

Studies in the genus *Machairophyllum* (Mesembryanthemaceae), with notes on some related genera

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ABSTRACT

Machairophyllum Schwantes is a small genus of the family Mesembryanthemaceae, confined to the southern part of central South Africa from the Little Karoo at Barrydale in the west to the Zuurberg near Kirkwood in the east. *Machairophyllum* is unusual in the Mesembryanthemaceae–Ruschioideae in that fynbos and renosterveld are the preferred habitats. The morphology, anatomy as well as the pollen, seed and leaf epidermis ultrastructure of the genus were examined. The taxonomy of *Machairophyllum* is revised on the basis of data presented. Of the ten names originally described, only four are upheld, *M. albidum* (L.) Schwantes, *M. stayneri* L.Bolus, *M. bijliae* (N.E.Br.) L.Bolus and *M. brevifolium* L.Bolus. All four species are very similar in their vegetative habit, and differ mainly in inflorescence and flower characters. Several presumably related genera, *Bijlia* N.E.Br., *Carruanthus* (Schwantes) Schwantes and *Cerochlamys* N.E.Br., are briefly discussed.

INTRODUCTION

Machairophyllum Schwantes is one of the few genera of the succulent plant family Mesembryanthemaceae which is almost exclusively found in fynbos or renosterveld. The species mostly prefer rocky habitats (Figure 1A, B), although occasionally they grow among grass and shrubs (Figure 1C). In its distribution *Machairophyllum* is, with two possible exceptions, entirely confined to Western and Eastern Cape, South Africa (Figure 2). Two localities have been reported in Northern Cape, but are doubtful and need to be verified (see chapter on phytogeography).

Plants of the genus *Machairophyllum* are unmistakable, with their clump-forming habit and the smooth trigonous leaves. The leaves have a sabre-like appearance, which is the origin of their botanical name ('*Machaira*', Greek, means sabre, and '*phyllon*' means leaf). Plants are seldom found in flower as flowering is stimulated by fire. Furthermore, flowers are mostly vespertine or nocturnal. The striking, fairly large flowers (Figure 1D, E) are yellow and frequently orange-red on the outside and on the petal tips.

Ten species have been described of which only four are recognized in the present study, *Machairophyllum albidum* (L.) Schwantes, *M. bijliae* (N.E.Br.) L.Bolus, *M. brevifolium* L.Bolus and *M. stayneri* L.Bolus. *M. albidum* is known from several sites in the Little Karoo and is easily recognized by the branched inflorescences and the normally long basal sheaths of the primary bracteoles ('bracts'). *M. stayneri* also has branched inflorescences, and is known only from the type collection made on the Zuurberg. *M. bijliae* is the most common and widespread species. Vegetatively it looks identical to *M. albidum*, but once flowers appear, the difference is obvious since the

inflorescences are always unbranched and have mostly short, basal, bracteole sheaths. *M. brevifolium*, as its name suggests, has short and rather wide leaves. It is known only from the red conglomerate hills between Oudtshoorn and De Rust.

Machairophyllum albidum and *M. bijliae* are fairly abundant. In some cases the populations that were visited by the first author comprised hundreds of individuals. It has been suggested to rate *M. vanbredai* L.Bolus as 'Critically Endangered' (Kurzweil & Linder-Smith 2001), but we now consider this taxon synonymous with the widespread *M. bijliae*. *M. stayneri* is only known from the type collection, and the fact that the species was never recollected may indicate that it is indeed very rare or extinct. Populations of the two dwarf species from the crumbling silcrete hills around De Rust (*M. brevifolium* and the synonymous *M. latifolium*) appear to be declining in numbers due to the erosion of their habitat (Smith *et al.* 1998: 220).

Machairophyllum is not very popular among succulent growers because of the often large plant size and the sporadic flowering. Plants are therefore rather uncommon in cultivation although well-grown specimens may be remarkably showy. *M. albidum* was introduced into Europe in 1715, but is rather scarce now (Hammer 1991). The plants can endure fairly low temperatures, and due to their fynbos habitat they can tolerate considerably more watering than many other mesembs (Kurzweil pers. obs.). Propagation can take place through seeds or cuttings (Jacobsen 1977). *M. brevifolium* is not uncommon in collections in California and England, probably because seeds were sent overseas by Mrs Van der Bijl, a well known South African succulent collector (Hammer 1991: 77).

The objective of this study is to examine the character distribution in *Machairophyllum* with the aim to resolve the taxonomy of the genus. For the purpose of phylogenetic interpretation, the presumed relatives in Hartmann's

