Bothalia 24,2: 187–194 (1994)

The taxonomic value of epidermal characters in the leaf of *Heteromorpha* and some related genera (Apiaceae)

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Keywords: Apiaceae, epidermis, *Heteromorpha*, *Polemannia*, *Polemanniopsis*, stomata, taxonomy, trichomes, vestiture

ABSTRACT

All 17 species of *Heteromorpha* Cham. & Schltdl. (sensu Humbert 1956), all three species of *Polemannia* Eckl. & Zeyh. and the monotypic *Polemanniopsis* B.L. Burtt were investigated for leaf epidermal characters. Stomatal type was anomocytic, with an exception in only one Madagascar species, *H. betsileensis*. The distribution and density of stomata (on both leaf surfaces) are diagnostic for some species. The number, size and outline of normal epidermal cells are different in juvenile and adult leaves and these differences vary between species. Seven trichome types are recognized which, when combined with dispersion pattern, also serve to characterise the various species and forms.

UITTREKSEL

Al 17 spesies van *Heteromorpha* Cham. & Schltdl. (sensu Humbert 1956), al drie spesies van *Polemannia* Eckl. & Zeyh. en die monotipiese *Polemanniopsis* B.L. Burtt se blaar-epidermale kenmerke is ondersoek. Die stomata-tipe was anomosities, met 'n enkele uitsondering by een Madagassiese spesie, *H. betsileensis*. Die verspreiding en digtheid van stomata (op beide oppervlakke) is diagnosties vir sommige spesies. Die aantal, grootte en buitelyn van gewone epidermisselle verskil by jeug- en volwasse blare en hierdie verskille varieer tussen spesies. Sewe trigoomtipes word onderskei wat, saam met verspreidingspatroon, kenmerkend is vir die verskillende spesies en vorme.

INTRODUCTION

Heteromorpha Cham. & Schltdl. (*sensu stricto*) is a genus of trees, shrubs or suffrutices occurring throughout most of temperate and subtropical Africa. Seven species are restricted to the African continent and Yemen. Humbert (1956) broadened the generic concept to include eight Madagascar species. The African contingent shares the woody habit with the related *Polemannia* Eckl. & Zeyh. from the Drakensberg region, and fruit characters with the Western and Northern Cape genus *Polemanniopsis* B.L. Burtt (Burtt 1988), which have been included here as potential outgroups.

Most species 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 to distinguish *H. trifoliata* from species with basally tuberculate trichomes, and to characterise *H. papillosa* and *H. gossweileri* (Townsend 1985, 1989). Epidermal characters are therefore clearly of taxonomic value in *Heteromorpha*, especially when the paucity of information on other characters is considered.

Stomatal type has been recorded for only one of the woody African Apiaceae, namely *H. arborescens*, which was found to be anomocytic (Guyot 1971).

This investigation forms part of a complete revision of the genus *Heteromorpha*. The formal taxonomic treatment will be published elsewhere.

MATERIALS AND METHODS

Leaves from FAA material or from herbarium specimens of all known species of *Heteromorpha sensu lato* (including the Madagascan 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.

Specimens examined:

Heteromorpha (African species)

1A *involucrata* Conrath, typical form, suffrutex, Transvaal, Swaziland & Natal, *Winter 61, 68* (JRAU); *Gerstner 3763* (PRE).

1B *involucrata* Conrath, 'kassneri' form, suffrutex, Malawi & Zambia, *Quarré 5919* (PRE); *Phillips 1295* (MO).

1C *involucrata* Conrath, 'Zimbabwe' form, suffrutex or weak shrub, Zimbabwe & Angola, *Jacobsen 2891* (PRE); *Bayliss 10686* (PRE); *Kers 3491* (S).

1D *involucrata* Conrath, 'Malawi' form, weak shrub, Malawi & SA, *Torré & Paiva 11897* (PRE); *Winter 67* (JRAU).

2 *pubescens* Burtt Davy, suffrutex or weak shrub, Transvaal, *Winter 66, 69* (JRAU); *Junod 143* (PRE).

3 *papillosa* C.C. Towns., well-branched shrub, Namibia, *Merxmüller & Giess 28004* (PRE); *Dinter 3499* (PRE); *Hanekom 135* (WIN).

4 *gossweileri* (Norman) Norman, suffrutex, Angola, *Milne-Redhead 3981* (PRE); *Mendes 2069* (PRE); *Hundt 727* (PRE); *Hooper & Townsend 325* (K).

5 *stenophylla* Wolff ex Schinz, suffrutex, Namibia, Angola & Malawi, *Le Roux 295* (PRE); *Giess 8602* (PRE); *Dinter 5487* (PRE).

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MS. received: 1993-02-09.

