 3127 (Lady Frere): Indwe, Ida forest (-BC), Von Gadow 360 (GRA).
- 3225 (Somerset East): Boschberg (-DA), Levyns 5576 (BOL).
- 3226 (Fort Beaufort): Alice, Hoggsback lookout post (-DB), Hoole 110G (GRA); Hoggsback (-DB), Rattray 232 (GRA), Von Gadow 443 (GRA); 6.3 miles on Fort Beaufort to Grahamstown road (-DC), Story 1259 (PRE); Sandile's Kop (-DD), Giffen 367 (PRE).
- 3227 (Stutterheim): Pirie, Maden [Madem] dam (-CB), Osborne 230 (GRA); Pirie, Murray's Ridge (-CB), sub RUH 291 (GRA); Dohne hill (-CB), Bot. Survey of SA 2104 (NU), Sim 2101 (NU [mixed with var. collina]), 19870 (NU); King William's Town, Mount Coke forest (-CD), Comins 1669 (GRA); King William's Town, Buffalo [river] at Heynes Mill (-CD), Tyson 381 (BOL); Komgha (-DB), Flanagan 559 (BOL, MO); East London, Between Quinera & Gonubi rivers (-DD), Rycroft 1896 (GRA).
- 3325 (Port Elizabeth): Krakakamma (-CD), Ecklon & Zeyher 2204 (GRA); Adow [Addo] (-DA), Ecklon & Zeyher 2204 (GRA).
- 3326 (Grahamstown): Sheldon (-AB), Bayliss 384 (PRE); Sidbury, Rockliffe (-AC), Daly 784 (GRA); Coldsprings (-AD), Jacot Guillarmod 9705, 9356 (GRA); Coldstream [Cold Springs (-AD) ?], Hoole sub GRA A7593 (GRA); Highlands road (-AD), Wells 3022 (GRA); Ecca pass c. 1300 ft (-BA), Schönland 769 (GRA); Ecca pass, old road, c. 15 km from Grahamstown (-BA), Brink 128 (GRA, PRE); Breakfast Vlei, Keiskamma valley (-BB), Acocks 11864 (PRE); Committees---Fish river valley (-BB), Dyer 2176 (GRA, PRE); Queen's road near Grahamstown (-BC?), Holland 3967 (BOL); Urbem Grahamstown (-BC), Zeyher s.n. sub SAM 37104 (SAM); Prope urbem "Grahamstown" (-BC), Ecklon & Zeyher 2204 (GRA), Zeyher 2204 (SAM); Albany Museum garden (-BC), Brink s.n. sub GRA A7592 (GRA, PRE), Brink 485 (GRA), Booij 160 (GRA); Ad fluvium "Karregarivier" (Albany) (-DA), Ecklon & Zeyher 2204 (GRA), Zeyher 2204 (SAM); Bathurst (DB/BD?), Karsten sub BOL 25204 (BOL); Alexandria, Boknesstrand (-DA), Burrows 3742 (GRA).
- 3327 (Peddie): East London, 200 ft (-BB), Thode 9225 (STE); East London, Potter's pass (-BB), Jacot Guillarmod & Brink 90 (GRA).
- 3319 (Worcester): Ceres (-AD), Thode A2247 (PRE).

Precise locality unknown: Ethiopia, In monte Scholoda, Schimper s.n. [1844?] (P, Z); Ethiopia: Choa (Shoa), Quartin Dillon et Petit s.n. (P); Ethiopia: Amba Sea (Lea?), "26/9 62", Schimper 268 (SAM, Z); Congo Belge, Muremera--Usumti, Robyns 2335 (K); Tanzania, Paget-Wilkes 394 (MO); Tanganyika territory, Schlieben 422 (MO); Malawi, Nyika Plateau, 2340 m, Brass 17342 (MO); Malawi, Lunyangwa, La Croix 3782 (MO); Lesotho, Southern

district [c. 3027BD], Archibald 660 (PRE); Lesotho, Staples 299 (PRE); Compton 29980 (NBG); Zimbabwe, Victoria, Makoholi Exp. Sta., Sederayi 34 (PRE); Dest S. Rhodesia, Rogers 13358 (SAM); Hutton 513 (GRA); Sydenham, 3--5000 ft, Wood 10797 (NU); Natal, Wood 775 (STE).

1.4. var. *montana* Winter var. nov. var. *trifoliatae similis*, sed fructis minoribus, usque ad 4.5(--5) mm longa et 1.5--2.5 mm lata. Differt foliis typice decompositis, pinnis lateralibus plus valde decursivis secus rachim et pinnulis lateralibus saepe decursivis secus rachillam supra tantum, et pinnis angustioribus, saepe falcatis, quae gradatim angustatae sunt pro maxima parte versus apicem acuminatum.

TYPUS. --- Malawi: Vipya Plateau, 37 miles SW of Mzuzu, Vernal Pool Dome, 5500 ft, 14 May 1973, Pawek 6736 (PRE, holotypus--Figure 7.6; MO, isotypus). 

*Diagnostic characters.* *H. arborescens* var. *montana* is similar to var. *trifoliata*, but with smaller fruit, up to 4.5(--5) mm long and 1.5--2.5 mm wide [(5--)6--9 mm long and 2--4 mm wide in var. *trifoliata*]. It also differs by its typically decomound leaves, with lateral pinnae more strongly decursive along rachis and lateral pinnules often decursive along upper side of rachilla only, and by its narrower, often falcate pinnae, which taper gradually for a greater part of the leaf toward an acuminate apex (Figure 3.16). The petioles are up to 42--68 mm long and the leaves are glabrous or with few sparse hairs only at the base of the adaxial midrib.



**Figure 7.6** The holotype of *Heteromorpha arborescens* (Spreng) Cham. & Schlechtd. var. *montana* Winter in the National Herbarium, Pretoria (PRE).

*Distribution and ecology.* Restricted to central African mountainous habitats from Tanzania to Zimbabwe (Figure 7.1), sometimes in the same general area as var. *trifoliata* or var. *frutescens*.

#### Specimens examined

TANZANIA---0933: Rungwe, Kiejo volcano (-BB), *Hepper, Field & Mhoro* 5397 (MO).

MALAWI---1133: Vipya Plateau, 37 miles SW of Mzuzu, Vernal Pool Dome (-DA), Pawek 6736 (MO, PRE); Mzimba, Makatupe, 9 miles N of Chikangawa (-DC), Phillips 3341 (MO).

---1434: Dedza, Dedza mountain (-AB), Pawek 11568 (MO).

---1535: Zomba mountain, near Ngondala village (-AB), *La Croix* 2898 (MO); Zomba Plateau (-AC), Brass 16078 (MO, PRE); Leach 10423 (MO); Blantyre, Ndirande mountain (-CC), Brummit 8872 (PRE); Lichenya Plateau, Mlanje mountain (-CC), Brass 16483 (MO); Mlanje mountain, Lichenya Plateau (-CD), Chapman 520 (PRE); Mount Mulanje, Likhubula Valley, Chapaluka track (-DC), Chapman & Chapman 7361 (MO); Mount Mulanje, Edge of Chipalombe Shelf (-DC), Chapman & Chapman 7863 (MO).

MOZAMBIQUE---1433: Tete, Macanga (Furancungo), Monte Furancungo (Elefante) (-DA), Pereira et al. 1745 (MO, NBG).

---1537: Estacao Pecuaria do Gurue, 18 km do Gurue, 14 km de Mt. Namuli (-AC), De Koning 7420 (MO, NBG).

ZIMBABWE---1832 (Umtali [Mutare]): Umtali (-DC), Chase 4417 (MO, PRE).

---1932 (Melsetter [Chimanimani]): Umtali, W end of Valhalla Estate (-BB), Pope & Muller 2075 (MO, PRE); Chimanimani National Park, North waterfall (-DB), De Castro 149 (JRAU).

1.5. var. *frutescens* Winter var. nov. differt a var. *trifoliata* habitu frutescente parciter ramoso, e basi surculis, usque ad 2 m alta, habens diametri truncum maxime 50 mm, cortice exfoliare non facile, foliis et caulis juvenibus plerumque glaucis, petiolulis plerumque longioribus. Pinnulae, ubi adsunt, oppositae vel suboppositae secus rachillam.

TYPUS (Figure 7.7). --- Transvaal: Crest of Abel Erasmus Pass, Winter 57 (PRE, holotypus; JRAU, K, NBG, NH, PRE, isotypus).

[*Heteromorpha transvaalensis* Schlechter & H. Wolff *sensu* C.C. Townsend (1985) p.p.]

*Diagnostic characters.* *H. arborescens* var. *frutescens* differs from var. *trifoliata* by the weakly branched shrubby habit, suckering from the base, up to 2 m high, trunk not wider than 50 mm, bark not readily peeling, leaves and young stems usually glaucous (rarely glaucescent in var. *trifoliata*), petiolules usually longer. Pinnules, when present, opposite or sub-opposite along the rachilla (Figure 3.16) in var. *frutescens* (alternate in var. *trifoliata*). The leaves are glabrous or with few sparse hairs only at the base of the adaxial midrib, trifoliolate to decreasingly pinnately decomound (Figure 3.16), with long petioles up to 25--62(--75) mm, and usually petiolulate. Synflorescences are lax, borne clear of vegetative leaves, and with bracts reduced in size (Figure 4.2 B). Fruit wings are well-developed in this variety, even at the flowering stage.

*Distribution and ecology.* *H. arborescens* var. *frutescens* occurs in (mesic) open woodland (Wolkberg) or dry grassland (Abel Erasmus Pass), and is distributed from southern Malawi to



**RAU HERBARIUM (JRAU)**  
JOHANNESBURG

2430 DA	LAND REF. HETAR/PRM	REGIO Transvaal
P Winter 57	SECT & NO	ANNO 3/5/1992 ALT 1500m
<i>Heteromorpha arborescens</i> Cham. + Schlechtd. var. <i>frutescens</i> Winter		
Thelabourie district, coast of Abel Erasmus pass; Open shrubland/ grassland. Shrub up to 1.8m; coppery from woody canes; General gaudous appearance		
P J D Winter 15/3/92		

**Figure 7.7** The holotype of *Heteromorpha arborescens* (Spreng) Cham. & Schlechtd. var. *frutescens* Winter in the National Herbarium, Pretoria (PRE).

Zululand, Natal (Figure 7.1). The proximity with *H. stenophylla* var. *transvaalensis* suggests the possibility of hybrid introgression.