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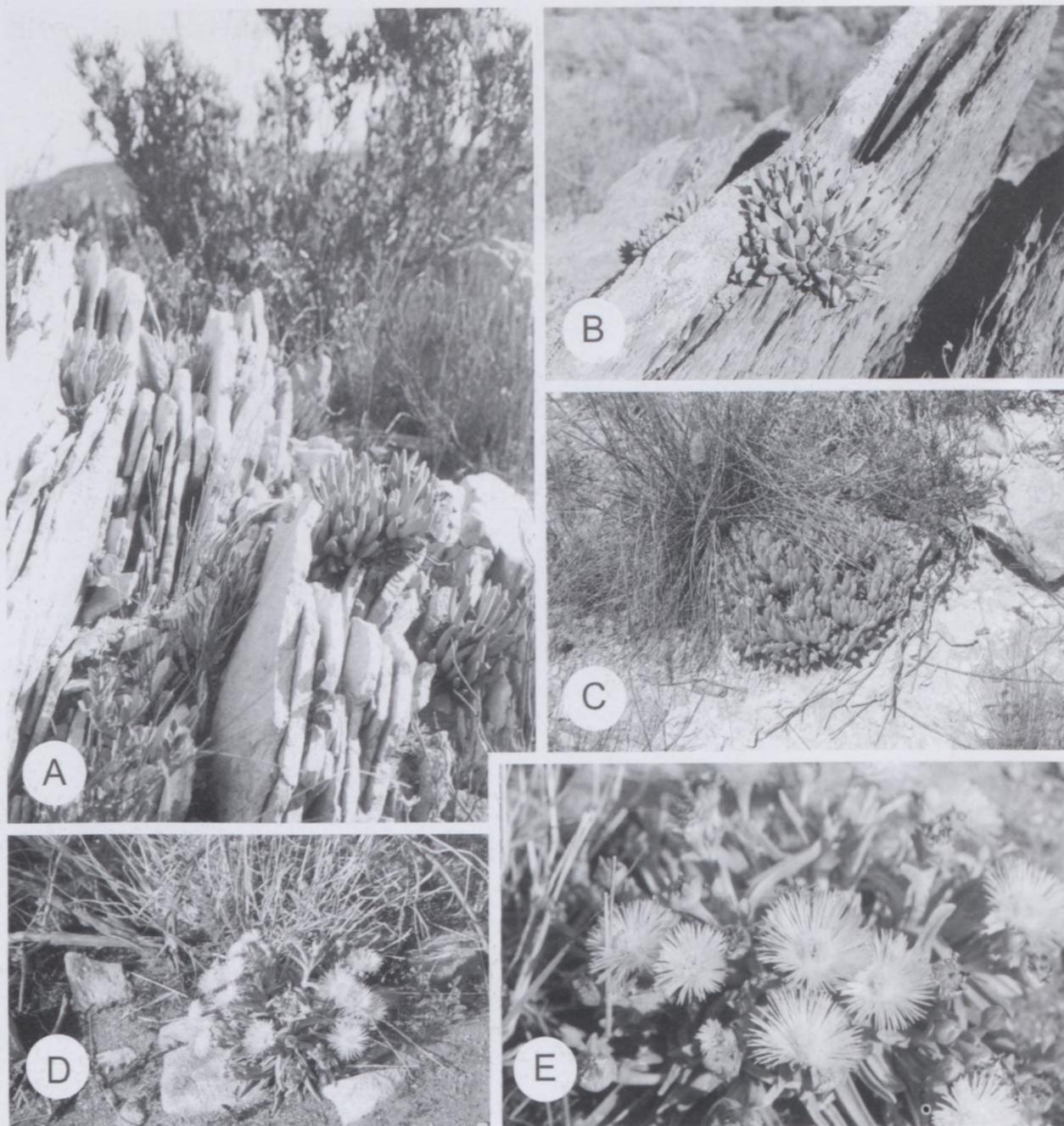


FIGURE 1.—A–C, habitat. A, *Machairophyllum albidum*, Kurzweil 1890. B, C, *M. bijliae*: B, Kurzweil 1896; C, Kurzweil 1913. D, E, flowering plants in previously burnt veld, photographed at around 17h00, Kurzweil 1902.

(1991) *Bergeranthus* group, i.e. the minor genera *Bijlia* N.E.Br., *Carruanthus* (Schwantes) Schwantes and *Cerochlamys* N.E.Br., which all share smooth and dotless leaves with *Machairophyllum*, were briefly surveyed. Out of these, *Bijlia* and *Carruanthus* were found to form a very close-knit group with *Machairophyllum*, which is here referred to as the '*Machairophyllum* complex'.

Taxonomic position and history

On account of having an inferior ovary with parietal placentation and lophomorphic (crest-shaped) nectaries, *Machairophyllum* is placed in Mesembryanthemaceae–Ruschioideae (Herre 1971). The Ruschioideae is the larger of the two subfamilies of Mesembryanthemaceae with 107 genera mainly in southern Africa. Ruschioideae was classified into 12 tentative groups according to the

then state of knowledge (Hartmann 1991, 1993, 1998a). *Machairophyllum* was listed in the *Bergeranthus* group which comprises perennial plants that mostly have free leaves with homocellular xeromorphic epidermis, exserted inflorescences and flowers with separate lophomorphic nectaries. Distinguishing characters of the capsules are the complete, firm and straight covering membranes and the reduced valve wings. Closing bodies can be present or absent. The genera included in this group are *Bergeranthus* Schwantes, *Bijlia*, *Carruanthus*, *Cerochlamys*, *Hereroa* (Schwantes) Dinter & Schwantes, *Rhombophyllum* (Schwantes) Schwantes and *Machairophyllum*. Many members of the group also have semi-terete or trigonous linear to lanceolate leaves. The genera included in the *Bergeranthus* group share a similar distribution in the southern and eastern parts of central South Africa. *Hereroa*, however, has a wider distribution ranging into