6A *arborescens* (Spreng.) Cham. & Schltdl., tree, Cape, *Van Wyk 3313* (JRAU); *Vlok 2633* (JRAU); *Ward 7538* (PRE).

6B *trifoliata* (Wendl.) Eckl. & Zeyh., typical form, tree, Eastern Cape to Arabian Peninsula, *Brink 128* (PRE); *Winter 71* (JRAU); *De Wilde 6041* (K); *Semsei 4122* (PRE); *Stolz 24699* (PRE); *Pope & Muller 2075* (PRE).

6C *trifoliata* (Wendl.) Eckl. & Zeyh., frutescent form, shrub, Natal to Malawi, *Winter 51, 57* (JRAU); *Rogers 22197* (PRE).

6D *trifoliata* (Wendl.) Eckl. & Zeyh., W African form, suffrutex, *Letouzey 5680* (K); *Meurillon 1396* (K); *Milne-Redhead 762* (K).

7 *transvaalensis* Schltr. & Wolff, suffrutex, *Winter 50, 52, 55* (JRAU).

Heteromorpha (Madagascan 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 *marojejyensis* 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 shrubs, NW Cape)

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

Polemannia (woody shrubs, Drakensberg)

P1 *montana* Schlecht. & Wolff, *Smook 7181* (PRE); *Schmitz 9077* (PRE); *Jacobs 3097* (PRE).

P2 *simplicior* Hilliard & B.L. Burtt, *Hoever 2016* (PRE); *Pole Evans 19654H* (PRE); *Pentz sub PRE 48118* (PRE).

P3 *grossulariifolia* Eckl. & Zeyh., *Ratray 35* (PRE); *Giffen 1296* (PRE); *Galpin 8359* (PRE).

Mean stomatal densities were determined under the light microscope, by a minimum of six counts per specimen 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.

After germinating seeds of five African species [*H. arborescens*, *H. trifoliata*, *H. involucrata*, *H. pubescens* and *H. transvaalensis*], juvenile leaves were available to investigate ontogenetic changes during leaf development. Trichome types were studied by SEM on one specimen of each taxon. To investigate the structure of each trichome type, mature leaves were embedded in glycol methacrylate (GMA) according to a modification (Tilney 1986) of the method of Feder & O'Brien (1968). Sections were obtained with a Porter Blum MT-1 ultramicrotome and stained according to the so-called periodic acid—Schiff/Toluidine Blue (PAS/TB) staining method. Drawings were done with the aid of a camera lucida attachment on a Zeiss compound light microscope. Vestiture (trichome distribution) was studied on several specimens with the aid of a dissecting stereomicroscope. The investigation was limited to the laminar region of the leaf.

RESULTS AND DISCUSSION

Five characters were chosen for analysis:

Stomatal apparatus

The stomatal apparatus proved difficult to interpret because cell boundaries were indistinct in the stomal region and because cells adjacent to the stomata differed superficially from the surrounding epidermal cells. The cuticula 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. Stomata are juxtaposed

