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Leaf anatomy of the southern African species of *Brachylaena* (Asteraceae)

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Abstract. The leaf blade anatomy of *Brachylaena discolor* DC., *B. elliptica* (Thunb.) DC., *B. glabra* (L. f.) Druce, *B. huillensis* O. Hoffm., *B. ilicifolia* (Lam.) Phill. & Schweick., *B. neriifolia* (L.) R. Br., and *B. rotundata* S. Moore was studied by light and scanning-electron microscopy. The studied species can be divided into two groups on the bases of stomatal type and the presence or absence of cuticular flanges, cuticular ribs, conjugated palisade cells, and hypodermis. The taxonomic significance of leaf blade anatomy is briefly discussed.

Key words: Anatomy; *Brachylaena*; Lamina; Southern Africa; Taxonomy.

Introduction

The genus *Brachylaena* R. Br. (Asteraceae) consists of 12 species of which seven occur in southern Africa (Cilliers, 1993). The southern African species are *B. discolor* DC., *B. elliptica* (Thunb.) DC., *B. glabra* (L. f.) Druce, *B. huillensis* O. Hoffm., *B. ilicifolia* (Lam.) Phill. & Schweick., *B. neriifolia* (L.) R. Br., and *B. rotundata* S. Moore (Cilliers, 1993).

Considerable information on the leaf morphology of these species is available, but little is known about the leaf anatomy. The only contribution on the anatomy of the genus *Brachylaena* was the study on wood anatomy of "*B. hutchinsii*" = *B. huillensis* by Metcalfe (1935). From a general discussion by Metcalfe and Chalk (1965) on the anatomy of the Asteraceae, it is clear that its anatomical characters are of taxonomic value. The current anatomical study was therefore undertaken to establish if any of the anatomical characters of the leaf blade of the southern African *Brachylaena* species are taxonomically useful.

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According to Metcalfe (1979, 1983) and Wilkinson (1979a, b, c), it is not an easy task to decide whether anatomical characters are directly induced by the environment (temperature, light intensity, and water availability) or genetically determined. We collected plant materials from a variety of habitats to ensure that a wide spectrum of ecological influences on leaf anatomy could be taken into account.

Materials and Methods

All the materials studied are listed in Table 1. Voucher specimens are housed in PUC. Pieces of the leaf lamina between the median vein and the leaf margin at the widest part of the leaf were removed. Care was taken to collect only leaves on the third node from the growing point, from the lowest branches on the north facing side of each plant to minimize the possible affect of the environment on leaf anatomy. Three samples (10 × 2 mm) were taken from each of three different leaves on each plant. All of the different habitats occupied by each species were included in the sampling. Habitats were described in Cilliers (1993).

For light-microscope studies, material was fixed

Table 1. *Specimens of* ***Brachylaena*** *used in the leaf blade anatomical studies*

Taxon	Collector and number
B. discolor DC. subsp. *discolor*	Cilliers 35, 42, 101, 108, 112, 117, 135
B. discolor DC. subsp. *transvaalensis* (Phill. & Schweick.) Paiva	Cilliers 84, 87, 91, 111, 119, 134, 137, 139
B. elliptica (Thunb.) DC.	Cilliers 22, 27, 28, 38, 40
B. glabra (L.f.) Druce	Cilliers 57, 61, 64, 133
B. huillensis O. Hoffm.	Cilliers 79, 95, 95, 100, 104
B. ilicifolia (Lam.) Phill. & Schweick.	Cilliers 37, 43, 53, 99, 147
B. neriifolia (L.) R. Br.	Cilliers 65, 67, 69, 72, 75
B. rotundata S. Moore	Cilliers 78, 80, 148, 150

with 3% glutaraldehyde in 0.1 M phosphate buffer and dehydrated in an alcohol series (Feder and O'Brien, 1968).Segments were impregnated with and embedded in glycol methacrylate according to the method of Feder and O'Brien (1968), and were transversely sectioned at 3 μm thickness. The PAS reaction and/or staining with toluidine blue O was conducted for the sections (Feder and O'Brien, 1968).

Epidermal segments obtained from the intercostal region of both leaf surfaces were fixed in FAA (Johansen, 1940) and further prepared according to the method of Kiger (1971). The epidermal preparations were stained with safranin (Johansen, 1940), rinsed in water, dehydrated for 5 minutes in methylcellosolve and mounted in Entellan.

It was impossible to determine trichome and stoma indices on the abaxial leaf surfaces, because of the dense trichome covering. Attempts to remove these trichomes beforehand with adhesive tape were partially successful. The shape of the epidermal cells could be determined, but the number of cells per surface area could not be counted. The number of linear trichomes on the adaxial surface and the number of linear and glandular trichomes and stomata on the abaxial surface were determined in an area of 33,750 μm^2 this being the field of the microscope used. This area is be referred to as a surface area unit. In each case the mean number of trichomes were taken from a total of ten surface area units.

The size and shape of the epidermal cells in surface view were also determined. The following measurements were made of the adaxial and abaxial epidermal cells as seen in transverse sections of the lamina:

a) Periclinal diameter: The maximum distance between the outer margin of the two anticlinal cell walls.

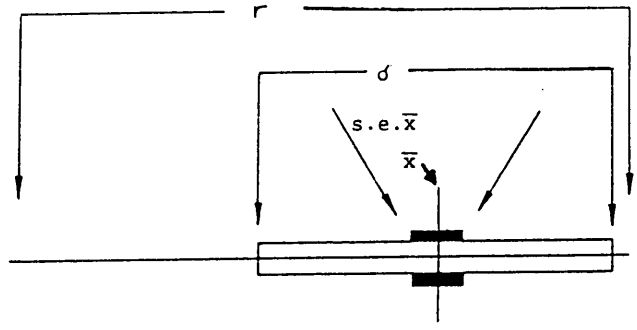
b) Anticlinal diameter: The maximum distance between the outer margin of the two tangential cell walls, excluding the cuticle.