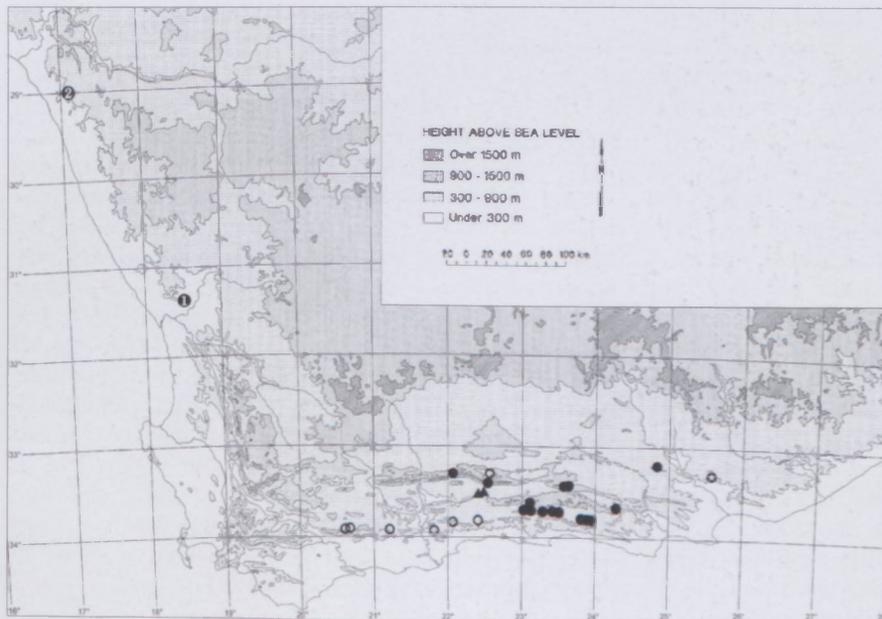


FIGURE 2.—Distribution of the genus *Machairophyllum*: *M. albidum*, ○; *M. bijliae*, ●; *M. brevifolium*, ▲; *M. stayneri*, ◻. Doubtful records in Northern Cape: ◐, *vide* Herre (1971: 198; near Vanrhynsdorp, no comment on source of information or identity of species was made); ◑, *Viviers s.n.* (NBG, hort.; Richtersveld; probably *M. bijliae*).

the Free State, Northern Cape, Gauteng and Namibia. Most genera of the *Bergeranthus* group share a similar pollination syndrome—with *Cerochlamys* as the only exception, all have yellow flowers which are open in the afternoon, evening or at night.

The genus *Machairophyllum* was described by Gustav Schwantes in May 1927, based on *M. albidum* and *M. cookii* (here also included in the concept of *M. albidum*) which he had previously incorporated into the genus *Carruanthus*. The species were said to differ from *Carruanthus* mainly by having many stigmas. Schwantes selected the former as the type species. Four years later *M. stenopetalum* was described by Louisa Bolus (1931), followed by *M. acuminatum* and *M. baxteri* in 1935 (all three are here included in *M. bijliae*). *M. brevifolium* and *M. latifolium* (here regarded as synonymous) were described by L. Bolus in 1938. In the same year L. Bolus also transferred *Perissolobus bijlii* to *Machairophyllum*. The last two additions to the genus *Machairophyllum* were *M. stayneri* (Bolus 1960) and *M. vanbredai* (Bolus 1964) (here included in *M. bijliae*).

In 1960 L. Bolus published a brief review of *Machairophyllum* together with a key to the species; *M. bijliae* was not included as it was insufficiently known. Later this key was used by Jacobsen (1977) in *Lexicon of succulent plants*. In her review, Bolus (1960: 156) pointed out that most species were known only from their type collections, and that 'it is quite possible that, when more intensive collecting and study have been done, *M. bijliae* (in spite of the much smaller size of the type, perhaps due to adverse conditions), *M. stenopetalum*, *M. acuminatum* and *M. baxteri* may prove to be forms of one variable species'. This statement is very much in agreement with the results of the present study. It is interesting that Bolus doubts the validity of her own species (except for the species that *M. bijlii* is based on, all were described by herself). However, this did not prevent her from describing another species a few years later, namely *M. vanbredai* in 1964, which is also merely a form of this 'variable species' (*M. bijliae*).

The species that *Machairophyllum bijliae* is based on was first described in a monotypic genus *Perissolobus* (Brown 1931). According to Brown, the main reasons for the recognition of *Perissolobus* were its eight sepals; affinities to *Machairophyllum* were not mentioned in his paper. Bolus (1938) pointed out the striking similarity of the two genera and transferred *Perissolobus bijlii* to *Machairophyllum*. She regarded the eight sepals of the species as being 'but a further variation of the already variable calyx of *Machairophyllum*' (Bolus 1938: 135). Bolus (1950: 229) pointed out that the reason for there not being any reference to *Machairophyllum* in Brown's paper was probably the fact that at the time *Machairophyllum* was erroneously thought to occur in Namaqualand in Northern Cape, whereas *Perissolobus bijlii* was described from Eastern Cape.

A synopsis of *Machairophyllum* was presented by Hartmann (2001). Both species with five or six sepals and \pm double the number of locules were considered conspecific, namely *M. albidum* and *M. cookii*. Also *M. bijliae* and *M. vanbredai* on the one hand as well as *M. brevifolium* and *M. latifolium* on the other hand were united as they were considered to differ only in minor characters. Thus the number of species was reduced to seven. It was also pointed out that a study of the genus may show that only four or five species are distinguishable, namely *M. albidum*, *M. bijliae*, *M. brevifolium*, *M. stayneri* and, possibly, a new species, allegedly from the Richtersveld.