### Specimens examined

- MALAWI**---1535: Zomba, Naisi spur (-AC), Tawakali & Balaka 85 (MO). [Grid reference not found: S region, Chiradzulu, Njuli, La Croix 3075 (MO)]
- MOZAMBIQUE**---2435 (Inharrime): Zavora beach, 16 km after crossing with LM [Maputo] to Beira road (-CA), De Lemos & Balsinhas 162 (PRE).
- 2532 (Lourenco Marques [Maputo]): Namaacha, Cascata (-CC), Groenendijk & De Koning 250 (MO).
- ZIMBABWE**---1832 (Umtali [Mutare]): 2 km N of Inyanga [Nyanga] village (-BB), Rushworth 810 (MO); Umtali [Mutare], S of Morning suburb (-DC), Chase 6053 (PRE); 32 miles N of Umtali [Mutare] (-DA), Biegel 1708 (MO).
- 1928 (Nyamandhlovu): Nyamandhlovu, Pasture Station (CD?), Plowes 1651 (MO).
- NAMIBIA**---1821 (Andara): Andara mission, River (-AB), De Winter & Marais 4807 (PRE, WIN).
- SWAZILAND**---2631 (Mbabane): Stegi, Hlova River (-BD), Compton 31320 (NH); Manzini, Tulwane (-CD), Compton 29015 (NBG).
- SOUTH AFRICA** (with included territories)---2230 (Messina): Louis Trichardt, Farm Rietbok 226MT (-CC), Venter 7801 (PRE); Vendaland, Tate Vondo, Tshirovha river, Mahovho-Hovho falls (-CD), A.E. Van Wyk 2856 (PRE); Vhurivhuri, 33 miles NE of Sibasa (-DA), Codd 6907 (PRE).
- 2329 (Pietersburg): Letjume, Farm Letjuma (-AB), Venter 7550 (PRE); 49 km from Pietersburg to Tzaneen (-DD), Winter 51 (JRAU).
- 2330 (Tzaneen): E of Eiland resort, Kondowe Lt 741, Private Nature Reserve, Magwena spruit (-DB), Van Jaarsveld 1211 (NBG, PRE).
- 2428 (Nylstroom): Naboomspruit, Mosdene (-DA), Galpin M159 (PRE).
- 2429 (Zebediel): Haenertsburg, Wolkberg / Strydpoort mountains near Island Blue Asbestos mine (-BB), Moffet 1774 (PRE).
- 2430 (Pilgrim's Rest): Abel Erasmus Pass, 49,5 km from turnoff to Pilgrim's Rest (-DA), Winter 57 (JRAU); California 228 KT (-DA), Raal 1428 ((PRE)).
- 2530 (Lydenburg): Sekukuniland, Farm Parys (-AA?), Barnard & Mogg 766 (PRE).
- 2531 (Komatipoort): Gorge of Crocodile Poort (-CA), Rogers 23901 (PRE); Kruger National Park, Hill near Malelane (-CB), Codd 5273 (PRE); Barberton (-CC), Rogers sub TRV 22197 (PRE); Fairview Mine (-CC), NEL 261 (NBG), 269 (NBG, PRE).

IHERB. HORT. KEW.



HOLOTYPE  
of *Heteromorpha papillosa* C.C.Townsend  
in Kew Bull. 40: 846 (1985).

*Vindhuk Herland*  
dCC!  
Botanica  
HERBARIUM DR. R. SEYDEL 124667

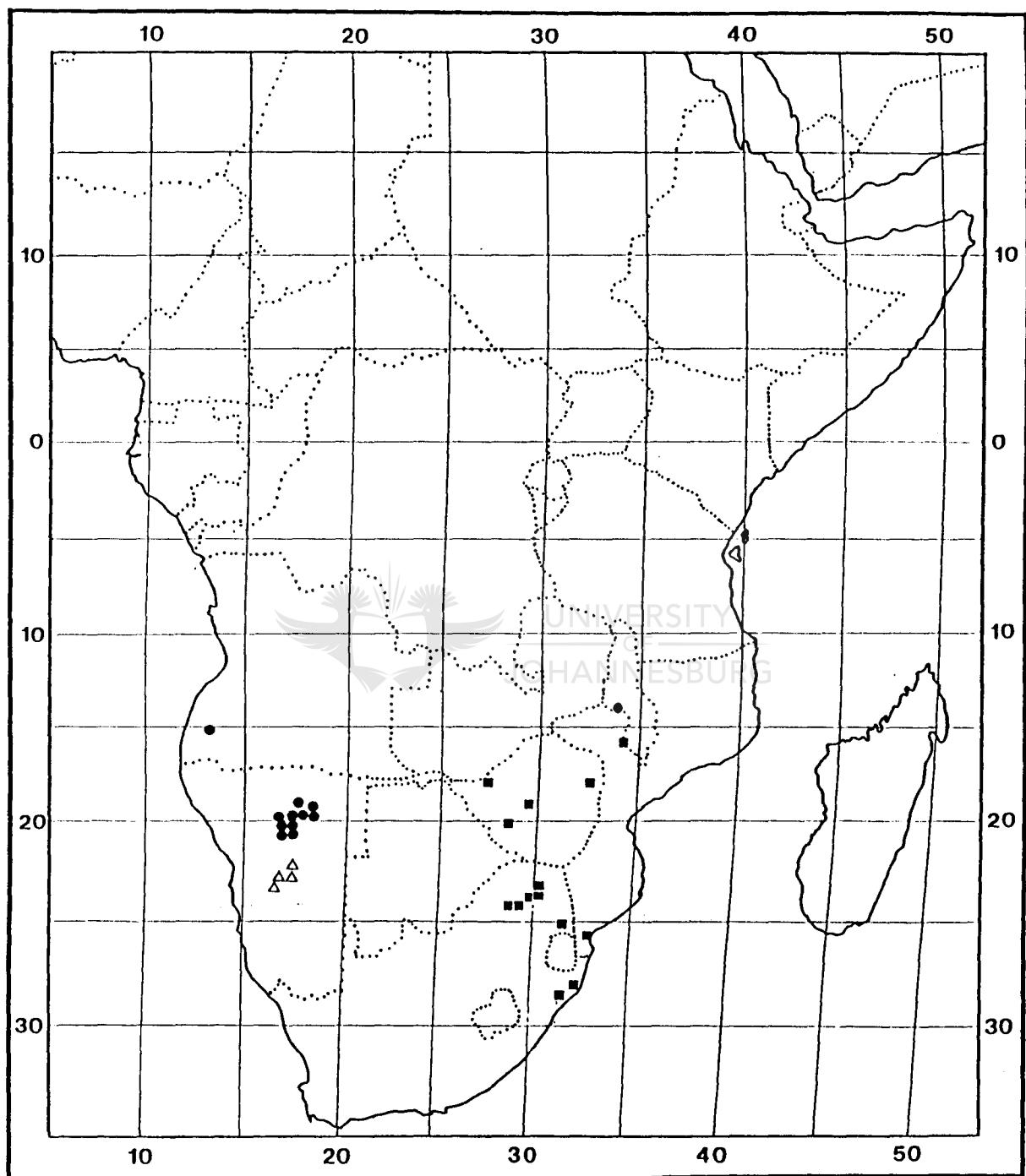
Herb No. \_\_\_\_\_ Regn. Asia.  
*Heteromorpha arborea* Chm. & Michl.  
Umbelliferae  
Auf den Berzen hier u da, im ranen  
-nicht häufig; wo ein "Pfeilbaum", dort  
-sieht auch ein lebender Pfeilbaum, wach  
-mit geteilten Blättern, zelles Blätter  
Altitude ca. 1000 m Ann. 3-6 v.H. Lep. Dr. Seydel  
No. 4623

Figure 7.8 The holotype of *Heteromorpha papillosa* C.C.Townsend in Kew herbarium (K).

mm wide; glabrous or with some short hairs only on the upper surface of the midrib. Inflorescence a shortly pedunculate, single compound umbel or rarely a panicle of compound umbels, bracts not markedly reduced; main florescence of (12--)17--23(--27) rays, 14--15(--22) mm long, (10--)12--20 raylets, 2--4 mm long. Involucral bracts small, lanceolate. Petals cream-coloured to greenish yellow, higher than, or as high as broad, usually papillose. Stylopodium and ovary usually papillose. Fruit glabrous or usually slightly pilose, narrowly obovoid to obpyriform, 6--10 mm long, 3 mm wide, strongly laterally compressed; vittae solitary in the valleculae, two on the commissure.

*Diagnostic characters.* *H. papillosa* is similar to *H. arborescens* in the well branched habit, but is of smaller stature and has very narrow pinnae (Figure 3.16), more than four times longer than wide. The leaves are glabrous or with some short hairs only on the upper surface of the midrib. The umbels are very shortly pedunculate, and the sepals, petals, ovary and in several specimens even the stylopodia are papillose. The adaxial stomatal density is up to 43 per  $\text{mm}^2$ .

*Distribution.* *H. papillosa* has been collected only in the region around Windhoek in Namibia (Figure 7.9). This constitutes a vicariant distribution range, the closest occurring species being *H. stenophylla*, with a distribution range which only commences several hundred km to the north (Figure 7.9).



**Figure 7.9** The known geographical distribution of *Heteromorpha papillosa* ( $\Delta$ ), *H. stenophylla* var. *stenophylla* ( $\bullet$ ), and *H. stenophylla* var. *transvaalensis* ( $\blacksquare$ ).



**Figure 7.10** The lectotype of *H. stenophylla* Welw. ex Schinz in Zürich herbarium (Z).



**Figure 7.11** The lectotype (specimen on the right) of *Franchetella arborescens* (Spreng.) Kuntze var. *stenophylla* (Schinz) Hiern in the British Museum (BM).

### Description

Suffrutex, 0,5--1,0(--1,8) m tall, glabrous. *Stems* simple or weakly branched; smooth to longitudinally grooved, glabrous to pilose. Pith predominant. *Bark* absent or weakly developed. *Leaves* with a maximum length of 110--127(--320) mm; distinctly petiolate, petioles with a maximum length of (25--)35--43(--102) mm, canaliculate, somewhat carinate, or sometimes terete, usually widely or deeply sulcate, glabrous to sparsely pilose in the groove, base non-amplexicaul, rarely amplexicaul; outline variable, trisect or pinnately and/or pedately compound, or bipinnatifid; incision usually decursive. *Pinnae* very narrowly elliptic to lanceolate or obovate; apex acuminate to truncate, mucronate; margins entire or somewhat crenulate, glabrous; base attenuate to cuneate; with a maximum length of 35--83(--160) mm and 5--10(--20) mm wide; midrib rarely with a few sparse hairs at the base. *Inflorescence* a lax panicle of compound umbels, bracts markedly reduced only in var. *transvaalensis*; main florescence of few, (10--)14--19(--25), thin rays, 29--50 mm long, and (9--)11--16(--28) raylets, 3--7(--10) mm long. *Involucral bracts* small. *Petals* cream-coloured to greenish yellow, higher than, or as high as broad. *Ovary* more than twice as long as the stylopodium. *Fruit* glabrous, ovoid, 3--9 mm long, 2--5 mm wide; vittae solitary in the valleculae, two on the commissure. *Chromosome number:* 2n=22.

*Diagnostic characters.* The suffrutescent habit distinguishes this species from *H. arborescens* and *H. papillosa*. It is distinguished from other suffrutescent species by the virtual glabreity of the entire plant, rather few (10--)14--19(--25), thin rays up to 50 mm long, lax inflorescence, and the ovary which is more than twice as long as the stylopodium (3.1 & 3.2 in Figure 4.3).

*Distribution.* The known distribution (Figure 7.9) can be divided into a western centre in northern Namibia, reaching north into south western Angola, and an eastern range comprising Malawi, Zimbabwe, northern and eastern Transvaal, Zululand and southern Mozambique. The apparent absence in the area in between (e.g. south eastern Angola, Zambia, and the Caprivi strip of northern Namibia), is possibly due to undercollecting.

Two varieties are recognised on the basis of morphological trends supported by micro-morphological discontinuity. The variation is generally correlated with geographical distribution (Figure 7.9), although some intermediates occur in Malawi and Zimbabwe.