Ten adjacent epidermal cells were measured and the average was taken.

Terminology for the shape of the epidermal cells and for the stomatal type follows Dilcher (1974). Other terms prescribed by Metcalfe (1979) and Wilkinson (1979a, b, c) are also used.

For SEM (scanning electron-microscope) studies material was fixed in 4% aqueous paraformaldehyde (pH 7.2), rinsed in 70% ethanol, and dehydrated in an ethanol series. The material was studied with a Cambridge 250 SEM after critical point drying and sputter coating with gold.

Anatomical differences between species are more quantitative in nature than qualitative (Metcalfe and Chalk, 1950). The data were therefore treated statistically according to the methods of Sneath and Sokal (1973). The variation in these quantitative characters was shown in the form of dice diagrams (Radford, *et al.*, 1974), as follows:



$\bar{x}$ = mean
s.e.$\bar{x}$ = standard error
σ = standard deviation
r = range

A principal component analysis was conducted with the PRINCOMP program (SAS Institute Statistical Analysis System, 1985). The final results give the coordinates in which each operational taxonomic unit (OTU) can be presented in a spatial relation, as well as a graphic exposition of principal components 1, 2, and 3. The following characters were used:

Characters 1-17 were taken from transverse sections of leaf blades (all measurements in μm)
(1) Thickness of the outer periclinal cell wall of the adaxial epidermal cells (A).
(2) Thickness of the adaxial cuticle (B).
(3) Relation of A to B.
(4) Shape of the adaxial epidermal cells.
(5) Presence or absence of cuticular flanges.
(6) Extension of cuticular flanges.
(7) Lamellar appearance of the outer periclinal cell walls of adaxial epidermal cells.
(8) Mean anticlinal diameter of ten adaxial epidermal cells.
(9) Mean periclinal diameter of ten adaxial epidermal cells.
(10) Presence or absence of subsidiary cells.
(11) Presence or absence of inner and outer stomatal ledges.
(12) Presence or absence of hypodermis.
(13) Composition of mesophyll.
(14) Presence or absence of conjugated palisade cells in the mesophyll.
(15) Diameter of median vein (X) from the outside of the adaxial cuticle to the outside of the abaxial cuticle.
(16) Diameter of the leaf blade (Y) between the veins, from the outside of the adaxial cuticle to the outside of the abaxial cuticle.
(17) Relation of X to Y.
Characters 18-24 were obtained from surface studies of the epidermis (all measurements in μm)
(18) Mean length (longest axis of the cells) of ten adaxial epidermal cells.
(19) Mean width (shortest axis of the cells) of the same ten adaxial epidermal cells.
(20) Relation of the number of linear non-glandular trichomes to the number of glandular trichomes per adaxial surface area unit (33,750 μm^2).
(21) Relation of the number of linear non-glandular trichomes to the number of glandular trichomes per abaxial surface area unit (33,750 μm^2).
(22) Shape of anticlinal cell wall of adaxial epidermal cells (straight or undulated).
(23) Presence or absence of cuticular ribs around guard cells.
(24) Stomatal type.
Characters 25-32 were taken from vegetative morphological studies (all measurements in mm)
(25) Length of leaf blade (P).
(26) Width of leaf (Q).
(27) Relation of P to Q.
(28) Petiole length.
(29) Leaf shape.
(30) Shape of leaf base.
(31) Shape of leaf apex.
(32) Shape of leaf margin.

Results

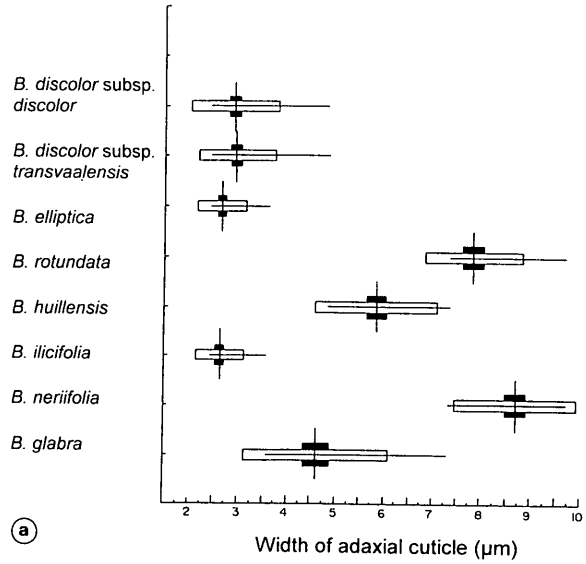
Epidermis

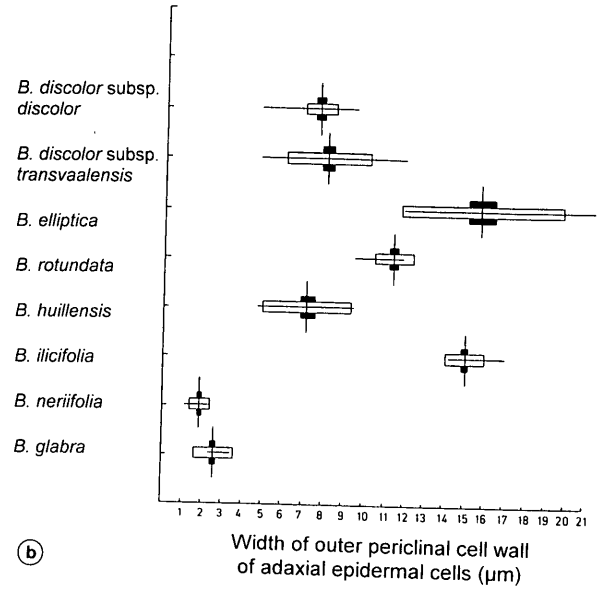
The adaxial cuticle of most of the taxa is smooth, but may possess long continuous striae which may be branched and extend over several cells.