MATERIAL AND METHODS

Dry and liquid-preserved material of *Machairophyllum*, as well as live seeds, were collected in the field in South Africa. For comparative purposes, material of *Bijlia*, *Carruanthus* and *Cerochlamys* was also collected. Herbarium material on loan from the Bolus Herbarium of the University of Cape Town (BOL) and the Herbarium, Royal Botanic Gardens Kew, London (K) was examined. Additional material was obtained from the Compton Herbarium of the National Botanical Institute, Cape Town (NBG) and from living plants cultivated in the National Botanical Garden, Kirstenbosch.

Herbarium, live and liquid-preserved material was used for gross-morphological investigations. The scanning electron microscope (SEM) technique had to be employed for the study of fine details. With this technique the examination of seeds, pollen and epidermal surfaces was done without previous treatment of samples. SEM investigations of floral structures as well as anatomical studies required the previous fixation of the material in FAA (ethanol 70% : glacial acetic acid : formaldehyde = 18 : 1 : 1). Material was treated with FAA for a few days and later stored in ethanol 70%. For SEM studies it was dissected in ethanol. Subsequently, samples were chemically dehydrated in formaldehyde–dimethylacetal and critical-point-dried directly from this reagent without the use of an intermedium, using CO₂ as the carrier gas (technique after Gerstberger & Leins 1978). Samples were sputter-coated with AuPd and viewed and photographed with a CAMBRIDGE STEREOSCAN S200 scanning electron microscope at voltages ranging from 10 to 30 kV. Anatomical studies were undertaken using a standard dehydration and wax embedding technique; samples were stained with alcian blue and safranin.

MORPHOLOGICAL CHARACTERS (SEE TABLE 1)

Growth forms

Machairophyllum species are vegetatively fairly uniform. The plants are compact, glabrous succulents with short stem internodes and trigonous leaves (Figure 1A–C). Old plants may form mats of up to 1.2 m in diameter. Even in large clumps the side branches normally do not form adventitious roots and are thus not anchored to the ground. Superficially, plants of *Machairophyllum* may be mistaken for *Carpobrotus*, which also occurs in fynbos, although these have somewhat longer and greener leaves and have well-developed stem internodes; however, the flowers and the fruit structure of *Carpobrotus* are very different.

Leaf

Morphology

The leaves are opposite with members of a pair ± equal and basally connate to form a sheath 10–15 mm long; in early ontogenetic stages leaves of a pair are often weakly unequal (anisophylly). The lamina is linear to lanceolate, entire, trigonous in the central portion but basally semi-terete because the dorsal (abaxial) keel disappears; the apex is acute to acuminate. Leaves are pale green often with a whitish tinge, or frequently flushed with red in sun-exposed specimens. Old leaves die off and turn black, but persist on the plant for a long time. Near the base, just above the union of a pair, an obscure swelling is visible on the upper side, which stretches as a curved structure over the entire width of the leaf. It marks the point up to which the leaf is tightly adpressed to the following leaf pair. However, this swelling is not developed as a prominent pustule, which is found in many other mesembs (Hartmann 1991).

Plants growing wild have leaves 10– ± 145 × 8–26 mm. The variation in length and width is continuous and does not allow a clear-cut separation of taxa (Figure 3). Whereas *M. brevifolium* always has short leaves, a few specimens referable to *M. bijliae* also have very short leaves, namely *Van der Bijl 93* (the type), *Desmet 2158*, *Pocock NBG627/26* and *Kurzweil 1919*. Particularly long leaves are found in *M. albidum*. It appears that leaf length and width are mainly the result of environmental factors and are not genetically fixed. The leaf size was previously considered a major key character (Bolus 1960).

Leaf surface

The leaf surface belongs to the 'xeromorphic type' defined by equal or nearly equal epidermis cells, a strongly thickened outer cell wall and a prominent wax cover (Ihlenfeldt & Hartmann 1982) (Figure 4); epidermis cells are irregularly polygonal-isodiametric to elon-

TABLE 1.—Important features of the *Machairophyllum* species recognized

Feature	<i>M. albidum</i>	<i>M. stayneri</i>	<i>M. bijliae</i>	<i>M. brevifolium</i>
Leaves, length	40–145 mm	70–80(–100?) mm	(20–)32–70(–85) mm	10–30 mm
Leaves, width	9–20 mm	13–16 mm	8–15(–18) mm	10–26 mm
Inflorescence	branched	branched	unbranched	unbranched
Bracteole, length total	(25–)50–130 mm	up to 52 mm (Bolus 1960)	(18–)25–40(–60) mm	7–23 mm
Bracteole, length sheath	(19–)42–80(–97) mm	up to 15 mm (Bolus 1960)	7–18(–42) mm	5–10 mm
Flowering season	mainly Nov.–Dec.	Oct.	mainly Aug.–Nov.	Aug.–Sept.
Flowers, open time of day	nocturnal or vespertine, sometimes open from 3 p.m. on	nocturnal	mainly nocturnal	open in the afternoon or vespertine
Flowers, diameter	45–65 mm	50–62 mm	30–55 mm	30–45 mm
Sepals, number	5 or 6	6–8	(5)6–8	6
Sepals, size	6–18 × 5–14 mm	14–20 × 5–8 mm	(3–)8–22 × 3–8(–11) mm	8–14 × 4–8 mm
Petals, size	18–35 × (0.3–)0.6–1(–1.5) mm	17–27 × 0.5–1 mm	(8–)15–25(–28) × 0.3–1(–2) mm	13–20 × 1–2 mm
Stamens, length	10–15(–19) mm	13–17 mm	(5–)7–14(–15) mm	9–10 mm
Nectaries	(8–)10–12	6–8	(5)6–8(–10)	6
Stigmas, number	(8–)10–12(–15?)	6–8	(5)6–8(–10)	6
Stigmas, length	8–15(–16) mm	12–14 mm	(4–)7–14 mm	10–12 mm
Locules	(8–)10–12(–15?)	6–8	(5)6–8(–10)	6