#### Key to the varieties of *H. stenophylla*

- 1a Leaves (3.1 in Figure 3.16) trifoliolate or pinnate, usually with 3--5 lanceolate pinnae (rarely up to 9 segments); pinna apices acuminate, rarely rounded; adaxial stomatal density up to 52 per  $\text{mm}^2$ , abaxial stomatal density lower than 100 per  $\text{mm}^2$  . . . . . 3.1 var. *stenophylla*
- 1b Leaves (3.2 in Figure 3.16) decursively pinnate to bipinnatipartite, usually with more than five segments, pinnae not lanceolate; pinna apices

acute to rounded, rarely acuminate; adaxial stomatal density up to 11 per  $\text{mm}^2$ , abaxial stomatal density more than 140 per  $\text{mm}^2$  . . . . . 3.2 var. *transvaalensis*

### 3.1 var. *stenophylla*

*H. stenophylla* Welw. ex Engl. nom. nud. in Hochgebirgsfl.  
Afrika: 317--318 (1892). Based on *Welwitsch* 2508 (see below).

*Welwitsch* 2508 (Figure 7.11) was the only specimen cited by Engler (1892), and was probably a B specimen.

*Franchetella arborescens* (Spreng.) Kuntze var. *stenophylla*  
(Schinz) Hiern, Cat. Welw. Afr. Pl. 2: 424 (1898).  
[as *Franchetella arborescens* O. Kuntze var. *stenophylla* (Welw.  
ms. in Herb.)]. Type: Welwitsch 2508 (BM, specimen on the right,  
lecto!, here designated, Figure 7.11; B†?; COI; G!; K, photo!;  
PRE p.p., mixed with *Peucedanum* ? sp.!)

Hiern obviously worked from BM duplicate material, being based there, as he also refers to *Welwitsch 2508 b*, which is mounted on the same BM sheet (Figure 7.11, specimen on the left).

*Welwitsch* 2508 (BM), as well as the duplicate in Genève, has fruit, which were mentioned in Schinz' description, while Newton 132 unfortunately does not.

Schreiber (1967), and Cannon (1970), both cited *H. stenophylla* Welw. ex Schinz as a synonym of *H. trifoliata* (Wendl.) Eckl. & Zeyh.

*Diagnostic characters.* Similar to *H. stenophylla* var. *transvaalensis*, but with only up to 5 lanceolate pinnae per leaf (9 segments are exceptionally rare), apices usually acuminate (3.1 in Figure 3.16), adaxial stomatal density generally higher, up to 52 per mm<sup>2</sup>, abaxial stomatal density < 100 per mm<sup>2</sup>. Petiole terete or semi-terete in transverse section. Bracts not markedly reduced on synflorescence branches. There are (10--)18--25 rays in the main florescence.

*Brummit 9316* (PRE) and *Robson 1521* (PRE) are atypical and have a situation disjunct from the rest of the taxon in the Dzalanyama area of Malawi (Figure 7.9). This may even prove to be a different species when more material is available (possibly a glabrous form of *H. involucrata*).



*Distribution.* With the exception of the two specimens from Malawi mentioned above, var. *stenophylla* is limited to Angola and the northern part of Namibia (Figure 7.9).

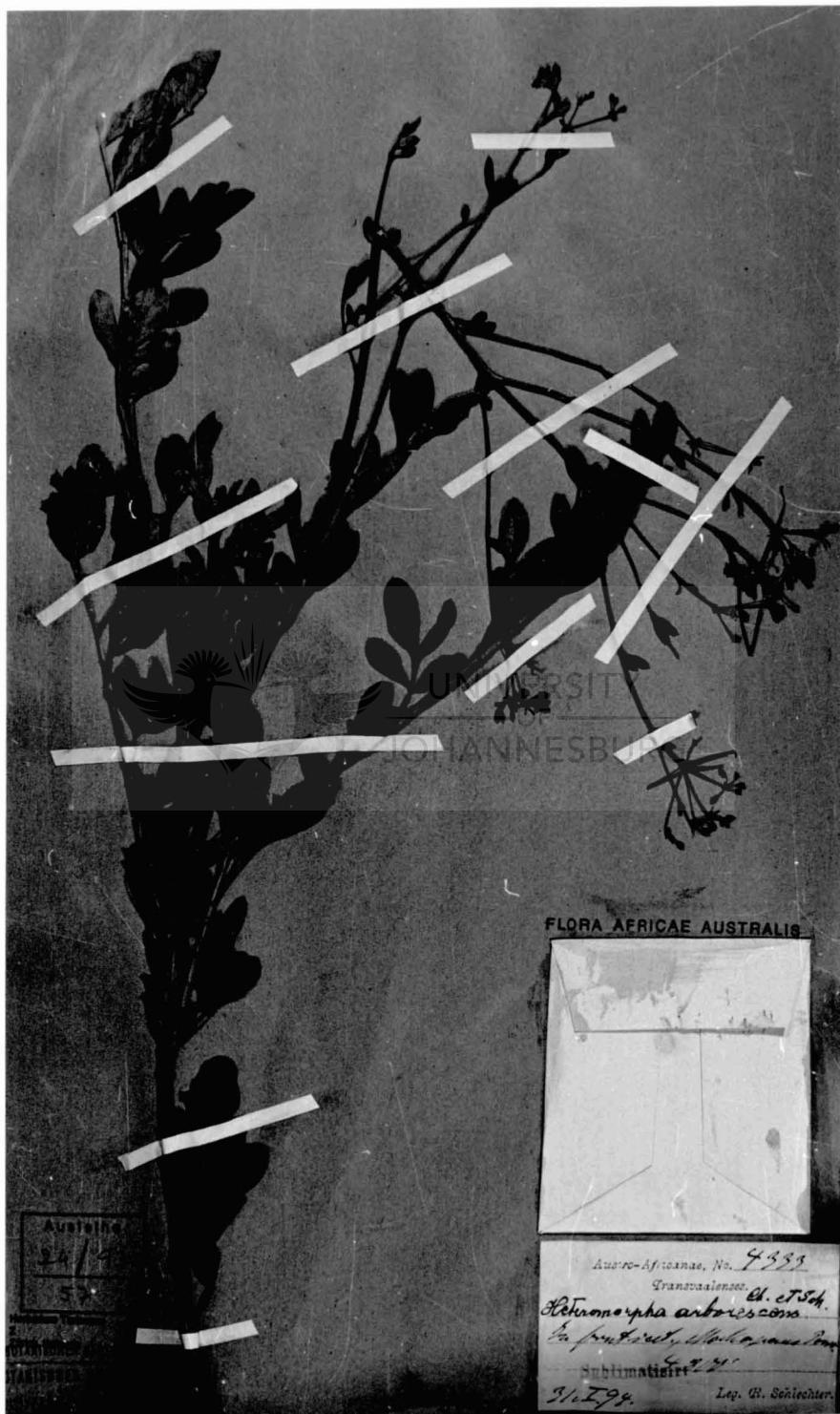
### Specimens examined

**ANGOLA---1513:** Mossamedes, Humpata (-AA), Newton 132 (Z); Benguela, inter Humpata et rivum Quipumpunhime (-AA), Welwitsch 2508 (BM, G, K, photo).

**MALAWI---1433:** Lilongwe district, Dzalanyama Forest Reserve, Chiungiza (-BA), Robson 1521 (PRE); Chiunjiza road, c. 5 km SE of Chaulongwe falls (-BA), Brummit 9316 (PRE).

**NAMIBIA---1916** (Gobaub): Rynefeld OU367 (-DC), Giess 8602 (PRE, WIN); Tölken & Hardy 884 (WIN).

---1917 (Tsumeb): 35,3 km SW of Tsumeb on Otavi road (-BA), De Winter 2914 (PRE, WIN); 35 km from Otavi on Tsumeb road, Khorab Ost 328 (-BC), Wanntorp 501 (PRE); Elandshoek GR771, Dolomitberghang (-BC), Giess 15120 (WIN); Elandshoek GR77, Steilem Dolomittfels (-BC), Giess 15139 (PRE); Grootfontein, Bergen GR668 (-BD), Giess, Volk & Bleissner 6457 (WIN); Otavi (-CB), Dinter



**Figure 7.12** The lectotype of *H. stenophylla* Welw. ex Schinz var. *transvaalensis* (Schlechter & H. Wolff) Winter in Zürich herbarium (Z).

---2428 (Nylstroom): Magalakwin [Mogalakwena], Sterkwater (-BB), *Smuts 2003* (PRE); *Smuts sub PRE 48177* [seems like rest of inflorescence of 2003] (PRE).

---2429 (Zebediela): Potgietersrus, Prinzen (-AA) *Burtt-Davy 2292* (PRE, 2 sheets); Makapans Poort/Pass (-AA), *Schlechter 4333* (BOL, GRA, K, PRE, S, SAM, STE, Z); 20,5 km from Potgietersrus on Pietersburg road, S of old road (-AA), *Winter 50* (JRAU); Lebowa Highlands mountains, Farm Portugal 55 (-AA), *Venter 12372* (NU).

---2531 (Komatipoort): Kruger National Park, Mutshidaka, c. 10 miles from Nahpe road (-AB), *Van der Schyff 606* (PRE).

---2831 (Nkandla): Umhlatuzi, Dornfeld (-C/D), *Gerstner sub NH 22766* (NH).

---2832 (Mtubatuba): Hlabisa, Hluhluwe Game Reserve (-AA), *Ward 2992* (NH, NU).

**Precise locality unknown:** S Rhodesia [Zimbabwe], *Rand 17* (GRA); (Gwanmpa ?) For. Res. S. R. [Zimbabwe ?], *Savony 146* (NU); N Zululand, *Baker 575* (NH).

4. *H. occidentalis* Winter, *sp. nov.* *Suffrutex robusta* *H. involucratae* similis ob caules medullosos plerumque non ramosos sub synflorescentia, sed a speciebus praecedentibus distincta ob duas vittas laterales cum vitta carinales in quoque lobo calycis.

TYPUS (Figure 7.13). --- Cameroun: Hossere NGO, 80 km NW de Tibati, *Letouzey 5680* (K, holotypus).

This specimen was selected since it has well-preserved flowers where the trivittate calyx lobes can be clearly seen.

*Franchetella arborescens* (Spreng.) Kuntze var. *platyphylla* Welw. ex Hiern *nom. nud.*, Cat. Afr. Pl. Welwitsch I. 2: 424 (1898). Type: Angola, Pungo Andonga, Candumba, Cuanza river, *Welwitsch 2507* (BM, lecto!, here designated; K, COI, LISU)



**Figure 7.13** The holotype of *Heteromorpha occidentalis* Winter in Kew herbarium (K).

As Hiern worked mainly in the British museum, that specimen is selected as lectotype.

[*Heteromorpha trifoliata* auct. non (Wendl.) Eckl. & Zeyh.: Jac.-Fel., Adansonia 10: 46 (1970); Cannon pro parte in CFA 4: 340--342 (1970)]

[*Heteromorpha abyssinica* auct. non Hochst. ex A. Rich.: Jac.-Fel., in Fl. Cameroun 10: 74 (1970)]

The original invalidly published varietal epithet has been used in synonymy of what is now considered *H. arborescens*. Various authors have used the name in this way up to the present, starting with H. Wolff (1910).