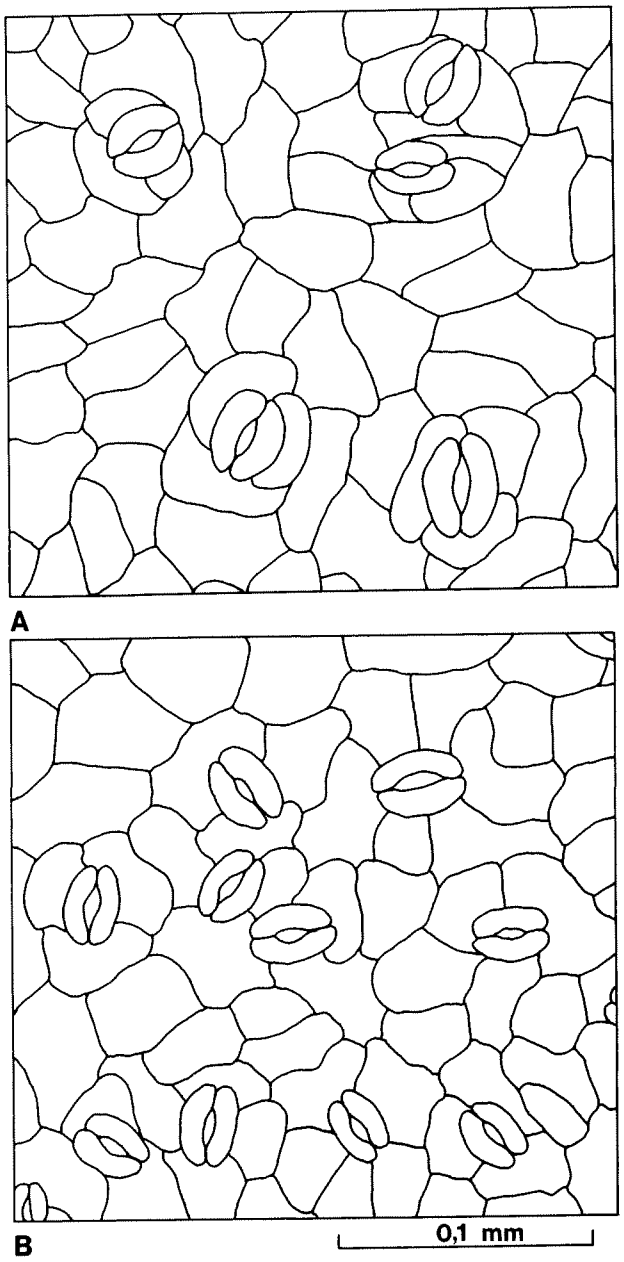

FIGURE 1.—Stomatal apparatus types in *Heteromorpha*. A, *H. betsileensis*: anisocytic type. B, *H. coursii*: anomocytic type.

in some instances, or separated by one cell only (Figure 1B), 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 our 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 related genera, all possess the anomocytic type stomatal apparatus (Figure 1B). 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 single exception, the Madagascan species *H. betsileensis*, has an anisocytic type stomatal apparatus (Figure 1A). The radial 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).

Stomatal dispersion

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

Four main patterns of stomatal dispersion over the adaxial surface were identified. Stomata are either absent, occur along margin and/or midrib only, occur mostly along margin and veins, or occur throughout the entire surface. These data are listed in Table 1. In the Madagascan 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 and *H. gossweileri* differ from the other African species in their stomatal dispersion pattern which is shared with all *Polemanniopsis* and *Polemannia* species, but with only two Madagascan species (*H. andohahelensis* and *H. bojeriana*). In *H. papillosa* this state co-occurs with states 2 and 3 of Table 1.

Stomatal distribution and density

The results of the stomatal density study are presented in Figure 2. The data show that the variation in this character is independent of habit and 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 2A), having values of around 110 per mm^2. Across *Heteromorpha*, most species have between 100 and 200 stomata per mm^2 on the abaxial surface. There are three Madagascan species with much higher values. These are *H. marojejyensis* (M2: mean = 279), *H. tsaratananensis* (M3: mean = 293) and *H. coursii* (M4: mean = 265).

In the African *Heteromorpha* group, notable outliers are H. *involucrata 'kassneri'* form (1B: mean = 229), *H. gossweileri* (4: mean = 220), and *H. stenophylla* (5: mean = 88). The West African form of *H. trifoliata—H. abyssinica sensu* Jacques-Félix (1970)—is clearly distinguishable from all the central African forms of *H. involucrata* (1B, 1C & 1D; means = 229, 131 & 119 respectively). Most species examined had none or virtually no adaxial stomata (Figure 2B), whereas *Polemannia* has on average just over 40 stomata per mm^2, and a relatively high variation per species. Adaxial stomata are rare (mean less than 5 per mm^2 or absent in most *Heteromorpha* species except *H. papillosa* (3: mean = 16), *H. gossweileri* (4: mean = 88), *H. stenophylla* (5: mean = 27), *H. andohahelensis* (M7: mean = 8) and *H. bojeriana* (M8: mean = 17).

Epidermal ontogeny

As the leaves develop from the juvenile to the mature stage, the proportion of stomata to normal epidermal cells (Figure 3) remains constant in *H. involucrata* and *H. pubescens*, whereas it decreases in both the typical and the frutescent forms of *H. trifoliata*. 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.

Trichome type

The variation in mature trichome types as well as their distribution is summarized in Table 1. Various types comprising seven character states were recognised and are shown in Figure 4 and Figure 5. The papillate type (Figures 4A; 5C2), 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 Madagascan group where only the filamentous, multicellular type is found in *H. betsileensis* alone, the African species show a high diversity of form.

Papillate trichomes, similar to those shown in Figure 4A and 5C, 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 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 5C) or with one (Figures 4C; 5A, B & E) or many (Figure 4E) trichomes of another type affixed apically. This condition was described by Townsend (1985) as papillose, and is characteristic of *H. pubescens* and most forms of *H. involucrata*. The term 'verruculose' used by Townsend (1985) to describe the vestiture in *H. gossweileri* suggests the simple tuberculate type of trichome (Figure 5C1). Although the SEM survey showed only the papillate type (Figure 4A), which does bear a superficial resemblance to the tuberculate type, light microscopy confirmed the presence of both types (Figure 5C).