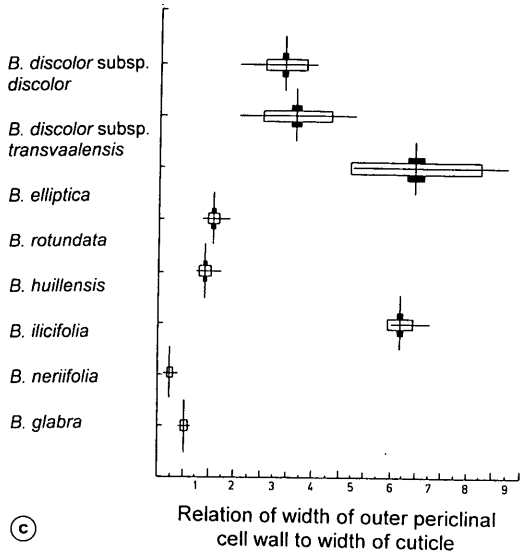
On the basis of adaxial cuticular thickness, two groups are distinguished within the *Brachylaena* taxa. The adaxial cuticle of *Brachylaena discolor, B. elliptica* and *B. ilicifolia* (Fig. 1a) was relatively thin (2.4-4.8 μm). The cuticle of the representatives of the second group (*B. neriifolia, B. huillensis* and *B. rotundata*) was thicker (4.8-9.7 μm) (Fig. 1a). *B. glabra* (3.6-7.3 μm) fit into both groups. In all taxa, the abaxial cuticle was thinner than the adaxial one.

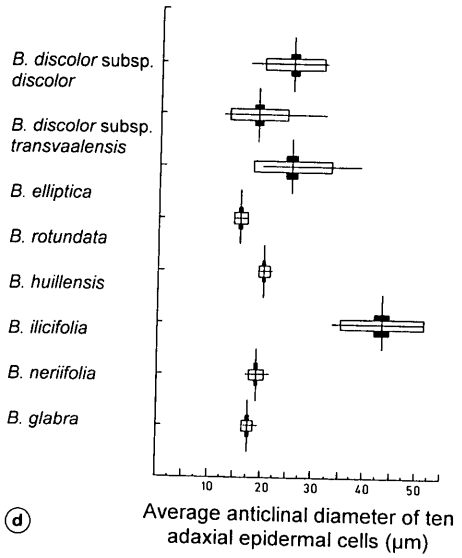
Cuticular flanges, as described by Haberlandt (1914), were observed only in *B. glabra, B. neriifolia,* and *B. huillensis* (Figs. 2a and 2b). These cuticular flanges sometimes reached the inner periclinal cell walls of the epidermal cells in *B. glabra* and *B. neriifolia*.

In transverse sections the epidermal cells on both adaxial and abaxial sides of the main vein appeared dome-shaped (sub-papillose) and much smaller than the intercostal epidermal cells on both adaxial and abaxial sides of the mesophyll. The outer periclinal









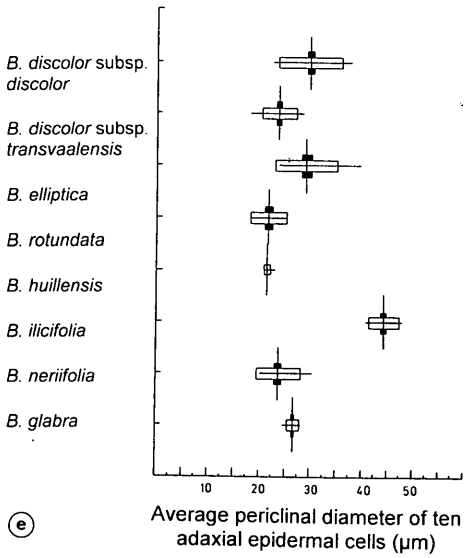


Fig. 1. Dice diagrams of certain quantitative leaf characters of the studied *Brachylaena* taxa, showing: (a) Width of adaxial cuticle. (b) Width of outer periclinal cell wall of the adaxial epidermal cells. (c) Relation between width of outer periclinal cell wall and width of cuticle of the adaxial epidermal cells. (d) Average anticlinal diameter of ten adaxial epidermal cells. (e) Average periclinal diameter of ten adaxial epidermal cells.