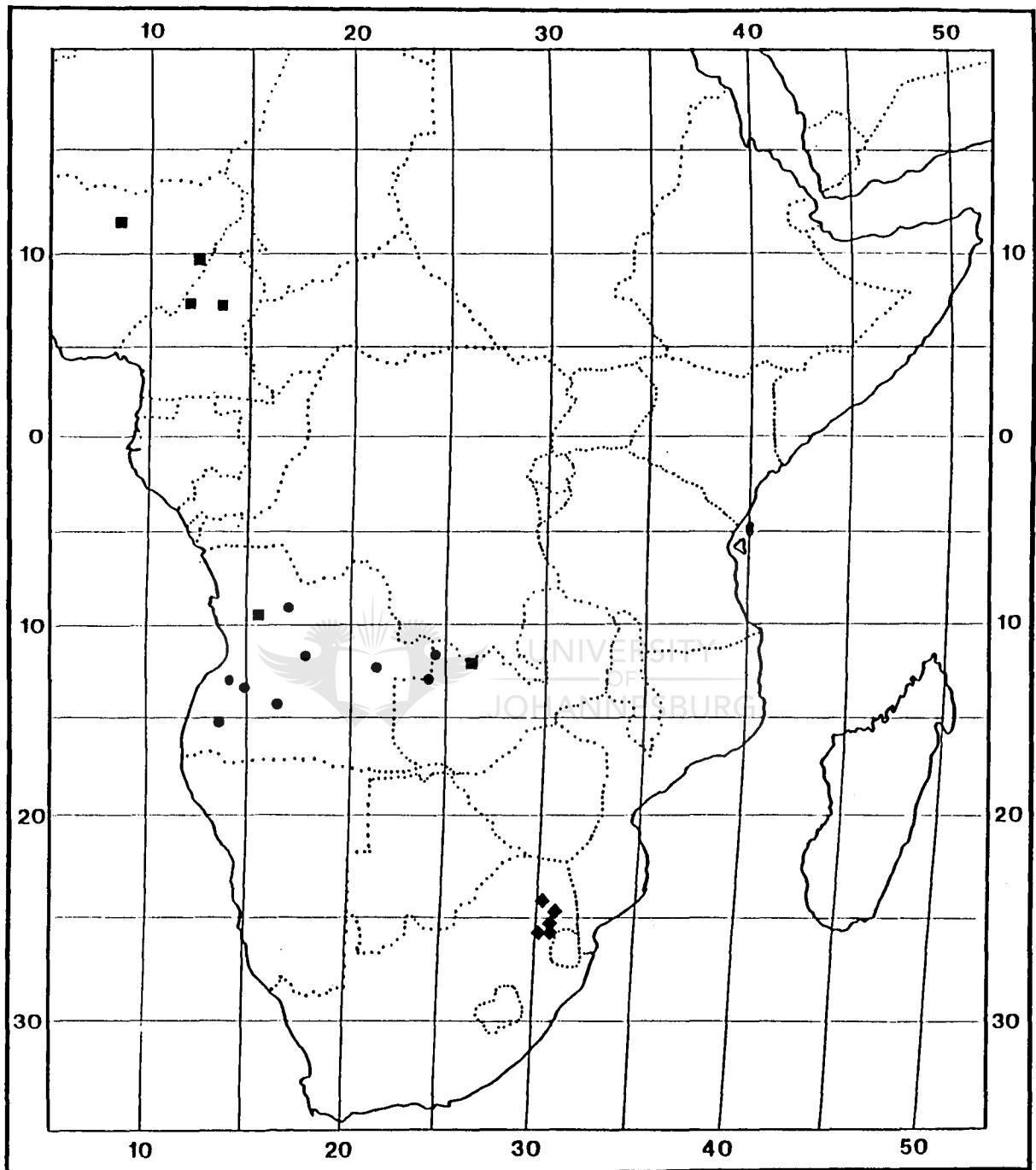
### Description

Robust suffrutex. Stems pithy, 2,5--3 m high, smooth, with very fine longitudinal striations, usually only branched in the inflorescence. Bark absent or weakly developed. Leaves distinctly petiolate, petioles with a maximum length of 23--54 mm, carinate or semiterete, sometimes terete, usually widely or deeply sulcate, often glabrous to pilose, base non-amplexicaul (< 1/3 circumference); outline invariably trifoliolate. Pinnae elliptic to widely elliptic; apex acute to rounded, mucronate; margin entire or somewhat crenulate, slightly tuberculate or papillate or with occasional short, broad-based trichomes; base

attenuate to cuneate; with a maximum length of 85--115 mm, and 23--45 mm wide; midrib glabrous to adaxially sparsely pilose with short, broad-based trichomes associated with occasional tubercles. *Inflorescence* a panicle of compound umbels, bracts not markedly reduced; main florescence large, 20--25 rays with a maximum length of 54 mm, and 10--15 raylets with a maximum length of 10 mm. *Involucral bracts* small, lanceolate, interspersed with up to 2 larger foliose, elliptic bracts. *Calyx lobes* long, with two lateral vittae in addition to the carinal vitta. *Petals* cream-coloured to greenish yellow, higher than, or as high as broad. *Fruit* glabrous, narrowly elliptic to ovoid 4--7 mm long, 2--4 mm wide; vittae solitary in the valleculae, two on the commissure.

*Diagnostic characters.* *H. occidentalis* is a robust suffrutex similar to *H. involucrata*, with pithy stems usually unbranched below the synflorescence, but is set apart from all other species by the presence of two lateral vittae in addition to the carinal vitta on each calyx lobe (Figure 4.3). It is further distinguished from *H. arborescens* and also *H. stenophylla* by the leaf margin and midrib which are slightly tuberculate or papillate or with occasional short, broad-based trichomes, whereas only simple cylindrical trichomes (if any) are found in the former two species.

*Distribution.* This taxon has a western distribution range with a tropical disjunction (Figure 7.14), and is limited to northern and southern latitudes between 7 and 12,5 degrees. Specimens are known from northern and eastern Nigeria, the Cameroun highlands,



**Figure 7.14** The known geographical distribution of *Heteromorpha occidentalis* (■), *H. gossweileri* (●), and *H. pubescens* (◆).

north eastern Angola and northern Zambia. (See note under *H. arborescens* var. *trifoliata*)

### Specimens examined

**NIGERIA**---0912: NE region: Mambila district, Nguroye, near Kusuku CRIN *Coffea* plantation on Nguroje to Kakara road, *Latilo* 132 (K).

---1108: NE region, Mambilla district, Kakara (-CD), *Ekwuno* 235 (K).

**CAMEROUN**---07N13: Plateau de Adamaoua, Wakwa, Cattle breeding centre (-DC), *Breteler* 292 (K).

[Grid reference not found: E Cameroun, W region, T-alus, 1300 m, *Meurillon* 1396 (K)]

---07N12: Hossere NGO, 80 km NW de Tibati, *Letouzey* 5680 (K).

**ZAIRE** [Grid reference not found: Katanga, Forêt claire, 1025 m, A. 0,3 km au S de Kabiashia, *Malaisse* 5433 (K)]

**ANGOLA**---0915: Pungo Andongo (-DA), *Welwitsch* 2507 (BM).

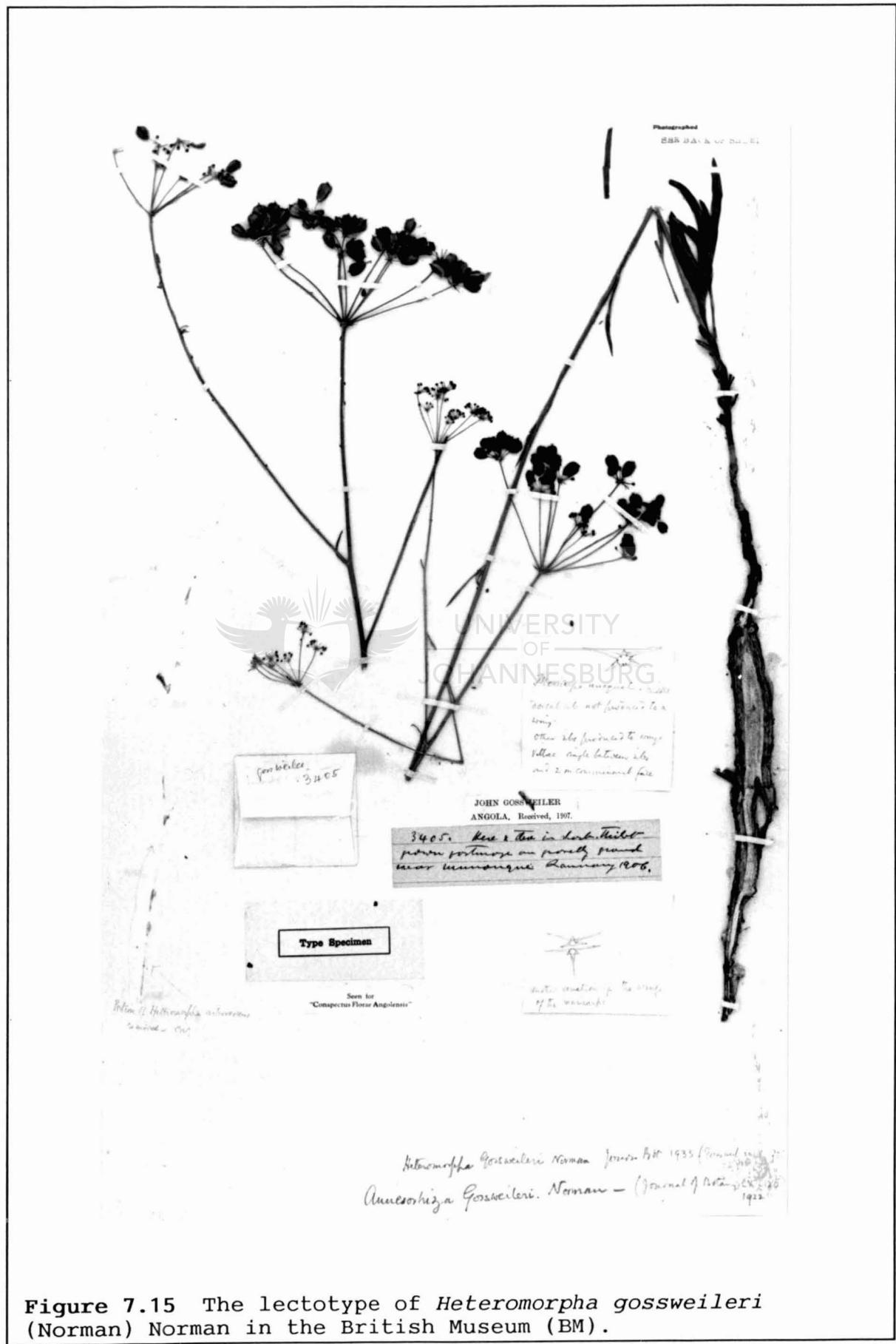
**ZAMBIA**---1226: Solwezi (-AB), *Milne-Redhead* 762 (K), 2 sheets.