The filamentous/filiform type (Figures 4E; 5E) is found only in *H. pubescens* and *H. betsileensis*, and in addition to distribution and density of hairs, characterizes these species. Short cylindrical hairs (Figures 4B; 5D) are char-

TABLE 1.—Epidermal character state distribution for leaves of *Heteromorpha*, *Polemannia*, and *Polemanniopsis*

Taxon	Adaxial stomatal dispersion				Trichomes: Type (character state)							Trichomes: Distribution						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Heteromorpha (African species)																		
involucrata																		
typical form	–	+	+	–	+	+	–	–	–	+	–	+	+	+	+/–	+	+	–
'kassneri' form	+	–	–	–	–	–	+	–	–	+	+	+	+	+	+	+	+	–
'Zimbabwe' form	–	–	+	–	–	+	+	–	–	+	–	+	+	+	+/–	+	–	–
'Malawi' form	+	–	–	–	–	+	+	–	–	+	–	+	+	+	–	R	–	–
pubescens	+	–	–	–	–	–	–	–	+	+	–	+	+	+	+	+	+	+
papillosa	–	+	+	+	–	–	–	+	–	–	–	B	B	–	–	–	–	–
gossweileri	–	–	–	+	+	–	–	–	–	+	–	+	+	+	–	+	–	–
stenophylla	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
arborescens	–	+	+	–	–	–	–	+	–	–	–	F	+	–	–	–	–	–
trifoliata																		
typical form	+	+	+	–	–	–	–	+	–	–	–	–/F	+/F	R	–	R	–	–
frutescent form	–	+	+	–	+	–	–	–	–	–	–	–/F	–/B	–	–	–	–	–
W African form	+	+	–	–	+	+	–	–	–	+	–	+	+	–	–	–	–	–
transvaalensis	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heteromorpha (Madagascan species)																		
laxiflora	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
marojejyensis	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
tsaratananensis	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
coursii	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
betsileensis	+	–	–	–	–	–	–	–	+	–	+	–	–	–	–	B	R	–
andringitrensis	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
andohahelensis	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
bojeriana	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polemanniopsis marlothii	–	–	–	+	+	–	–	–	–	–	–	+	–	–	–	–	–	–
Polemannia																		
montana	+	–	–	+	+	–	–	–	–	–	–	+	–	–	–	–	–	–
simplicior	–	–	–	+	+	–	–	–	–	–	–	+/–	+/–	–	–	–	–	–
grossularifolia	–	–	–	+	+	–	–	–	–	–	–	+/–	+	IMV	–	–	–	–

Adaxial stomatal distribution: 1, absent; 2, margin only; 3, mostly margin and 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.
+, present; –, absent; F, few; R, rare; B, basal only; IMV, intramarginal vein.