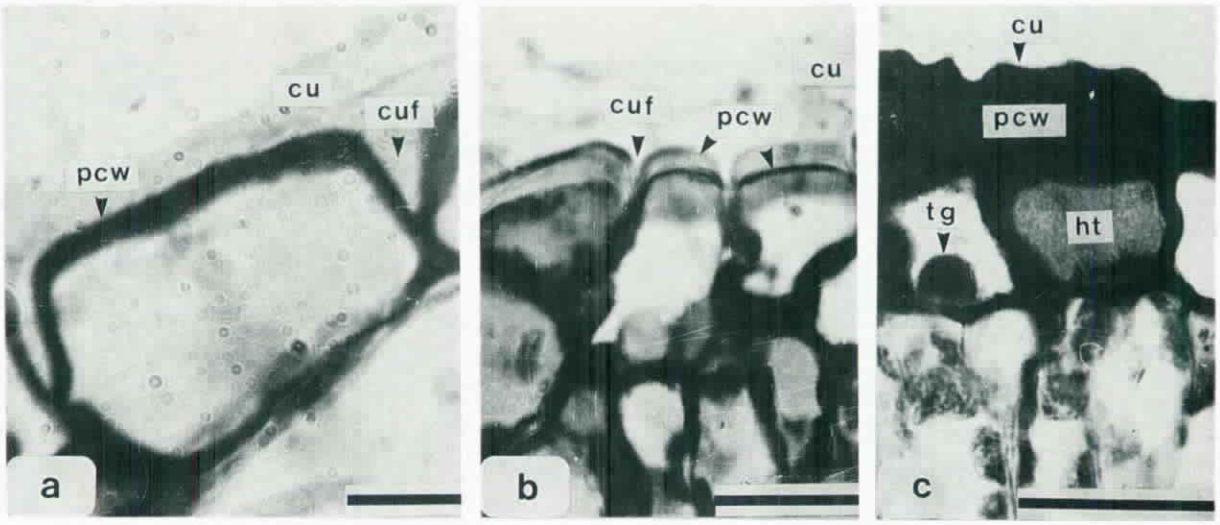


Fig. 2. Light micrographs of cross sections through adaxial epidermal cells of the leaves of: (a) *B. glabra* (*Cilliers 133*) showing the thick cuticle (cu), thin outer periclinal cell wall (pcw), and cuticular flange (cuf). Scale bar = 10 μm. (b) *B. huillensis* (*Cilliers 104*) showing the thick cuticle (cu) cuticular flange (cuf) and lamellar outer periclinal cell walls (pcw). Scale bar = 10 μm. (c) *B. rotundata* (*Cilliers 80*) showing the thin cuticle (cu), thick outer periclinal cell walls (pcw), homogenous tanniniferous contents (ht), and tanniniferous globules (tg). Scale bar = 20 μm.

walls of the epidermal cells on both adaxial and abaxial sides of the main vein formed projections into the cuticle. In *B. glabra, B. neriifolia* and *B. huillensis* the epidermal cells on the adaxial side of the intercostal region were sometimes dome-shaped (sub-papillose).

A considerable intraspecific variation existed in *B. discolor, B. elliptica,* and *B. huillensis* (Fig. 1b) with respect to the thickness of the outer periclinal cell walls of the intercostal adaxial epidermal cells. In spite of this variation, three species groups were distinguished within the *Brachyalena* taxa on the basis of this character. The thickness of the outer periclinal cell walls of the first group (*B. elliptica* and *B. ilicifolia*) varied between 12.2 and 21.96 μm. *B. discolor, B. rotundata,* and *B. huillensis,* which belong to the second group, had thinner outer periclinal cell walls (4.8–12.2 μm), while those of *B. glabra* and *B. neriifolia* were much thinner (1.2–3.6 μm). It was not always possible to distinguish between the members of the first and the second group (Fig. 1b).

B. huillensis can be distinguished from the other species by the lamellar appearance of the outer periclinal cell walls of the adaxial epidermis (Fig. 2b).

Although not always well defined, four species groups were distinguished within *Brachylaena* on the basis of the relation of the thickness of the outer periclinal cell wall of the adaxial epidermal cells to the thickness of the adaxial cuticle (Fig. 1c). This relation was smaller than 1:1 in *B. glabra* and *B. neriifolia*. In the second group (*B. rotundata* and *B. huillensis*) the relation varied from 1:1 to 1.7:1. *B. discolor* was the only member in the third group, where the relation varied from 2:1 to 5:1. The relation of the fourth group (*B. elliptica* and *B. ilicifolia*) varied between 5:1 and 9:1.

In a transverse section of the leaf the periclinal cell walls of the adaxial and abaxial epidermal cells appeared longer than the anticlinal walls. The epidermis contained tanniniferous substances in homogenous deposits, spherical globules, or granular deposits (Fig. 2c). In surface view the epidermal cells appeared isodiametric and/or hexagonal (rarely pentagonal) in the intercostal regions. In costal regions the cells were rectangular and/or hexagonal. The anticlinal walls of the adaxial epidermal cells of *B. huillensis* were undulated, but they were straight in the other taxa.

The size of the adaxial epidermal cells in surface view varied considerably (18–57.1 μm × 14.15–44.41 μm in most of the taxa). On the basis of this character, however, it was possible to distinguish between *B. ilicifolia* (33.18–57.1 μm × 25.38–44.41 μm) with large cells and *B. huillensis* (19.03–24.4 μm × 14.15–18.54 μm) and *B. rotundata* (20.5–31.23 μm × 14.64–23.42 μm)