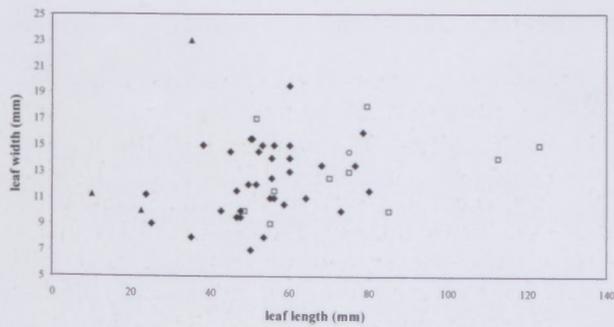


FIGURE 3.—Diagram showing relationship of leaf length and width in *Machairophyllum*. *M. albidum*, □; *M. stayneri*, ○; *M. bijliae*, ◆; *M. brevifolium*, ▲. Plotted measurements represent average values found in examined specimens.

gate, $\pm 61\text{--}146 \times 30\text{--}85 \mu\text{m}$; anticlinal walls are straight; stomata are superficial to slightly sunken (Figure 4F), on both sides of the leaf, paracytic (*sensu* Dupont 1976), $39.32 \times 22.00 \mu\text{m}$.

Leaves lack teeth, dots or hairs, are covered by a continuous wax layer, which is either smooth or breaks up into platelets (Figure 4A–F). Local wax projections mainly take the shape of elongate rodlets (Figure 4B–D), but round granules or flakes are also found occasionally (Figure 4B). In *Kurzweil 1914* structures resembling burst bubbles were observed next to a stoma (Figure 4F), but nothing can be said about their nature at this stage.

Anatomy

Leaves are mostly well differentiated into peripheral assimilation tissue and central water storage tissue (Figure 5A), which are parenchymatic and have intercellular spaces. Tannin idioblasts, a common feature in xeromorphic Mesembryanthemaceae (Hartmann 1991), as well as raphide idioblasts occur throughout the mesophyll, but are absent in the epidermis and hypodermis.

Epidermis is homocellular, cells with flat outer periclinal walls without papillae; cuticle 1 to 2 μm thick; outer wall is strongly thickened at 5–25 μm and contains crystal sand made up of minute grains of calcium oxalate as in other xeromorphic Mesembryanthemaceae (Ihlenfeldt & Hartmann 1982; asterisk in Figure 6A); inner periclinal walls and the anticlinal walls are 1–3 μm thick; hypodermis cells are elongate or more rarely isodiametric, walls 1–3 μm thick.

Assimilation tissue is compact, 10–15-seriate (Figure 6B); vascular bundles as well as fibre bundles are absent; a ring of small vascular bundles is present at the boundary of assimilation tissue and water storage tissue, referred to as secondary bundles (Dannemann 1883; arrowhead in Figure 6C). The central water storage tissue is 10–30-seriate, contains laxly arranged cells; large water storage cells are scattered throughout. Primary bundles: 1–3, are large with several smaller collateral vascular bundles (Figure 6D); the main bundle is normally broad, straight or slightly curved. Most of the pri-

