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

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**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. betuleaemis*. 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 characterize the various species and forms.

**INTRODUCTION**

*Heteromorpha* Cham. & Schltdl. (sensu stricto) is a genus of trees, shrubs or suffrutesces 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).

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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)

1. *involucrata* Conrath, typical form, suffrutex, Transvaal, Swaziland & Natal, Winter 61 (JRAU); Gerstner 3763 (PRE).
2. *involucrata* Conrath, 'kassen' form, suffrutex, Malawi & Zambia, Quatré 5919 (PRE); Phillips 1295 (MO).
3. *involucrata* Conrath, 'Zimbabwe' form, suffrutex, Zimbabwe & Angola, Jacobsen 2891 (PRE); Badiss 10695 (PRE); Kers 3491 (S).
4. *involucrata* Conrath, 'Malawi' form, weak shrub, Malawi & SA, Torre & Paiva 11897 (PRE); Winter 67 (JRAU).
5. *pubescens* Burtt Davy, suffrutex or weak shrub, Transvaal, Winter 66, 69 (JRAU); Janod 145 (PRE).
6. *papillosa* C.C. Townsend, well-branched shrub, Namibia, Merxmüller & Giess 28004 (PRE); Dinter 3499 (PRE); Henekont 135 (WIN).
7. *gossweileri* (Norman) Norman, suffrutex, Angola, Milne-Redhead 3981 (PRE); Mendes 2069 (PRE); Hanf 727 (PRE); Hooper & Townsend 525 (K).
8. *stemonifolia* Wolff ex Schinz, suffrutex, Namibia, Angola & Malawi, Le Roux 395 (PRE); Giess 3802 (PRE); Dinter 5487 (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 stomatal 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
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* can species and the other genera stomata are either absent or dispersed randomly across the entire surface. *H. involucrata*—*H. abyssinica sensu Jacques-Félix* (1970)—is clearly distinguishable from the median 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 mm², and a relatively high variation per species. Adaxial stomata are rare (mean less than 5 per mm²) 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 *Polemannia* has on average just over 40 stomata per mm², and a relatively high variation per species. Adaxial stomata are rare (mean less than 5 per mm²) 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).

**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 recognized and are shown in Figure 4 and Figure 5. The papillate type (Figures 4A; 5C1), which is also the juvenile type, has a wide occurrence (present in all three genera), and is also the only type for *Polemannioptis* 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-
| Taxon                      | Adaxial stomatal dispersion | Type (character state) | Trichomes | Distribution |
|---------------------------|-----------------------------|------------------------|-----------|--------------|
| Heteromorpha (African species) |                             |                        |           |              |
| involucrata               |                             |                        |           |              |
| typical form              | -                           | +                      |           |              |
| 'kassneri' form           | +                           | -                      |           |              |
| 'Zimbabwe' form           | -                           | +                      |           |              |
| 'Malawi' form             | +                           | +                      |           |              |
| pubescens                 | +                           | +                      |           |              |
| papillosa                 | -                           | +                      |           |              |
| gossweilleri              | -                           | +                      |           |              |
| stenophylla               | -                           | +                      |           |              |
| arborecens                | +                           | +                      |           |              |
| trifoliata                | +                           | +                      |           |              |
| typical form              | -                           | -                      |           |              |
| frutescent form           | -                           | +                      |           |              |
| W African form            | +                           | +                      |           |              |
| transvaalensis            | +                           | +                      |           |              |
| Heteromorpha (Madagascan species) |                     |                        |           |              |
| laxiflora                 | +                           | -                      |           |              |
| marojejensis              | +                           | -                      |           |              |
| tsaratanaunensis          | +                           | -                      |           |              |
| coursii                   | +                           | -                      |           |              |
| betsileensis              | +                           | -                      |           |              |
| andringitrensis           | +                           | -                      |           |              |
| andohahelensis            | +                           | -                      |           |              |
| bojeriaca                 | +                           | -                      |           |              |
| Polemanniopsis marlothii  | -                           | -                      |           |              |
| Polemannia                |                             |                        |           |              |
| montana                   | +                           | -                      |           |              |
| simplicior                | +                           | -                      |           |              |
| grossularifolia           | +                           | -                      |           |              |

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 cylindrical; 8, short cylindrical; 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.
HETEROMORPHA POLEMANNIOPSIS HETEROMORPHA

**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.

characteristic 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
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 polyphylectic 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...
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.

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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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