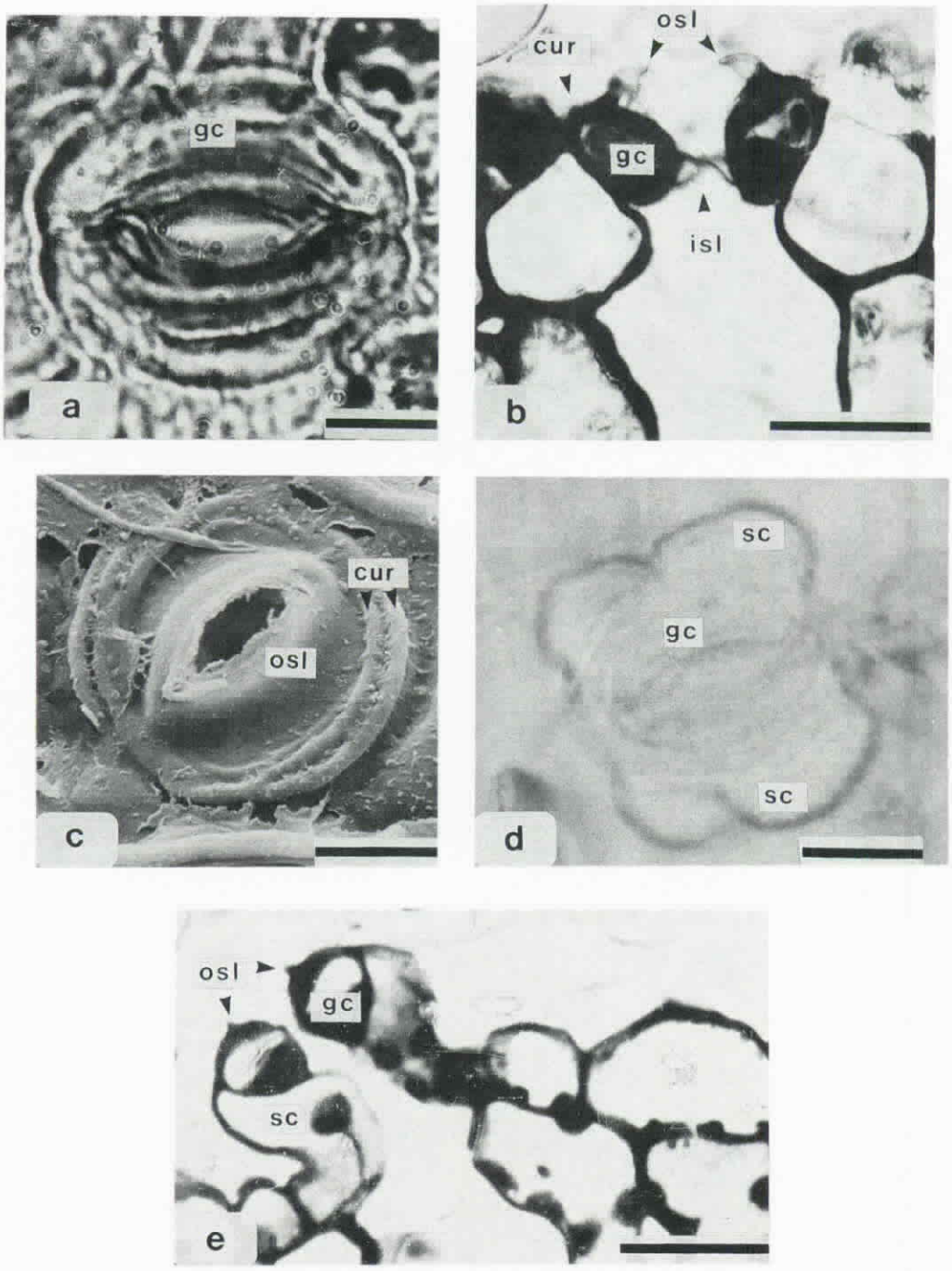


Fig. 3. (a) Light micrograph of a surface view of the abaxial epidermis of *B. neriifolia* (*Cilliers 72*) showing an anomocytic stomata with guard cells (gc). (b) Light micrograph of a cross section through the abaxial epidermis of the leaf of *B. neriifolia* (*Cilliers 75*) showing the guard cells (gc), inner stomatal ledges (isl), outer stomatal ledges (osl), and the cuticular ribs (cur). (c) Scanning electron-micrograph of the abaxial leaf surface of *B. glabra* (*Cilliers 57*) showing a stoma with outer stomatal ledges (osl) and cuticular ribs (cur). (d) Light micrograph of surface view of the abaxial epidermis of *B. discolor* subsp. *discolor* (*Cilliers 135*) showing a brachiparacytic stoma with guard cells (gc) and subsidiary cells (sc). (e) Light micrograph of a cross section through the abaxial epidermis of the leaf of *B. discolor* subsp. *transvaalensis* (*Cilliers 139*) showing subsidiary cells (sc), guard cells (gc), and the small outer stomatal ledges (osl). All scale bars = 10 μm.

with smaller cells.

B. ilicifolia could also be distinguished from most of the other taxa on the basis of the average anticlinal and periclinal cross section diameters of ten adaxial epidermal cells (Figs. 1d and 1e).

Trichomes

Linear, multicellular, non-glandular trichomes and glandular trichomes with unicellular or multicellular stalks and multicellular heads were present on the leaves of all the taxa. The different taxa could, however, be distinguished by the specific position and the number of trichomes per surface area unit. All trichome types were observed on both adaxial and abaxial sides of the main veins of the leaves in all taxa. On the adaxial side of the leaf blade (excluding the main vein) no trichomes were observed in *B. glabra, B. neriifolia,* and *B. huillensis.* All types were present in *B. ilicfolia* and only non-glandular trichomes in *B. discolor, B. elliptica,* and *B. rotundata.* With the exception of *B. rotundata* (10-22 linear trichomes per surface area unit), all taxa had less than eight linear trichomes per surface area unit, adaxially of the leaf blade. On the abaxial side of the lamina, more than twenty linear trichomes and more than two glandular trichomes per surface area unit were present in most of the taxa. *B. glabra* and *B. neriifolia* differed from the other taxa in this character, as they have five or fewer linear trichomes per surface area unit and no glandular trichomes.

Stomata

The leaves of all the taxa were hypostomatic. The guard cells, subsidiary cells (if present), and surrounding epidermal cells had very thick outer and inner periclinal cell walls, as well as homogenous tanniniferous material or tanniniferous bodies. The relation between the length and the width of the guard cells varied between 1.1:1 and 1.5:1; in surface view they appeared circular to widely elliptic.