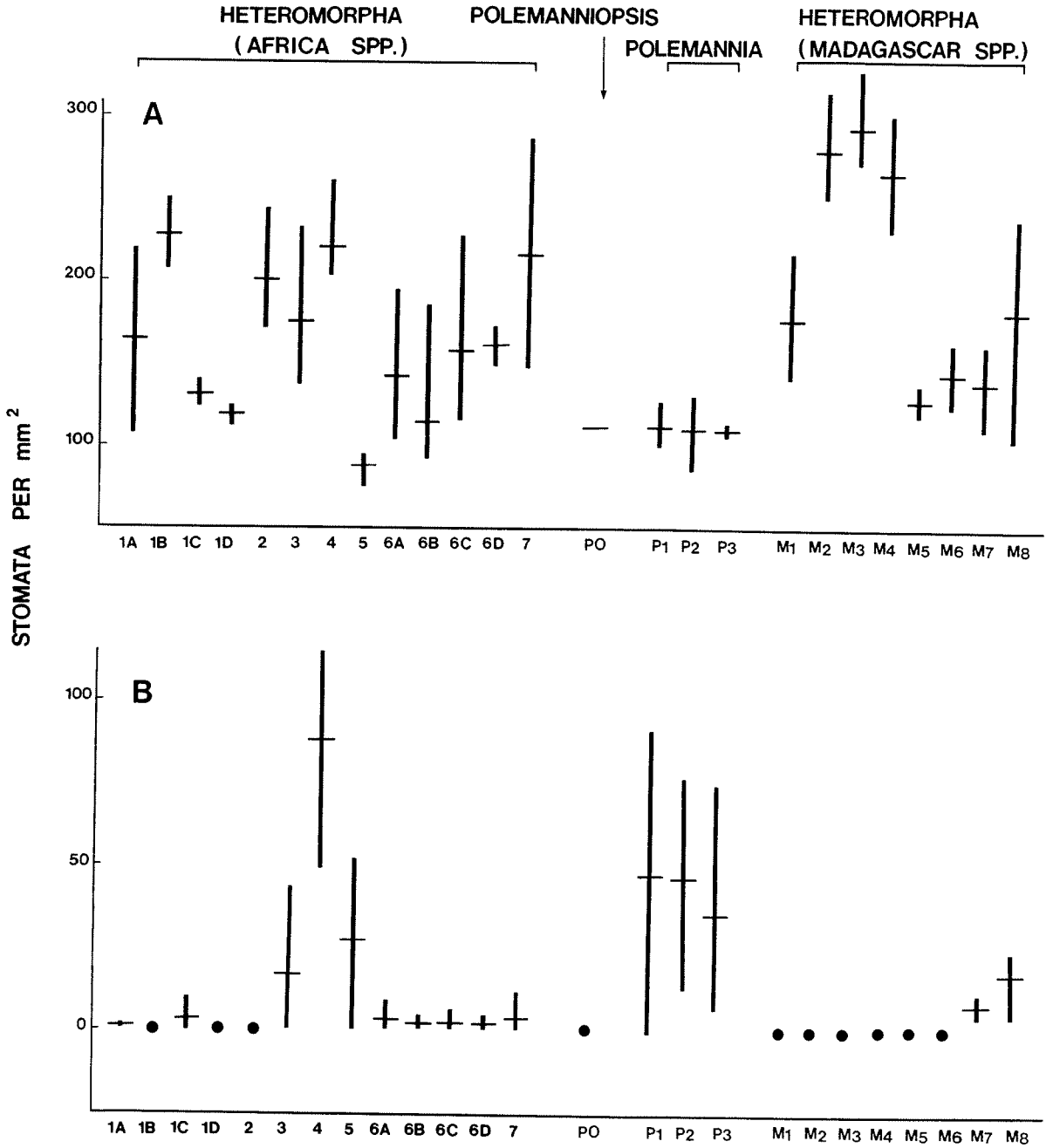

FIGURE 2.—A, abaxial density, and B, adaxial density of stomata in the genera *Heteromorpha, Polemanniopsis* and *Polemannia.* Range and mean values of specimens examined are indicated for each species/form; ●, absence of stomata; single values (n = 1) are denoted by a horizontal bar only. Taxa numbered and sampled as under Specimens examined.

acteristic of *H. arborescens* and *H. trifoliata*, but are also found in *H. papillosa*, the West African form of *H. trifoliata*, and occasionally (with other types) in some forms of *H. involucrata.*

Other types that can be identified are 1, a unicellular conical hair (Figures 4F; 5A), usually present in all forms of *H. involucrata*; and 2, a unicellular or multicellular long cylindrical hair (Figures 4D; 5B), present in the central African forms of *H. involucrata.*

Trichome distribution

Patterns of laminar distribution of trichomes are summarized in Table 1. Hairs, when present, are usually located at least on the adaxial midrib (Figure 6A). This is, however, only rarely the case in *H. involucrata*, where the abaxial midrib is usually more pilose than the adaxial midrib. The presence of trichomes along the leaf margin is the rule in *H. involucrata* (Figure 6B & C) and the exception in *H. trifoliata.* The West African form of *H. trifoliata* can be distinguished from the typical form by the presence of small tubercles, albeit sparse in some specimens, along the leaf margin. The leaf margin in typical *H. trifoliata* is usually glabrous, or if pubescent (commonly in young growth), then with short cylindrical hairs. Both forms have cylindrical trichomes along the adaxial midrib.

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

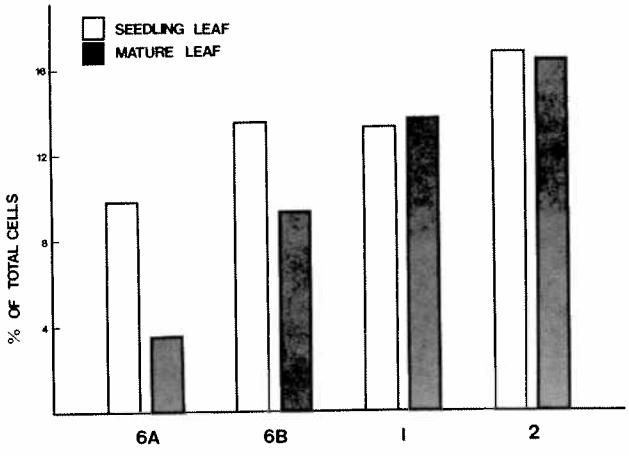

FIGURE 3.—Variation in leaf epidermal ontogeny in *Heteromorpha* indicated by differences in proportions of stomata to surrounding cells between seedlings and mature leaves. This is a function of the size and number of normal epidermal cells. 6B, *H. trifoliata*, typical form, *Winter 71*; 6C, *H. trifoliata*, frutescent form, *Winter 57*; 1, *H. involucrata*, *Winter 61*; 2, *H. pubescens*, *Winter*

morphological features in common with *H. involucrata*, and also shares the hairy abaxial midrib and presence of hairs on the adaxial secondary venation (Townsend 1985) in addition to those found elsewhere (Figure 6D).