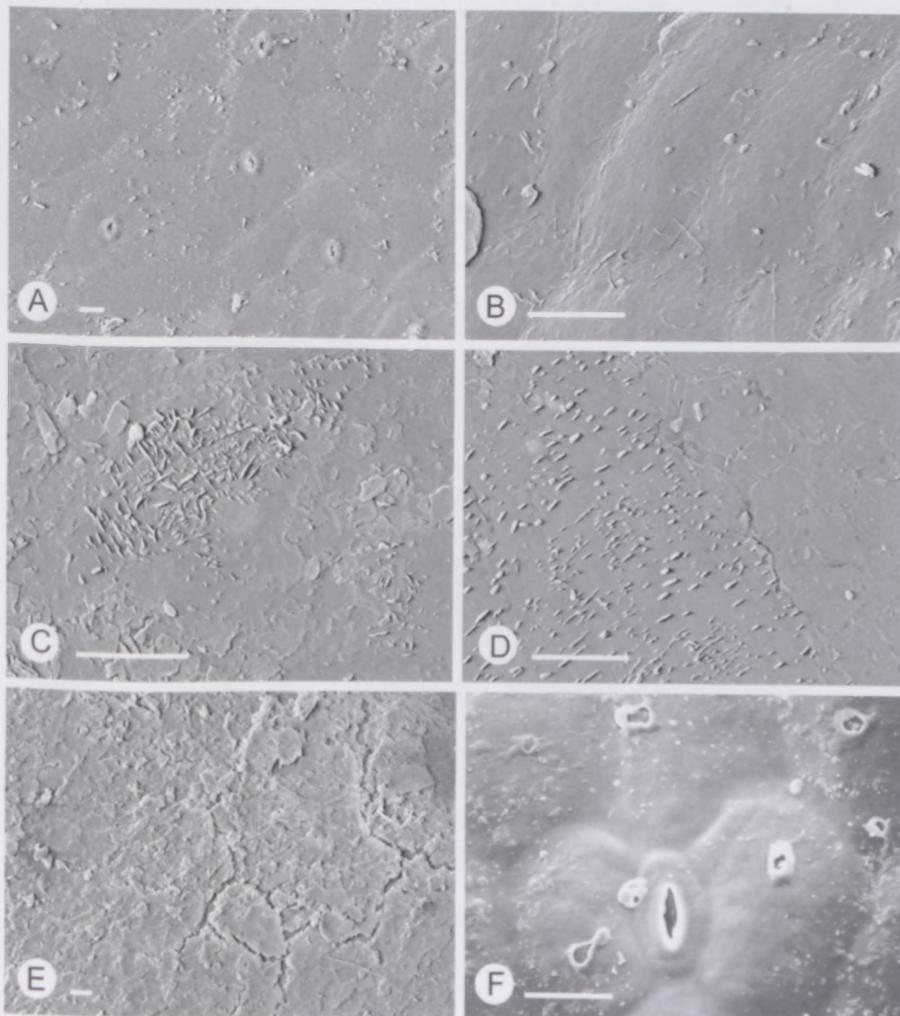


FIGURE 4.—SEM micrographs of leaf surfaces in *Machairophyllum*: A, E, *M. albidum*; B, *M. cf. bijliae*; C, D, *M. bijliae*; F, *M. sp. A*, *Kurzweil 1900*; B, *Bayer 7027*; C, *Kurzweil 1901*; D, *Kurzweil 1896*; E, *Kurzweil 1902*; F, *Kurzweil 1914*. Scale bars: 20 μm .

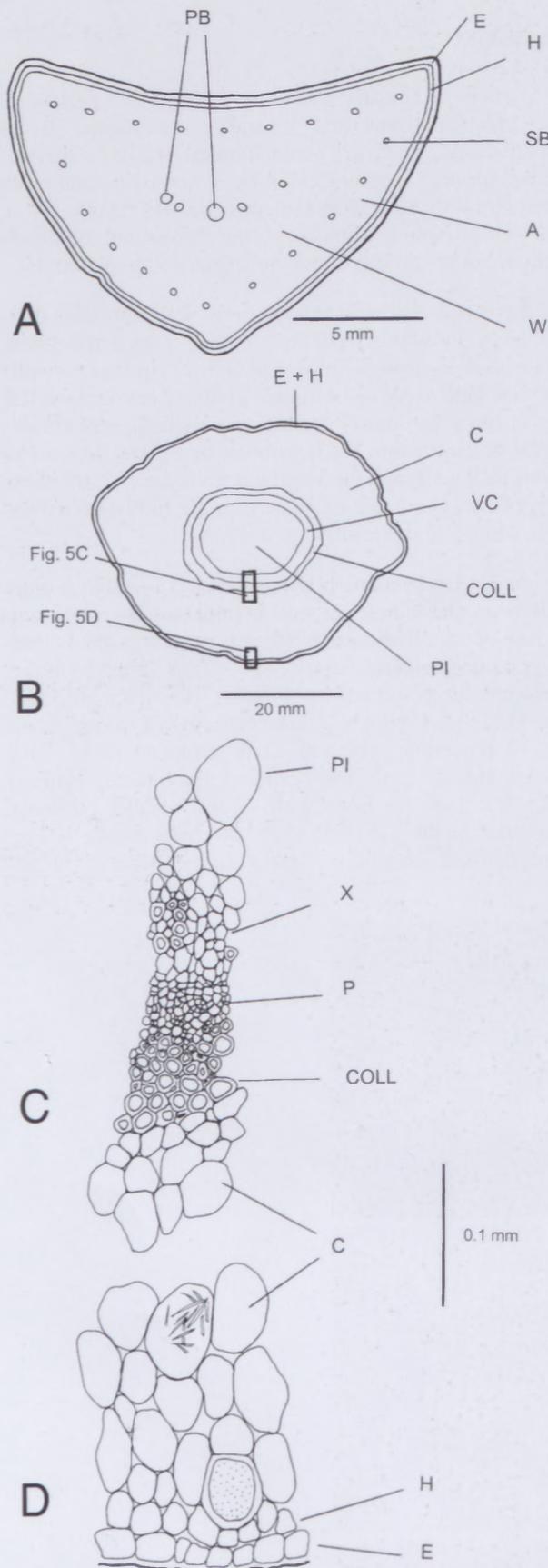


FIGURE 5.—Semi-diagrammatic representation of the anatomy of leaf and stem in *Machairophyllum*: A, *M. albidum*, Kurzweil 1890, leaf. B–D, *M. bijliae*, Kurzweil 1919: B, primary stem; C, D, enlarged sections of B. A, assimilation tissue; C, cortex; COLL, collenchyma; E, epidermis; H, hypodermis; P, phloem; PB, primary bundle; PI, pith; SB, secondary bundle; VC, vascular cylinder; W, central water storage tissue; X, xylem. Scale bars: A, 5 mm; B, 20 mm; C, D, 0.1 mm. Drawn by P. Chesselet.

mary bundles have collenchymatic caps, and bundles plus their caps are surrounded by parenchymatic sheaths.