On the basis of stomatal type, structure of the guard cells and the surrounding epidermal cells, and the number of stomata per surface area, two groups of species were distinguished. The stomata of the first group are anomocytic (Fig. 3a), without subsidiary cells, guard cells on the same level as the surrounding epidermal cells (Fig. 3b), a rather large outer stomatal ledge, a smaller inner stomatal ledge (Fig. 3b), and four cuticular ribs (two on each side of each outer stomatal ledge) (Figs. 3b and 3c). The species in this group (*B. glabra* and *B. neriifolia*) have three to eight stomata per surface area unit. The stomata of the second group are brachyparacytic (Fig. 3d). The guard cells are raised above the leaf surface by the enlarged subsidiary cells (Fig. 3e). A relatively small outer stomatal ledge was detected, but no inner stomatal ledge or cuticular ribs (Fig. 3e). The representatives of this group (*B. discolor, B. rotundata, B. elliptica, B. ilicifolia,* and *B. huillensis*) have 10-22 stomata per surface area unit.

Hypodermis

B. glabra and *B. neriifolia* are distinguished from all the other taxa by the presence of one or two continuous adaxial hypodermal parenchyma layers (Fig. 4a). Opposite the vascular bundles of the main vein these cells may be collenchymatous. The hypodermal cells were much larger than the epidermal cells. Spherical tanniniferous bodies were sometimes present in these cells.

Mesophyll

The leaves of all the taxa were dorsiventral. The mesophyll of *B. discolor, B. elliptica, B. huillensis,* and *B. rotundata* consisted of four or five layers of palisade parenchyma cells (Fig. 4b). The leaves of these species were, however, not regarded as isobilateral, because individual cells in the two abaxial layers were sometimes sponge-like and were always shorter than the others. These palisadal cells may also contain rows of papillae on their longitudinal walls. Solereder (1908) referred to these cells as conjugated palisadal cells (Fig. 4c). According to Metcalfe (1979), these conjugated palisadal cells usually have taxonomic value because of their restricted appearance. In *B. ilicifolia* about two-thirds of the mesophyll consisted of two to three layers of palisade parenchyma and the remaining one-third of spongy parenchyma cells. *B. glabra* and *B. neriifolia* differed from the other taxa, as their mesophyll consisted of only one layer of adaxial palisade parenchyma cells while the spongy parenchyma occupied the largest part of the mesophyll (Fig. 4a).

Veins

The main vein of *B. ilicifolia, B. huillensis, B. glabra,* and *B. neriifolia* was somewhat sunken or on the same level as the rest of the leaf blade on the adaxial

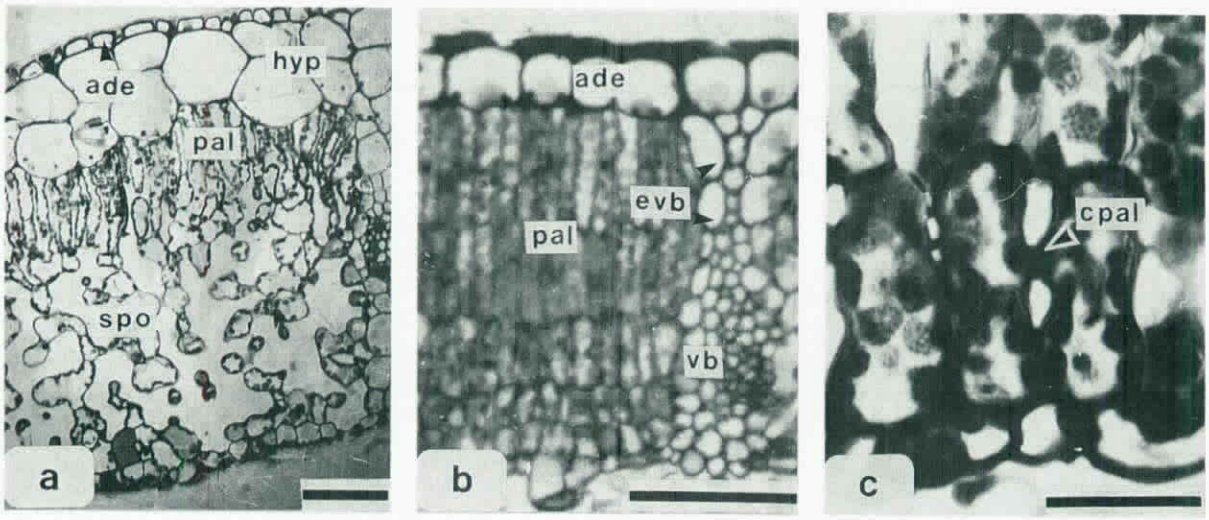


Fig. 4. Light micrographs of cross sections through: (a) leaf blade of *B. glabra* (*Cilliers 64*) showing the adaxial epidermis (ade), hypodermis (hyp), palisade parenchyma (pal), and spongy parenchyma (spo). Scale bar = 100 μm. (b) leaf blade of *B. discolor* subsp. *discolor* (*Cilliers 42*) showing the adaxial epidermis (ade), palisadal parenchyma (pal), vascular bundle (vb), and the extensions of the vascular bundle sheaths (evb). Scale bar = 100 μm. (c) part of the abaxial side of the leaf blade of *B. rotundata* (*Cilliers 78*) showing the conjugated palisade cells (cpal). Scale bar = 20 μm.

side. In the other taxa the main vein formed an adaxial ridge.

In all species three collateral vascular bundles of more or less the same size were arranged in a crescent in the main vein. All three bundles or only two of them may be fused. The protophloem consisted mainly of sclerenchyma fibres, while the metaphloem contained sieve tubes and companion cells. A cambial zone consisting of two to three layers of cells also occurs. Primary xylem consisted of vessels, fibres, and parenchyma cells. The secondary xylem consisted mainly of vessels and parenchyma cells, arranged in radial rows. No or very little secondary phloem was observed. Sclerenchyma fibres formed a continuous layer on the adaxial side of each vascular bundle.