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).

TAXONOMIC IMPLICATIONS

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 Madagascan species with any degree of vestiture on the laminar region. The occurrence of a second stomatal type could indicate a polyphyletic grouping of the Madagascan species, as this feature appears to be rather conservative, and is a potential character for tribal delimitation. A re-investigation of generic limits is suggested. Abaxial stomatal density is a potential grouping character within the Madagascan contingent, and could support the division of the group into two or more genera when these species are investigated further.

The typical and frutescent forms of *H. trifoliata*, for which seedlings were investigated, show an ontogenetic feature not present in *H. pubescens* and *H. involucrata*, namely a decrease in size of normal epidermal cells.

Three of the African species of *Heteromorpha* can be distinguished from the others on the basis of the uniformly dispersed adaxial stomata, a character which is shared with *Polemannia*, *Polemanniopsis* and two Madagascan species. This character may be logically correlated with

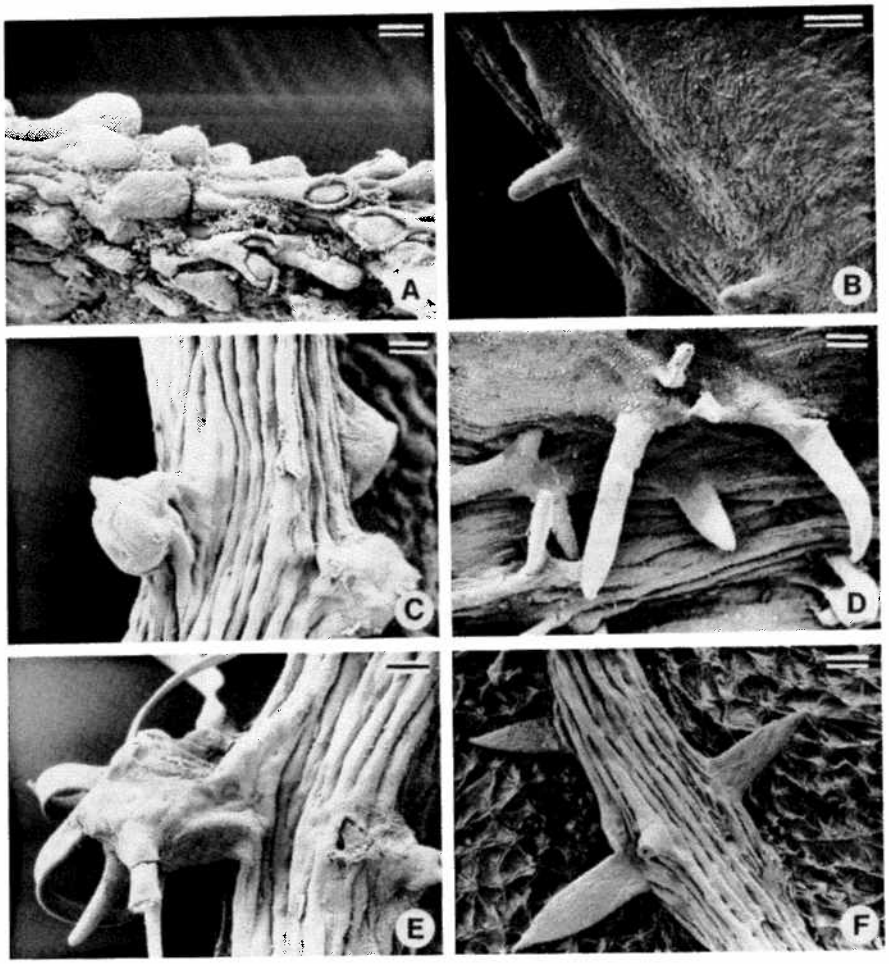

FIGURE 4.—Trichome types in *Heteromorpha sensu stricto*. A, *H. gossweileri*: papillate hairs, resembling juvenile state. B, West African form of *H. trifoliata*: short cylindrical hairs. C, *H. involucrata*, typical form: short conical hairs on tuberculate base. D, *H. involucrata*, '*kassneri*' form: multicellular long cylindrical hairs. E, *H. pubescens*: filamentous trichomes on tuberculate base. F, *H. involucrata*, 'Malawi' form: conical trichomes. Scale bars: 10 µm.

the high adaxial stomatal density in these species. *H. stenophylla*, previously considered to be merely a form of *H. trifoliata* (Schreiber 1967; Townsend 1985), is characterized by having less than 100 abaxial stomata per mm^2 and a substantially higher adaxial density than other African species.