5. *H. gossweileri* (Norman) Norman in Journal of Botany 71, Suppl.1: 236 (1933); Cannon in Consp. fl. Angol. 4: 342--343 (1970); C.C. Townsend in Kew Bull. 40(4): 846 (1985). Type (Figure 7.15): Angola, Menonque, *Gossweiler* 3405 (BM, lecto!, here designated; COI; K, photo!; LISJC).

Since Norman worked in BM, and since this is the only available specimen to be chosen, it is designated as lectotype. Both Cannon (1970), and Townsend (1985) considered this specimen the holotype.

*Annesorhiza gossweileri* Norman in Journ. Bot. 60: 120 (1922) & 67, Suppl. 1: 200 (1929). Type as above.



Judging by the note in Norman (1933), the BM specimen is indeed the type referred to in the original description.

*Bupleurum angolense* Norman in Journ. Bot. 71, Suppl. 1: 234 (1933). Type (Figure 7.16): Angola, Planalto de Malange, Kela, Gossweiler 9594 (BM, lecto!, here designated; K, photo!; LISJC).

Since Norman worked in BM, and as this specimen also appears to be the specimen used for Figure 3, accompanying the original description, it is selected as lectotype. Both Cannon (1970), and Townsend (1985) considered this specimen the holotype.

*Heteromorpha angolensis* (Norman) Norman in Journ. Bot. 72: 206 (1934); Cannon in Consp. fl. Angol. 4: 343, TAB. XXXIX (1970). Type as above.

### Description

Suffrutex, 0,2--0,7(--1,2) m tall. *Stems* thin, simple or weakly branched; smooth to longitudinally grooved, glabrous to pilose. Pith predominant (the xylem limited to a thin cylinder around it). *Bark* absent or weakly developed. *Leaves* with a maximum length of 80--90 mm; sub-sessile or shortly petiolate (only when trifoliolate), petioles 0--5(--30) mm long, canaliculate, widely sulcate, base non-amplexicaul or semi-amplexicaul, somewhat narrowly winged, glabrous to pilose; outline variable, unifoliolate or tripartite to trifoliolate; incision usually decursive. *Pinnae* narrowly or very narrowly elliptic to obovate;



**Figure 7.16** The lectotype of *Bupleurum angolense* Norman in the British Museum (BM).

apex acuminate to obtuse, mucronate; margin entire or somewhat crenulate, papillate to ciliolate, somewhat tuberculate; base cuneate to attenuate, mostly narrowly decurrent along petiole; with a maximum length of 60--80 mm and 7--17 mm wide; costal vein angle usually less than 45°; margins or veins partly verruculose. *Inflorescence* a lax panicle of compound umbels, bracts often reduced; main florescence of few, 9--10(--16), thin rays, 50--70(--80) mm long, (8--)11--18 raylets, (1--)3--7 mm long. *Involucral bracts* small, linear, up to 30 mm long. *Petals* yellow, broader than high. *Fruit* glabrous, typically roundish when young, becoming broadly obovoid, up to 10 mm long, 5--6(--7) mm wide, with well developed (half-winged) petaline ribs; vittae solitary in the valleculae, two on the commissure.

*Diagnostic characters.* Suffrutex with thin stems, distinguished from *H. stenophylla* by the sub-sessile or shortly petiolate leaves, the petioles with a maximum length of 5(--30) mm. The costal vein angle is usually less than 45 degrees, and the leaf margins or veins partly verruculose. The few, 9--16, long, 50--70(--80) mm, thin rays and the combination of high adaxial and abaxial stomatal densities, > 45 per mm<sup>2</sup> and > 200 per mm<sup>2</sup> respectively, distinguishes this from other species. The involucral bracts are slender, and the fruit has well-developed petaline ribs.

*Distribution and ecology.* *H. gossweileri* has been recorded only from Angola and northern Zambia (Figure 7.14).

### Specimens examined

ZAMBIA---1124: Mwinilunga district, 0,5 miles SW of Matonchi farm (-CB), Milne-Redhead 4315 (K, 2 sheets); Mwinilunga district, Between Kalene and Sakatwala (-CB), Hooper & Townsend 325 (K, 3 sheets).

---1224: 52 km S of Mwinilunga on road to Kabompo (-AB), Brummit, Chisumpa & Polhill 14107 (K).

ANGOLA---0917: Planalto de Malange, Kela [Quela], Luando-Lui (-BB), Gossweiler 9594 (BM, K, photo).

---1118: Bié, Menongue (-D?), Gossweiler 3405 (BM, K, photo).

---1214: Alto Catumbela, Ganda, Mambussoco, Capacca (-CC), Faulkner A423 (K, PRE).

---1314: Benguella hochland zwischen Ganda und Caconda, Facenda Xangorolo (-BD), Hundt 727 (PRE).

[Grid reference not found: Moxico district [c.1321], Between R. Lukaia and R. Ndamba (Mundamba), Milne-Redhead 3981 (PRE)]

---1416: Ganguelas, Vila Artur de Paiva, Quezô (-AD), Mendes 2069 (PRE).

----1513: Between Huilla and Quihita Mission (-BA), Pearson 2633 (K).

6. *H. pubescens* Burtt Davy, A manual of flowering plants and ferns of the Transvaal with Swaziland, South Africa II: xxiii, 520 (1932); C.C. Townsend in Kew Bull. 40: 843--850 (1985); B.L. Burtt in Edinb. J. Bot. 48: 214 (1991). Type (Figure 7.17): Transvaal: Shilouvane, Rochers du Sanatorium, Junod 878 (K, lecto., photo!, here designated; G!; Z! x2).

Since his 'Manual of the Flowering Plants and Ferns of the Transvaal' (1932) was written while Burtt Davy was in K, this specimen is selected as lectotype. This specimen was indeed annotated by Burtt Davy himself.



**Figure 7.17** The lectotype of *Heteromorpha pubescens* Burtt Davy in Kew herbarium (K).

### Description

Suffrutex to weakly branched, woody shrub, 0,6--1,5 m tall, filamentously pilose, trichomes often clustered. *Stems* simple or weakly branched, smooth; pith variable in thickness. *Bark* weakly to well developed. *Leaves* with a maximum length of 80--135 mm; distinctly petiolate, petioles with a maximum length of 20--26 mm, usually widely or deeply sulcate, canaliculate, carinate or semi-terete, base semi-amplexicaul; outline variable, trifoliolate, sometimes pinnately and/or pedately compound with rarely up to 7 divisions; incision usually decursive. *Pinnae* elliptic to obovate or ovate; apex acute to obtuse or rounded, mucronate; margins crenulate, often undulate, ciliate; base attenuate; with a maximum length of 65--115 mm, 25--50 mm wide; abaxial veins often raised above the surface; somewhat tuberculately pilose. *Inflorescence* a single compound umbel or a lax panicle of compound umbels, bracts not reduced in size; main florescence of (24--)28--32 rays, 15--30 mm long, and 15--27(--27) raylets, 2--3(--4) mm long, often larger than the lateral umbels. *Involucral bracts* small to broad and conspicuous (usually more than two foliose bracts). *Petals* cream-coloured to greenish yellow, higher than, or as high as broad, abaxially bearded, particularly along the keel. *Fruit* invariably filamentously pilose, elliptic to broadly elliptic, 4--6 mm long, 2--3 mm wide, with well developed (half-winged) petaline ribs, secondary ribs invariably present, bearded; c 16 irregular vittae surrounding the seed, occasional small vittae also not infrequently occurring in the tips of the ribs or part way along them. *Chromosome number:* 2n=22.

*Diagnostic characters.* Similar to *H. involucrata*, but the filamentously pilose aerial parts (Figure 3.16), additional (c. 16) irregular vittae surrounding the seed (Figure 4.7), and presence of secondary ribs (Figure 4.7) on the fruit surface, are unique to this species.

*Distribution and ecology.* *H. pubescens* occurs in open woodland or grassland on well-drained slopes in the eastern Transvaal (Figure 7.13). It seems to be restricted to dolomite outcrops and serpentine soils.

#### Specimens examined

SOUTH AFRICA (with included territories)---2430 (Pilgrim's Rest): Ohrigstad, Murchison range, Smuts Pass from the Downs (-AA), *Burrows* 2666 (PRE); Letaba, The Downs (-AA), *Codd* 9476 (PRE); Lekgalameetse Nature Reserve, Paris SE corner (-AB), *Stalmans* 419 (PRE); Shilouvane, Rochers du Sanatorium (-AB?), *Junod* 878 (K, photo, G, Z); Blydepoort (-DB), *A.E. Van Wyk* 385 (PRE).  
 ---2530 (Lydenburg): Sabie, Langverwag (-BB), *Louw* 2718 (STE); Rocky's drift on Nelspruit to White River road (-BD), *Buitendag* 1304 (PRE); Nelspruit, W slope of amajuba mountain, Schagen (-BD), *Liebenberg* 3341 (PRE); Sudwala Caves area, 4,5 km from Houtboschloop road to Rosehaugh (-CC), *Winter* 65, 66 (JRAU); Cythna Letty Nature Reserve (-DD), *Kluge* 2616 (PRE); Barberton, Moodies (-DD), *Thorncroft* 5 (NH); 8 km on Agnes mine road opposite mine dump (-DD), *Winter* 69 (JRAU).

Precise locality unknown: Pietersburg (2329-DD?), *Van Greuning* 586a (PRE).

#### Doubtful locality:

MOZAMBIQUE---2135 (Bazaruto): Macovane (-AC), *Junod* 143 (PRE).

7. *H. involucrata* Conr. in Kew Bulletin 1908: 224 (1908); H. Wolff in Engl., Pflanzenr. Heft 43: 193 (1910); Burtt Davy, Man. Fl. Pl. & Ferns Transvaal II: 519--520 (1932); Compton, Fl. Swaziland: 407 (1976); C.C. Townsend in Kew Bull. 40: 843--850 (1985); C.C. Townsend in Fl. Trop. E. Afr: 37--41 (1989); B.L. Burtt in Edinb. J. Bot. 48: 213 (1991). Type (Figure 7.18): Transvaal, Modderfontein, Conrath 328 (K, lecto., photo!, here designated).