Adjacent to the adaxial and abaxial epidermis four to eight layers of annular collenchyma cells occurred in the main vein, while parenchyma cells with large intercellular spaces surrounded the vascular bundles. The parenchyma and collenchyma cells appeared empty or contained granular or homogenous tanniniferous material. Isolated raphides were present in some of the cells. No bundle sheath was visible.

In the mesophyll a single row of smaller vascular bundles was situated closer to the abaxial epidermis. These small vascular bundles possessed a parenchymatous bundle sheath, which was sometimes sclerenchymatous. The vascular bundle sheaths were connected to the adaxial and abaxial epidermal cells by one to three layers of cells (Fig. 4b) which were usually parenchymatous, but sometimes sclerenchymatous. Solereder (1908) called this type of arrangement vertically transcurrent. In *B. glabra* and *B. neriifolia* the parenchyma cells extended only to the hypodermis and were continuous with the hypodermal cells. The xylem and phloem of the small vascular bundles consisted only of parenchyma cells.

A principal component analysis (PCA)

The principal component analysis (PCA) was conducted to show the taxonomic significance of leaf-blade anatomical characters in *Brachylaena*. A combination of vegetative morphological characters (Cilliers, 1993) and leaf blade anatomical characters was used in the PCA (S. S. Cilliers, 1990, unpublished M. Sc. thesis, PU for CHE).

From diagrams of these analyses it was clear that specimens belonging to the same species group together, mainly on the basis of principal components 1 and 2 (Fig. 5) and less so on the basis of principal component 3 (Fig. 6). A combination of anatomical and vegetative morphological characters is responsible for this

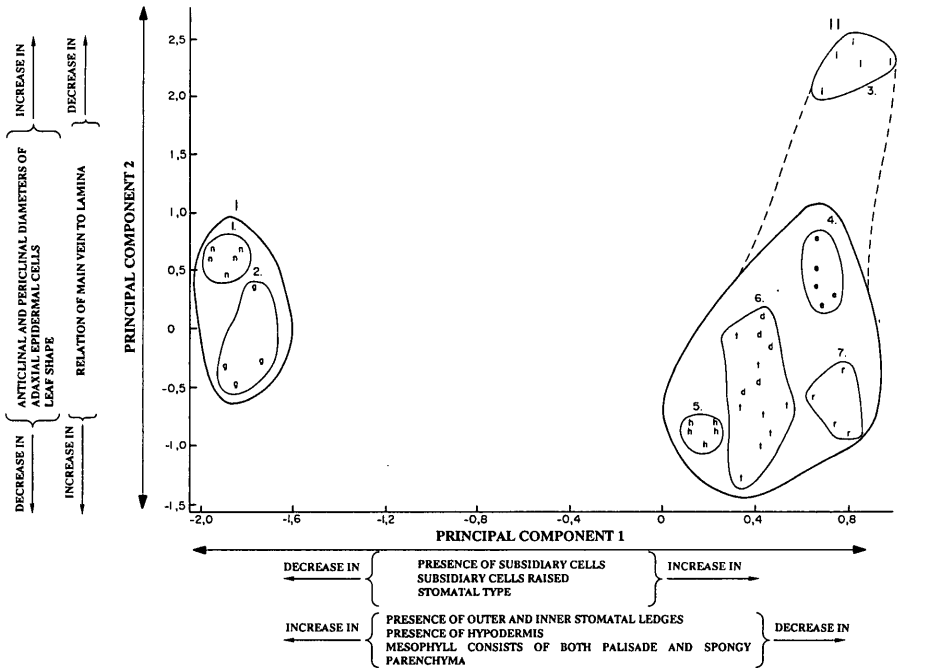


Fig. 5. Scatter diagram showing the ordination of the studied materials of *Brachylaena* according to main components 1 and 2, on the basis of a combination of morphological and anatomical characters. Group I: group 1 - *B. neriifolia,* - group 2 - *B. glabra;* Group II: group 3 - *B. ilicifolia;* - group 4 - *B. elliptica,* - group 5 - *B. huillensis,* - group 6 - *B. discolor,* - group 7 - *B. rotundata.*

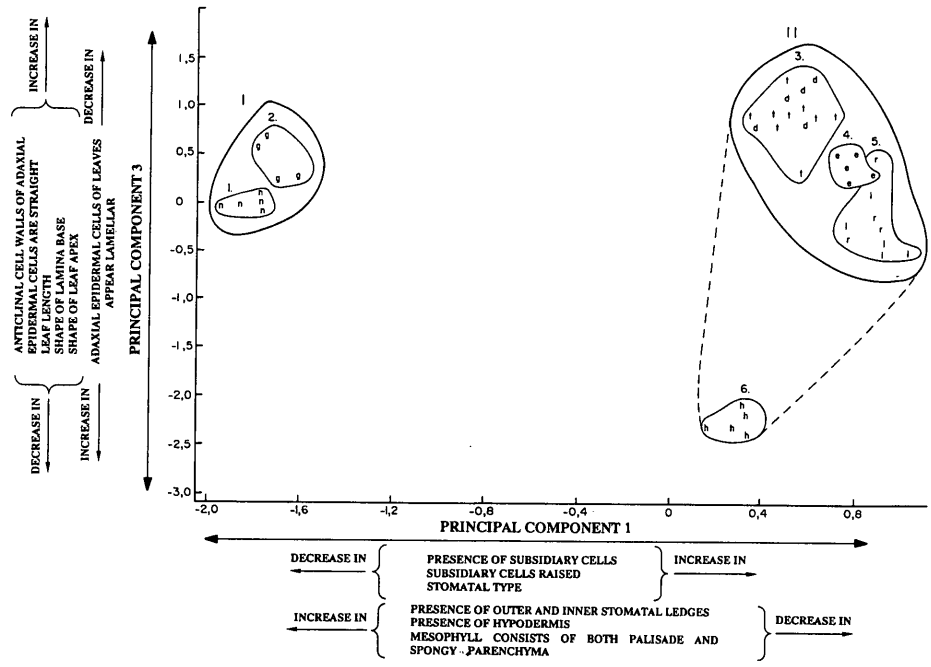


Fig. 6. Scatter diagram showing the ordination of the studied materials of *Brachylaena* according to main components 1 and 3, on the basis of a combination of morphological and anatomical characters. Group I: group 1 - *B. neriifolia,* - group 2 - *B. glabra;* Group II: group 3 - *B. discolor,* - group 4 - *B. elliptica,* - group 5 - *B. ilicifolia,* and *B. rotundata,* - group 6 - *B. huillensis.*