Papillate trichomes seem to be the primitive state from which other states were derived. If the cell differentiation in the development of the other trichome types were investigated, this could lead to a better understanding of the phylogeny of *Heteromorpha*. The presence of small tubercles (although sparse in some specimens) along the leaf margin of the West African form of *H. trifoliata* raises some doubt as to its present taxonomic position, and suggests a closer affinity to the suffrutescent species *H. gossweileri*, *H. involucrata* and *H. pubescens*. The abaxial stomatal density distinguishes it from other suffrutescent types with which it may be confused, namely some central African forms of *H. involucrata*. The formal description of this taxon has been indicated by other evidence, and will be published elsewhere.

H. pubescens and most forms of *H. involucrata* share, along with other morphological characters, the distribution of trichomes along abaxial midrib and venation, but are distinguished on the basis of trichome type. Some forms of *H. involucrata* exhibit deviation from the typical condition of a hairy abaxial midrib. As currently circumscribed, this species shows as much if not more variation than the *H. arborescens* complex, and formal recognition of infraspecific taxa may be useful.

CONCLUSIONS

Anomocytic stomata and papillate trichomes are conservative characters at the generic level. The density and distribution of stomata are of limited value at this level, but show some pattern at the species level. *Heteromorpha sensu stricto* differs in the diversity of trichome types, and this character is useful to distinguish some of the species.

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 in *Heteromorpha* species is an important character and would seem to be correlated with epidermal features. Without attention to habit, other characters tend to be difficult to interpret.

ACKNOWLEDGEMENTS

Financial support from the Foundation for Research and Development is gratefully acknowledged. We would like to thank Dr W. Oldewage for his instruction and assistance with the SEM.