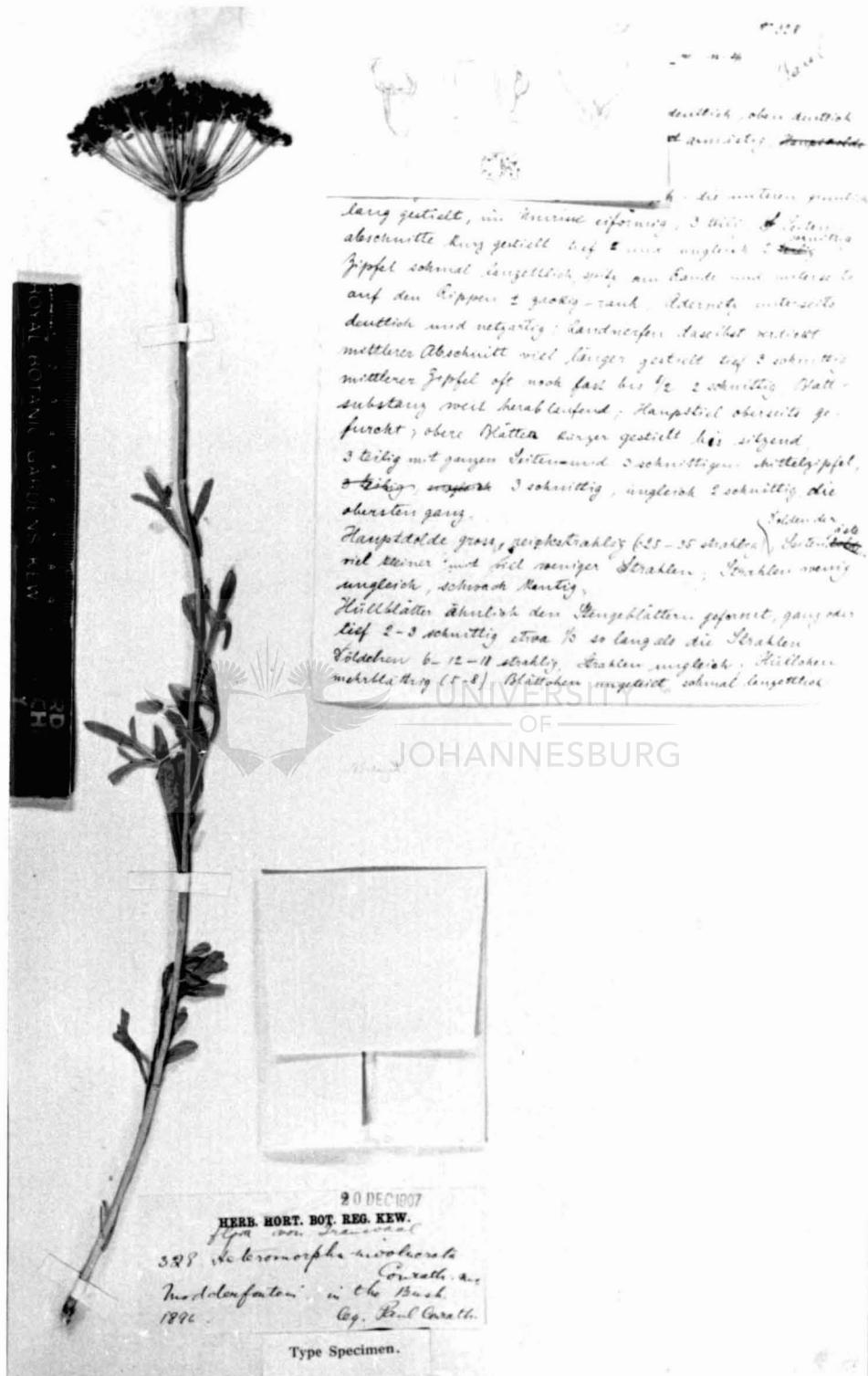
Since the K specimen has a detailed description in Conrath's handwriting, this specimen is selected as lectotype. An ambiguous note in parentheses cites *Wilms* 563 (Z!) from Transvaal, near Lydenburg (Figure 7.19), and *Wilms* 563b from Transvaal, near Pretoria, Rensburg's Farm as "The same plant.... - Otto Stapf."



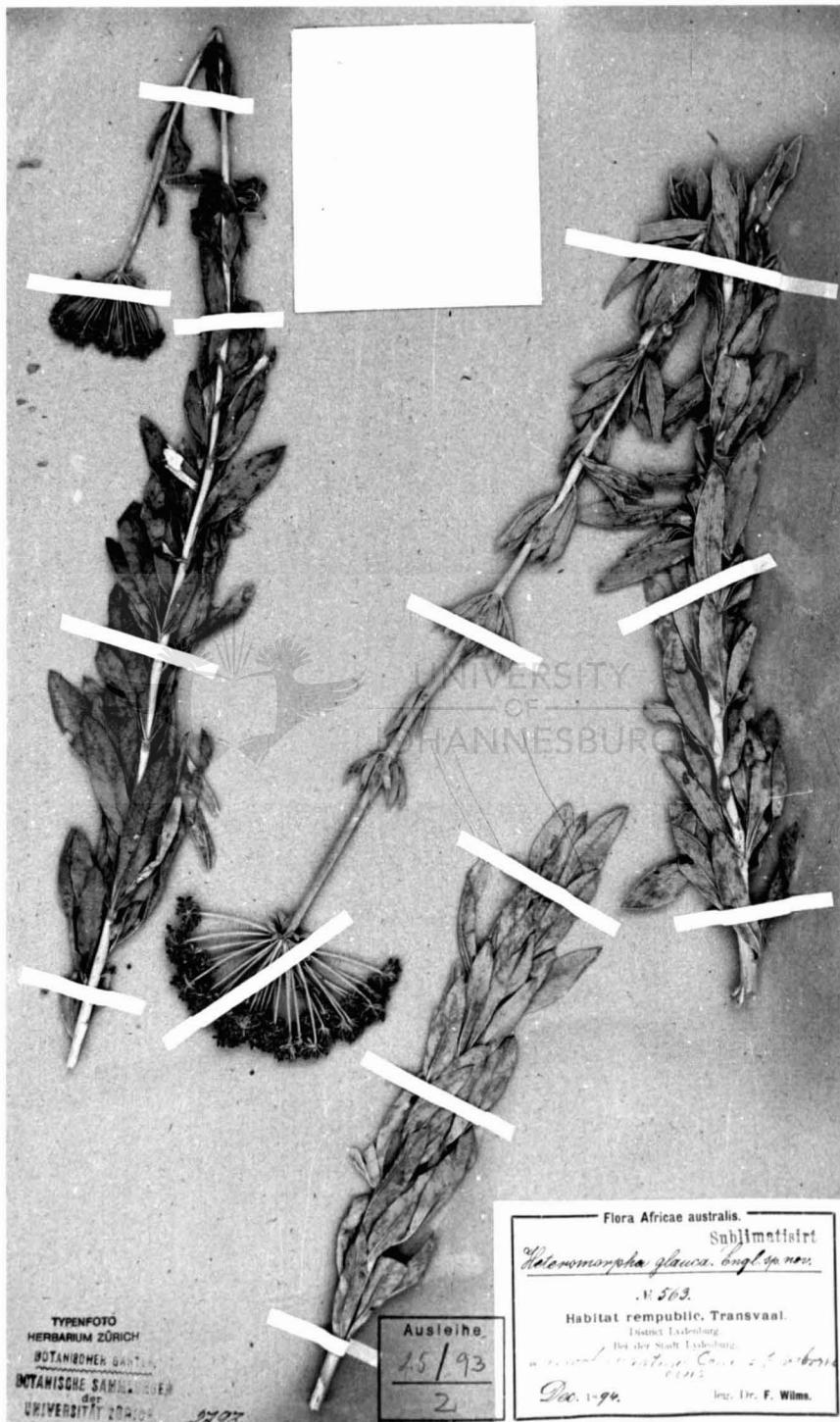
*Heteromorpha glauca* [Engl. nom. nud.; H. Wolff in Planzenr. Heft 43: 193 (1910), nom. nud. in syn.] Lemesle in Ann. Sci. Nat. Ser. 10, 8: 67 (1926); Burtt-Davy, Kew Bull. 4: 174 (1908).

According to Burtt (1991) the name *H. glauca* was validated by Lemesle's statement regarding anatomical differences between *H. glauca* and *H. arborescens*, and is based on *Wilms* 563 (Figure 7.19), distributed under this name by Engler (G; Z!).

*Heteromorpha kassneri* H. Wolff in Engl. Bot. Jahrb. 57: 226 (1921); Cannon in Fl. Zambeziaca 4: 581 (1978). Type (Figure 7.20): Belgian Congo [Zaire], Oberes Katanga: Luende, Kassner 2490 (K, lecto., photo!, here designated; B†?).



**Figure 7.18** The lectotype of *Heteromorpha involucrata* Conrath in Kew (K).



**Figure 7.19** The original specimen on which the name *Heteromorpha glauca* Engl. ex Lemesle was based, in Zürich herbarium (Z).



**Figure 7.20** The lectotype of *Heteromorpha kassneri* H. Wolff in Kew herbarium (K).

Since the holotype was not found, and was presumably destroyed in B, I select the K specimen as lectotype, as this is the only isotype available.

*Heteromorpha stolzii* H. Wolff in Engl. Bot. Jahrb. 57: 225 (1921), *synon. nov.* Type: Nördliches Nyassaland - Ukinga-Berge: Mwakalila-Landschaft [Mwakaleli], 2400 m ü. M., 19 Julie 1913, Stolz 2086 (B†?); Nyassa Hochland - Station Kyimbila, 1800 m, 1912, Stolz 2086 (Z, lecto.!, here designated--Figure 7.21; B!; G!; L!; MO!; PRE!; S!; SAM!).

No type with the original locality description was found, and is presumed to have been destroyed in B. All isotypes seen merely give the following details: Nyassa Hochland - Station Kyimbila, 1800 m, 1912, thus obviously a different collection!

Since the Zürich specimen has good leaves and fruit, I select this specimen as lectotype. The specimen in BM! is excluded as isotype. It is certainly not the same plant and is here identified as *H. arborescens* var. *trifoliata*.

#### Description

Suffrutex to woody shrub, 0,4--1,8 m tall. Stems simple or weakly branched; smooth to longitudinally grooved, glabrous to pilose. Pith variable in thickness. Bark absent or weakly developed. Leaves with a maximum length of 47--285 mm, distinctly petiolate to subsessile, petioles 0,5--94 mm long,