grouping. It was also apparent that two distinct groups of species (I and II) are formed, mainly on the basis of principal component 1 with anatomical characters the main contributors (Figs. 5 and 6). In group II, however, *B. ilicifolia* and *B. huillensis* tended to form subgroups (Figs. 5 and 6) distinct from the rest of the group.

Discussion

The anatomical characters correlate very well with the vegetative morphological characters used to distinguish the different species (Cilliers, 1993). It is, however, clear that leaf blade anatomical characters alone cannot be used to distinguish between all the southern African species of *Brachylaena*, but their contribution to the distinction between certain species cannot be overlooked. *B. ilicifolia* and *B. huillensis*, for example, can be distinguished from the other taxa mainly by the size of the adaxial epidermal cells and the presence of lamellae in the adaxial outer periclinal epidermal cell walls, respectively (Figs. 5 and 6). It is also clear that two groups of species are distinguished in the studied taxa on the basis of certain leaf blade anatomical characters (Figs. 5 and 6). The most important characters are summarized in Table 2. *B. glabra* and *B. neriifolia* are the only representatives of group I, while *B. discolor, B. elliptica, B. huillensis, B. ilicifolia,* and *B. rotundata* form group II.

Certain characters such as the structure and thickness of the cuticle, thickness of the cell walls, size of the epidermal cells, number of trichomes, presence of a hypodermis, and the relation of palisade to spongy parenchyma in the mesophyll may be induced by the environment (Metcalfe, 1979, 1983; Wilkinson, 1979a, b, c). The anatomical differences between groups I and II (Table 2) were, however, observed in all the studied samples of a taxon from different localities, and are therefore regarded as taxonomic characters for the southern African representatives of the genus. The only anatomical difference between the leaves of samples of *B. glabra* collected in Natal and from the eastern Cape was the number of hypodermal cell layers. Leaves from samples of *B. ilicifolia* collected in the very dry Potlake Nature Reserve in Secucuniland were much smaller with much finer toothed margins than those from samples collected in Natal and the eastern Cape (Cilliers, 1993), but no anatomical differences were observed.

Characters regarded as xeromorphic, such as thick cuticles, the presence of cuticular ribs, cuticular flanges, and a hypodermis, were observed in taxa such as *B. neriifolia* and *B. glabra* (Group I), which grow under more temperate conditions. These taxa also show mesomorphic characters such as smooth leaves, adaxial epidermal cells with thin outer periclinal cell walls, large areas of spongy parenchyma tissues, and few stomata per surface area.

Mesomorphic characters such as thin cuticles, raised stomata and very large adaxial epidermal cells occurred in taxa such as *B. discolor, B. elliptica, B. huillensis, B. ilicifolia,* and *B. rotundata* (Group II), which grow in more xerophytic habitats than the previous

Table 2. *Summary of the main anatomical distinctions between the leaf blades of Group I (**B. glabra** and **B. neriifolia**) and Group II (**B. discolor, B. elliptica, B. huillensis, B. ilicifolia,** and **B. rotundata**)*

Group I	Group II
Outer periclinal cell walls of adaxial epidermal cells very thin (1.2-3.6 μm).	Outer periclinal cell walls of adaxial epidermal cells much thicker (4.8-21.96 μm).
Stomata anomocytic. Guard cells on the same level as the surrounding epidermal cells.	Stomata brachyparacytic. Guard cells raised above the surrounding epidermal cells, because of the presence of swollen subsidiary cells.
Four cuticular ribs present around stomata.	No cuticular ribs present.
Inner and outer stomatal ledges present on guard cells.	Only outer stomatal ledges present on guard cells.
One or two-layered hypodermis present.	No hypodermis present.
Mesophyll consists of one layer of palisade parenchyma cells and clearly differentiated spongy parenchyma cells.	Mesophyll consists mainly of palisade parenchyma cells. If spongy parenchyma cells are present, two layers of palisade parenchyma cells occur.
No conjugated palisade parenchyma cells occur.	Conjugated palisade parenchyma cells are present.

two species. These taxa also had xeromorphic characteristics such as pubescent leaves, adaxial epidermal cells with thick outer periclinal cell walls, mainly palisade parenchyma cells in the mesophyll, and a large number of stomata per surface area unit.

It seems that different species of this genus developed different strategies to adapt to their respective habitats.

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南非產菊科 *Brachylaena* 屬之葉部解剖

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本文以光學顯微鏡及掃描電子顯微鏡研究南非產 *Brachylaena* 屬七個種的葉片解剖。這七個種包括 *B. discolor* DC., *B. elliptica* (Thunb.) DC., *B. glabra* (L. f.) Druce, *B. huillensis* O. Hoffm., *B. ilicifolia* (Lam.) Phill. & Schweick., *B. neriifolia* (L.) R. Br.及 *B. rotundata* S. Moore。根據氣孔型以及是否具有角皮層隆脊、條狀氣孔平孔突起、複合式柵狀細胞和 F 表皮層可將這七個種分爲兩群。文中亦簡略討論了葉片解剖其分類上的重要性。