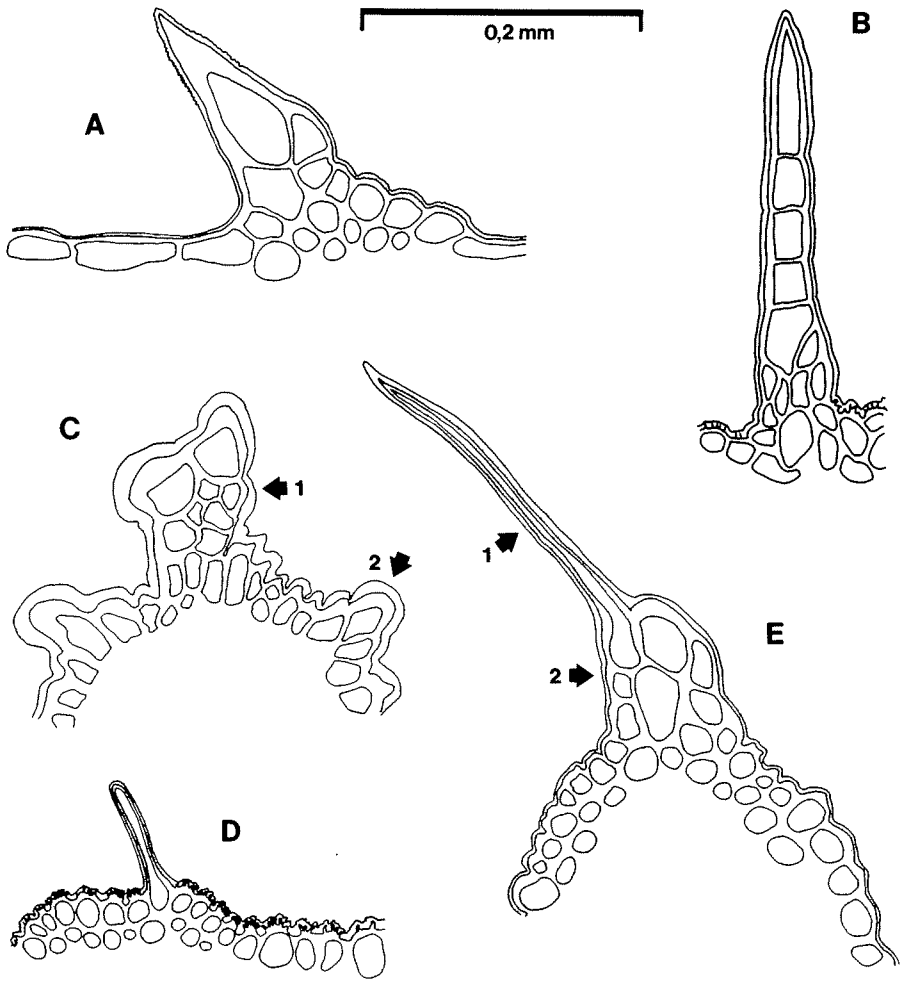

FIGURE 5.—Structure of trichome types, as seen in Figure 4, in leaf transverse sections of *Heteromorpha sensu stricto*. A, *H. involucrata*, typical form: conical trichome on a tuberculate base. B, *H. involucrata*, '*kassneri*' form: multicellular, long, cylindrical trichome. C, *H. gossweileri*: 1, tuberculate and 2, papillate trichomes. D, *H. trifoliata*, typical form: short, cylindrical trichomes. E, *H. pubescens*: filamentous trichomes on a tuberculate base.

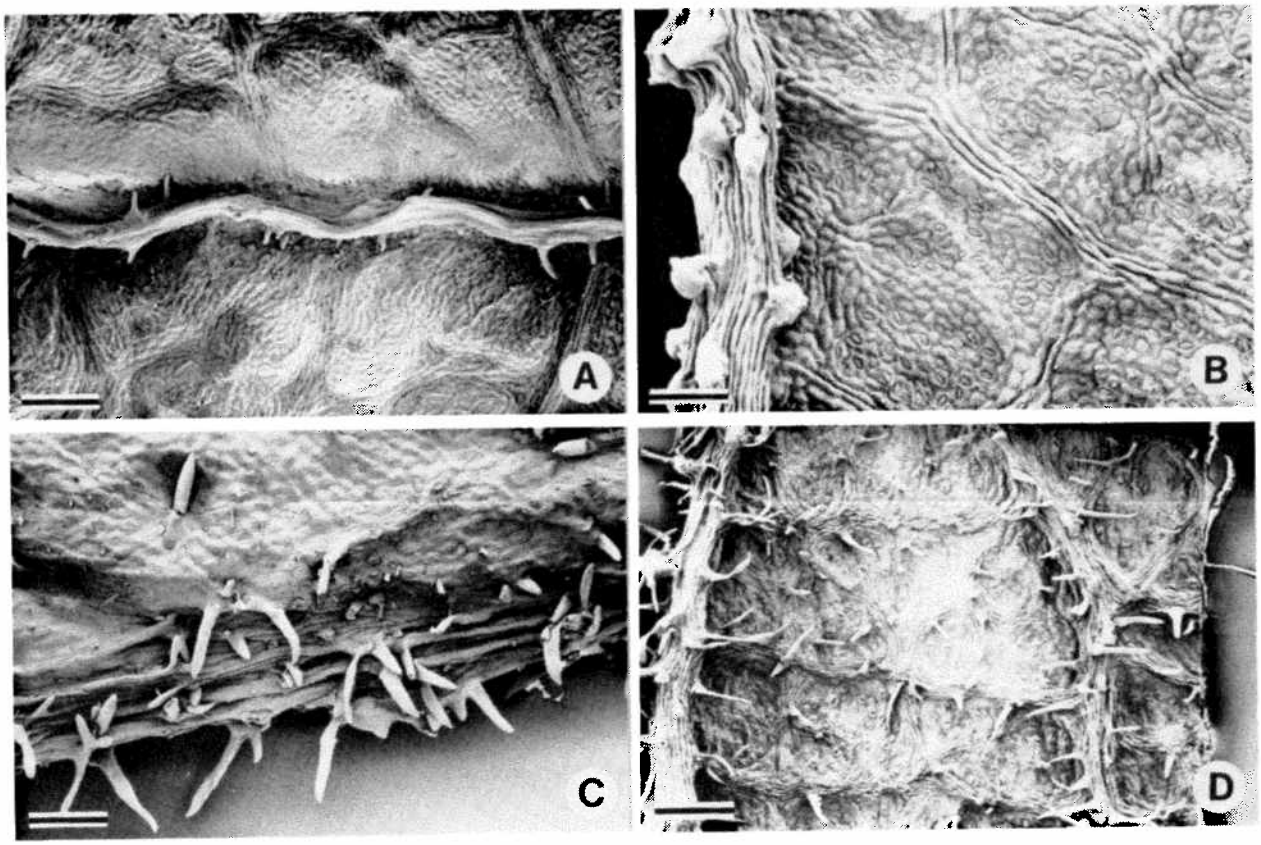

FIGURE 6.—Some examples of trichome distribution in *Heteromorpha sensu stricto*. A, *H. trifoliata*: adaxial midrib. B, *H. involucrata*: abaxial view, margin only. C, *H. involucrata*, '*kassneri*' form: margin and adaxial surface. D, *H. pubescens*: abaxial view, along entire venation. Scale bars: A–C, 50 µm; D, 100 µm.

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