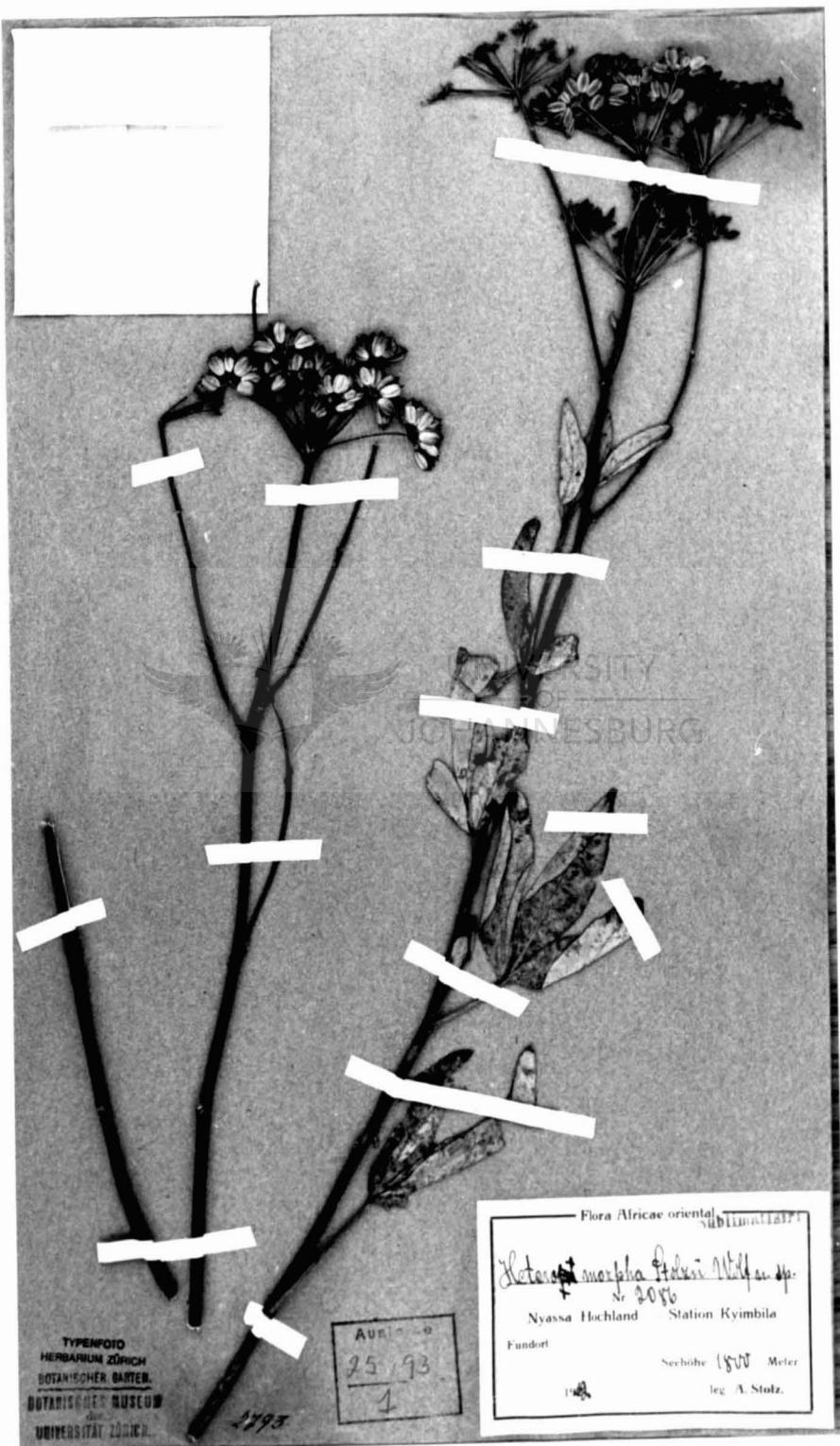


Figure 7.21 The lectotype of *H. stolzii* H. Wolff in Zürich herbarium (Z).

semiterete, rarely terete, usually widely or deeply sulcate, often carinate, glabrous to pilose; outline variable, trisect to pinnately and/or pedately compound, or bipinnatifid, terminal segment often bi- or tripartite. Incision usually decursive, second order incision never complete. *Pinnae* elliptic to very narrowly elliptic, ovate or obovate; apex acute to obtuse or rounded; margins entire or somewhat crenulate, papillate to ciliolate; base attenuate to cuneate; with a maximum length of 35--65 mm, 5--30 mm wide; at least abaxial and/or adaxial midrib and margins usually pilose, rarely glabrous, some trichomes, often clustered, set on low undulations or slight to pronounced tubercles, trichomes usually conical. *Inflorescence* a single compound umbel or a lax panicle of few to numerous compound umbels, bracts often reduced in size; main florescence of (16--)22--68 rays, 25--42(--75) mm long and (8--)13--24(--30) raylets, 2--6(--10) mm long, often larger than the lateral umbels. *Involucral bracts* small to broad and conspicuous (usually more than two foliose bracts), then sometimes dissected. *Petals* cream-coloured to greenish yellow, higher than, or as high as broad, abaxial surface often with short, conical or cylindrical trichomes. *Stylopodium* sometimes sparsely pilose at the rim, or at the bases of the styles. *Fruit* glabrous or usually lightly pilose, oval to broadly ovoid, 3--7(--9) mm long, 2--4(--5) wide, with well developed (half-winged) petaline ribs, secondary ribs occasionally present; vittae solitary [and conspicuous] in the valleculae, two on the commissure, occasional small vittae also not infrequently occurring in the tips of the ribs or part way along them. *Chromosome number:* 2n=22.

*Diagnostic characters.* Distinguished from *H. arborescens* by pilose leaves, which are usually pilose on the abaxial and/or adaxial midrib and margins. Some trichomes, often clustered, are set on low undulations or slight to pronounced tubercles (Figure 3.20). If all the vegetative parts are glabrous, then the terminal florescence is usually larger than the lateral umbels, with more than 25 stout rays. Two or more large foliose, sometimes dissected, involucral bracts are present (usually more than two in glabrous forms). *H. involucrata* is similar to *H. pubescens*, but lacks the filamentous trichomes, and has only six regular vittae surrounding the seed.

*Wilms 563 (Z)* has occasional nodes with a verticillate arrangement of four leaves. These may in fact be bracts, since they appear to be situated at the base of the peduncle, thus signifying the start of the reproductive growth phase.

*Distribution and ecology.* *H. involucrata* is found in Central Africa and has been recorded from Zambia, Malawi and northern Mozambique, adjacent regions of Zaire and Tanzania, and from the central and northern regions of Zimbabwe. Further south, it occurs in the south eastern Transvaal, Swaziland, and northern Zululand (Figure 7.22). Townsend (1989) describes the habitat in East Africa as "Almost invariably in rough upland grassland and pasture, also streamside bushland". The same could be said for the rest of its distribution in southern Africa.

There is a single record from Angola, Kers 3491 (S), but it is possible that this is merely an atypical form of *H. gossweileri*.

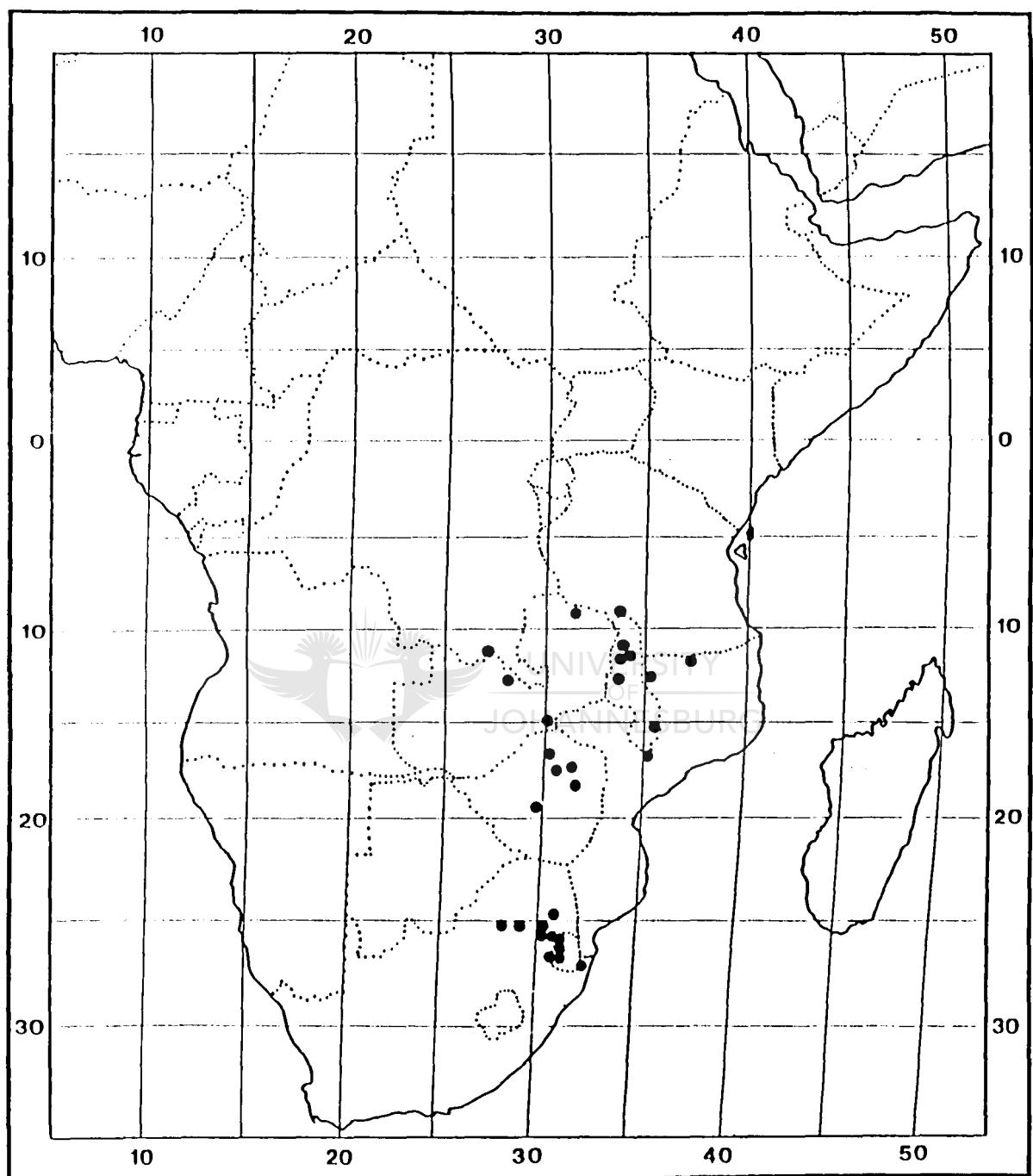


Figure 7.22 The known geographical distribution of *Heteromorpha involucrata*.

*Infraspecific variation.* This species is extremely variable, perhaps more so than is usually perceived of *H. arborescens*. As with *H. arborescens*, this species complex can be considered a paraphyletic assemblage until convincing autapomorphies are found. Several forms can be recognized, sometimes corresponding to geographical regions. In order to maintain nomenclatural stability, the variation is best described informally until it is better known.

The typical form of the species (South Africa and Swaziland), is extremely variable in leaf shape and vestiture. *Braun 614* (PRE) from Swaziland, is totally glabrous and has wide trifoliolate leaves with obovate leaflets. Although the stem on this specimen is quite woody, the leathery leaves and widely grooved petiole distinguish it from *H. arborescens*. The typical form generally has more rays (up to 68) than most central African forms (17 to 24, rarely 34). It is limited to rocky, well-drained, upland grassland habitats.

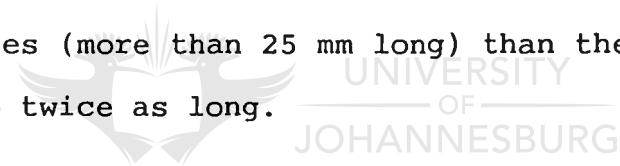
The '*H. kassneri*' form (Figure 7.20) has robust leaves (Figure 3.16: 7.2), which are pinnate with well dissected pinnae. Cylindric multicellular trichomes (Figure 3.21 & 3.22) are present on both abaxial and adaxial midribs, along the margins and on the adaxial surface. The abaxial leaf stomatal density is always more than 200 per  $\text{mm}^2$ , whereas in the typical form it varies between 106 per  $\text{mm}^2$  and 167 per  $\text{mm}^2$ , rarely up to 218 per  $\text{mm}^2$ . This form is otherwise similar to the typical form, also with numerous (25 to 41) rays in the terminal umbel. It occurs in Zaire, Malawi and Zambia.

The '*H. stolzii*' form has been overlooked by Townsend (1985, 1989), and was tentatively placed in synonymy under *H. trifoliata* by Cannon (1978). The characters of the isotypes of *H. stolzii* seem to overlap with those of the typical *H. involucrata* from the Lydenburg district (South Africa) and Swaziland, in the coriaceous leaves and large terminal umbels.