Stem

The anatomy of the stem conforms essentially to that of other Mesembryanthemaceae with similar compact growth (Hartmann 1976, 1977; Hartmann & Gölling 1993).

Epidermis and cortex are only visible as separate structures in the primary stem (Figure 5B, D). The epidermis is similar to that of the leaf, and the hypodermis is insignificant. The massive parenchymatic cortex probably acts as a storage organ. In older stems the cortex is successively replaced by a layered cork which originates in its inner part. In several specimens of small and compactly arranged collenchymatic cells is found just outside the vascular cylinder (Figure 5B, C), reminiscent of a similar collenchymatic ring in *Odontophorus* (Hartmann 1976) and *Fenestraria* (Hartmann 1982). The vascular tissue of the primary stem consists of a ring of collateral bundles, and takes the shape of a rounded rectangle with its long axis parallel to the axis of the first leaf. Leaf traces emerge in rapid succession from the shorter sides of the rectangle. Each pair emerges at an angle of 90° to the previous one, and the shape of the vascular cylinder therefore changes according to this pattern.

Secondary growth starts in the second internode. It is anomalous as in other Mesembryanthemaceae (Metcalf & Chalk 1950) in that numerous secondary bundles are developed by new cambium formed on the outside of the primary vascular cylinder (epifascicular cambium). These eventually form several concentric rings around the primary vascular cylinder (Figure 7A, B). An unusual cell pattern was observed in the pith of several specimens of *Machairophyllum bijliae* (Figure 7C), looking like pith cells with minute rounded 'cells' between them. It is possible that the latter are in fact intercellular spaces.

Root

Roots are mostly thin and slender, up to 2 mm in diameter. Anatomically the roots resemble stems. They also show an anomalous secondary growth (Metcalf & Chalk 1950). Roots are usually diarch (2-stranded) or triarch (3-stranded). Prominent collenchyma caps are found on the phloem of the bundles. In some specimens, strongly thickened sclereid cells are found below the xylem and form pronounced sclerenchyma caps.

Inflorescence and pedicel

In principle the inflorescence of *Machairophyllum* is a dichasium (Figure 8A) which is typical of Mesembryanthemaceae (Hartmann 1993). The number of flowers ranges from three to \pm seven. Frequently one of the side branches is aborted, which is probably the result of environmental factors, or may be caused by disease, or insect attack. In a large number of specimens the flowering shoot is consistently unbranched and has a single flower (Figure 8B), and lateral buds or vestiges thereof were not found. This is obviously the result of a reduction which is also found in some other mesembs and may be part of their life

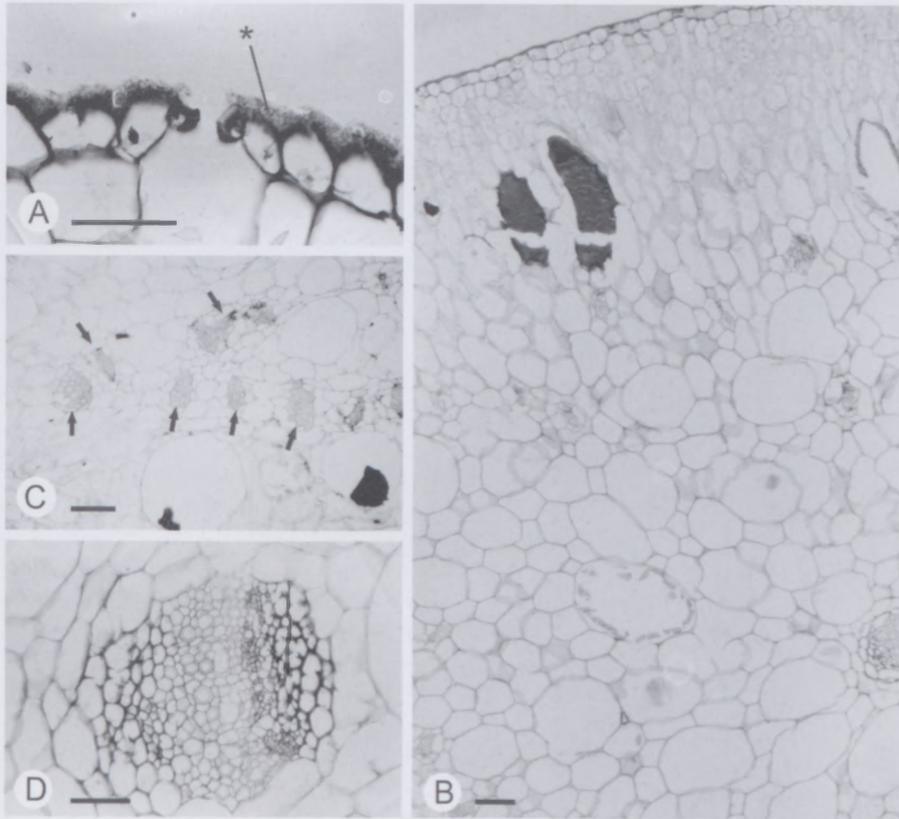


FIGURE 6.—Leaf anatomy in *Machairophyllum* in *vs.* A, *M. albidum*, Kurzweil 1902, epidermis. Asterisk indicates crystal sand in outer epidermis wall. B, D, *M. bijliae*, NBG806/83: B, assimilation tissue; D, central vascular bundle, note the dark colenchyma caps. C, *M. sp.*, NBG44/83: secondary vascular bundles, indicated by arrowheads. Scale bars: A, D, 50 μm ; B, C, 100 μm .

strategy, aimed at a synchronization of the flowering in order to improve the probability of successful pollination (Ihlenfeldt 1989: 80). It was found that the degree of branching is remarkably constant in *Machairophyllum*. In the present study the inflorescence type is considered a

character of major taxonomic importance, with the branched inflorescence characterizing *M. albidum* and *M. stayneri*, and the unbranched inflorescence characterizing *M. bijliae* and *M. brevifolium*. This corresponds exactly with the concepts of Bolus (1960: 157) and J. Vlok (pers.