Townsend (1985) does refer to the *H. trifoliata*-complex as being most difficult in central Africa, and mentions suffrutescent forms occurring in that region. Brenan (1954), reported what he considered an aberrant form of *H. trifoliata* from the Nchisi mountain in Malawi, with simple and usually solitary stems. Plants are 1 to 2 m high, with puberulous stems and leaves. He considered this form [voucher: Brass 16926 (MO)] worthy of separation once the complex was better known. Examination of central African material has shown that this 'Malawi' form has a distinct distributional centre in Malawi and Mozambique. Plants referable to this form have also been found in the Lydenburg district of South Africa [compare Strey 3808 (PRE)]. These plants lack the characteristic pilose abaxial midrib of *H. involucrata*, but the trichomes are conical or broad-based, often slanted toward the apex, sometimes set on tubercles, as opposed to the perpendicular cylindric trichomes found in *H. arborescens*. Some specimens also have the terminal umbel much larger than the lateral umbels [Torré & Paiva 11897 (PRE) from Mozambique], although this is not a constant character for the species. Most specimens of this particular form have a synflorescence similar to that of *H. arborescens*. The possibility of introgression with *H. arborescens* cannot be

excluded, and there are forms of the latter in southern Tanzania which are atypical in appearance, and have pilose abaxial midribs.

Specimens from Zimbabwe have umbels with long rays and fruit with pronounced wings, leaves with somewhat irregular trichomes, some of which are raised on slight tubercles. These tuberculate trichomes occur on the abaxial surface as well. This 'Zimbabwe' form seems to be a natural geographical group differing from the 'Malawi' form in the presence of abaxial midrib vestiture, although one specimen from the Harare district, Schneller 140 (Z), is intermediate in that it has slightly pilose midribs on both leaf surfaces. Both this form and the 'Malawi' form have longer petioles (more than 25 mm long) than the other forms, and raylets up to twice as long.



Kers 3491 (S) from Angola has been labelled *H. gossweileri*, but despite being the only representative in an area normally occupied by *H. gossweileri*, has broader leaflets, trichomes and stomatal characters more typical of the 'Zimbabwe' form of *H. involucrata*. It also lacks the prominent petaline wings typical of *H. gossweileri*.

The classification of all these forms under *H. involucrata* is tentative, given the limitations of herbarium specimens, and is intended as a provisional basis for further clarification through good field observation of habit, noting height, degree of branching of vegetative stems, and fire or disturbance history. The collection of more fruiting material across the

distribution range could confirm my suspicion that the plants reported as forms of *H. arborescens* with slender rays up to 50 mm long from Malawi, Zambia and Zimbabwe by Townsend (1985) are indeed better classified under *H. involucrata*. Alternately, these may turn out to be one or more distinct taxa, which would thereby allow for a closer circumscription of this species as a whole.

### Specimens examined

**TANZANIA**---0933: Makete, Kitulo plateau between Kitulo and Matamba (-BB), Lovett & Congdon 1861 (MO). Nyassa Hochland, Station Kyimbila, 1800 m (-BB), Stoltz 2086 (G, L, MO, PRE, S, SAM, Z).

**ZAIRE**---1127: Elizabethville (-CB), Quarré 5919 (PRE, x3).  
[Grid reference not found: Oberes Katanga, Luende, Kassner 2490 (K)]

**ZAMBIA**: Solwezi district, 20 km NW of Kansanshi, Drummond & Rutherford-Smith 7058 (PRE); 100--129 km E of Lusaka, Chakwenga headwaters, Robinson 6229 (B); Mbala district, Zombe border, Sanane 449 (B); Kitwe, Granite outcrop, Mutimushi 32 (B).

**MALAWI**---1033: Mpore, 2 miles E of Nyika (-DD), Phillips 1295 (MO).  
---1133: Nkhata Bay district, Kawalazi Estate, 640 m (-CB), La Croix 3770 (MO, PRE); N. Province, 5 miles W. of Mzuzu, grassland, 4200 ft (-DB) Phillips 1840 (MO); N. Province, Mzimba district, Mzuzu, Marymount (-DB), Pawek 5318, 6525, 8237 (MO).  
---1134: N province, Nkhata Bay, White Father's Beach (-CB), Pawek 8841, 8858 (MO).

---1233: Central region, Ntchisi district, Forest Reserve (-DD), Banda & Kaunda 2253 (PRE); Kota-Kota district, Nchisi mountain (-DD), Brass 16926 (MO).

---1535: Machinga district, Ukasi stream, Chindusi hills, Liwonde Forest Reserve (-AB), Salubeni & Kaunda 3818 (MO); Zomba (-BC), Msiska 40 (MO).  
---1635: Nsanje, Malawi Forest Reserve N of Chididi Mission (-CC), Banda & Balaka 1988 (MO).

**MOZAMBIQUE**---1137: Cabo Delgado, Macondes, andados 5 km de Chamba para Negomano (-CA), Torre & Paiva 11897 (PRE).

---1335: Niassa district (Fl.Z.), Vila Cabral, encosta sul da serra de Massangulo (-CB), Torre & Paiva 10763 (PRE).

**ANGOLA**---1413: Mocamedes district, Chela mountain, 4 miles before Huila district on road from Vila Arriaga to Sa da Bandeira (-CD), Kers 3491 (S).

**ZIMBABWE---1630** (Lomagundi): Mangula [Mhangura], Farm Whindale (-CC?), Jacobsen 2891 (PRE); Mangula [Mhangura], Farm Robbsdale (-CC?), Jacobsen 2144 (PRE).

---1730 (Sinoia [Chihoyi]): Central Umvukwe range, near Chrome Mine area, near Toroshanga [Mutorashanga] Pass (-BB), Rodin 4414 (PRE, MO); Mazoe (-BD), Eyles 279 (BOL).

[Grid reference not found: (c. 1730) Umvukwes, 5200 ft, Horseshoe mine, Leach & Brunton 9860 (MO)]

---1731 (Salisbury [Harare]): Bindura, Kerry farm, Shashi mountains (-AD), Mogg 34213 (PRE).

[Grid reference not found: Salisbury [Harare], Twentydales road, Rutherford-Smith 484 (MO)]

---1831 (Marandellas [Marondera]): Marandellas [Marondera] (-BA), Cosby 709 (PRE).

---1929 (Gwelo [Gweru]): Gwelo [Gweru] (-BD), Biegel 4206 (NU); Mwanza, Gwelo village (-BD?), Seyani 668 (MO); 8 miles S of Gwelo [Gweru] (-DB), Biegel 2003 (MO).

**SWAZILAND---2531** (Komatipoort): Havelock, Pigg's Peak (-CC), Compton 28738, 30641 (NBG, NH); Havelock Forest margin (-CC), Compton 29988 (NBG).

---2631 (Mbabane): Malolotja Nature Reserve, Majolomba block (-AA), Braun 614 (PRE); Ngwenya hills (-AA), Compton 26531 (NH, PRE); Hhoho, 20 km from Pigg's Peak, Nkomati [Komat] Bridge (-AA), Germishuizen 5974 (PRE); Compton 26942 (NBG, 2 sheets); Hlotwani hills (-AA), Compton 26501 (NBG); Malandela (-AB), Compton 31892 (NBG); Mbeluzi valley (-AC), Compton 25004 (NBG, NH); Usutu Forests (-CA), Compton 25476 (NBG); Hlatikula (-CD), Stewart 128 (SAM).

[Grid reference not found: Ukutula, Compton 25017 (NBG); Mpalaeni swamp, Compton 32267 (NBG, NH)]

**SOUTH AFRICA** (with included territories)---**2430** (Pilgrim's Rest): Ohrigstad Natuurreervaat, O van dam (-DC), Theron 3463 (JRAU, RUH); 25,8 km from Lydenburg to Ohrigstad (-DC), B-E. Van Wyk 3045, Winter 61 (JRAU); Frankfort Mine valley (-DD), Matthews 769 (PRE).

---**2529** (Witbank): Middelburg district, Buffelsvlei (-AA), Rudatis 243 (STE).

---**2530** (Lydenburg): Farm Nooitgedacht, Erasmus Pass (-AB), Strey 3808 (PRE); Sabie valley, N slope (-BB), Galpin s.n. (BOL); Houtboschloop road between Sudwala Cave turnoff and Rosehaugh (-BC), Hilliard & Burtt 14217 (NU, PRE); 2 km W of school at Weltevrede (-BC), Winter 67 (JRAU); Rosehaugh, swamp, paddock (-BD), Mogg 13963 (PRE); Farm 'Waterval' Palmers, near Spitzkop (-CA), Burtt-Davy 1641 (PRE); Waterval boven, 6 km on Slaaihoek road, Rocky Drift, Private Nature Reserve (-CB), Germishuizen 5018 (PRE); Nelspruit to Kaapsche Hoop, old road (-DB), Hilliard & Burtt 14287 (NU).

---**2531** (Komatipoort): Barberton, Saddleback Pass (-CC), Venter 1491 (PRE); 5 km from Barberton, Saddleback Pass (-CC), Winter 68 (JRAU); Barberton (-CC), Van Dam sub TRV 21116 (PRE); Barberton, 3000 ft (-CC), Brayshaw 166 (NU).

---**2628** (Johannesburg): Modderfontein, 1896 (-AA), Conrath 328 (K, photo!).

---**2630** (Carolina): Lochiel (-BB), Rogers 11485 (GRA); Amsterdam, 3 km on Nerston road (-DA), A.E. v. Wyk 2255 (PRE).

---**2732** (Ubombo): Ingwavuma (-AA), Gerstner 3763 (NH, PRE).

Precise locality unknown: Umvukwes, Bayliss 10686 (MO, PRE).

7.3.4. Species excluded (For reasons see sections 3.2.3.1; 4.3.1; 4.3.3 and Winter *et al.* 1993)

1. *H. laxiflora* (Baker) Humb.

var. <i>altilcola</i> Humb.	<i>Humbert &amp; Capuron</i> 25031 (P)
var. <i>laxiflora</i>	<i>De la Bâthie</i> 15168 (P) <i>Schatz</i> 2655 (MO)

2. *H. marojejyensis* Humb.

<i>Humbert</i> 22710 (P)
<i>Miller &amp; Lowry</i> 4160 (MO)

*Herbier de l'Alaotra* 3475 (MO)

3. *H. tsaratananensis* Humb.

<i>De la Bâthie</i> 6806 (P)
<i>Humbert</i> 18374 (P)
<i>De la Bâthie</i> 16411 (P)

4. *H. coursii* (Baker) Humb.

<i>Humbert et al.</i> 24702 (P)
<i>Herbier de l'Alaotra</i> 3825 (MO)

5. *H. betsileensis* Humb.

<i>Humbert</i> 3792 (P)
<i>De la Bâthie</i> 6815 (P)

6. *H. andringitrensis* Humb.

<i>De la Bâthie</i> 13741 (P)
<i>De la Bâthie</i> 6809 (P)
<i>De la Bâthie</i> 14430 (P)

7. *H. andohahelensis* Humb.      *Humbert 13654 (P)*

*Humbert 6466 (P)*

*Humbert 6192 (P)*

8. *H. bojeriana* (Baker) Humb.      *Bojer s.n. (P)*

*Dorr et al. 2889 (MO)*

*Catat 332 (P)*

9. *H. scandens* J.J. Clark in Kew Bull. 1911, 229 (1911) ==

*Pseudocarum eminii* (Engl.) Wolff.



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