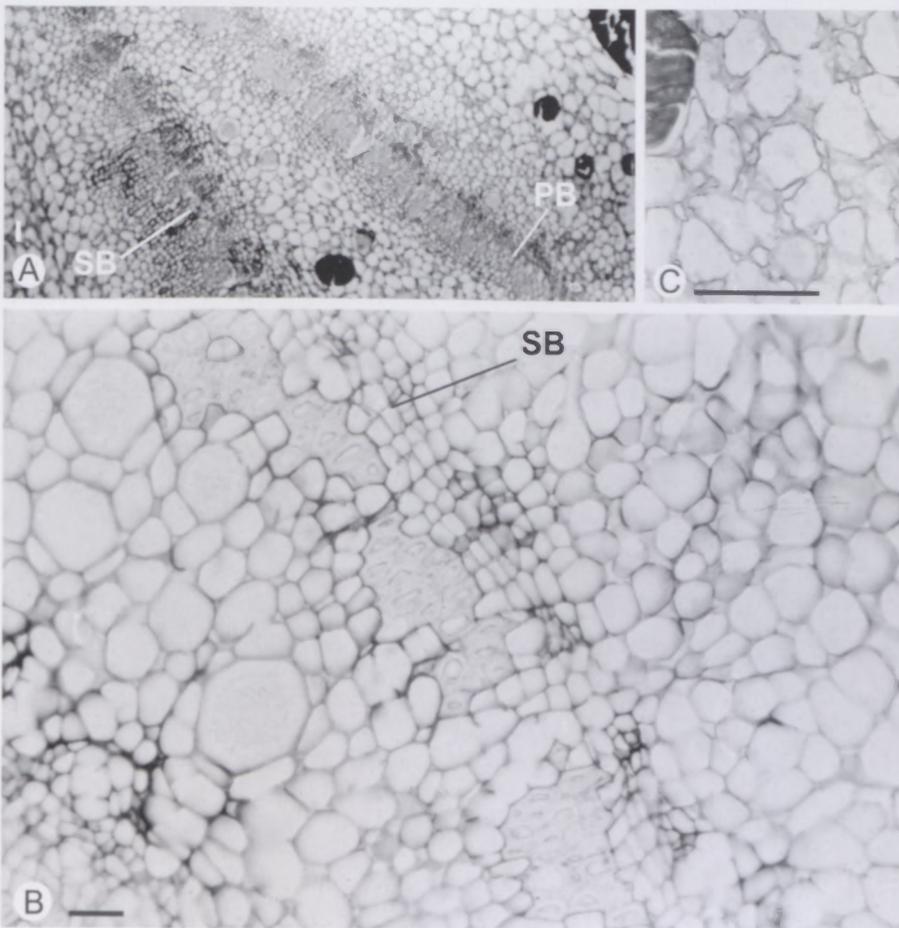


FIGURE 7.—Secondary stem in *Machairophyllum bijliae* in *vs.*, Kurzweil 1919. A, B, vascular bundles; C, pith. PB, primary bundles; SB, secondary bundles. Scale bars: 50 μm .



FIGURE 8.—Semi-diagrammatic representation of inflorescences in *Machairophyllum*. A, *M. albidum*, Kurzweil 1900; dichasium; B, *M. bijliae*, Kurzweil 1919; solitary flower. Scale bars: 10 mm. Drawn by P. Chesselet.

comm.). In the vast majority of cases the distinction of specimens with branched versus unbranched inflorescences is clear-cut but, rarely, poorly grown specimens of *M. albidum* were found to be single-flowered (however, they normally reveal their affinity to *M. albidum* in floral characters).

In all cases the flowers are subtended by an opposite pair of short bracteoles which resemble foliage leaves [These bracteoles have also been referred to as 'bracts', and it needs to be noted that their homology is disputed. However, the term 'bracteoles' was used in the most recent treatment of the genus (Hartmann 2001), and is therefore adopted here]. Bracteoles are 7–130 mm long, with their free upper portion ranging from 6–60 mm; bases are connate and form a sheath. The length of this sheath is strongly intercorrelated with the degree of inflorescence branching: *M. bijliae* and *M. brevifolium*, the two species with unbranched inflorescences, have predominantly basal bracteole sheaths of up to 25 mm long (total range 5–42 mm) whereas *M. albidum*, with branched inflorescences, has predominantly primary bracteole sheaths which are longer than 21 mm (ranging from 15 to almost 100 mm) (Figure 9). The single specimen of *M. stayneri* (branched inflorescence) has primary bracteole sheaths of 15 mm. The term 'primary' is here used for the terminal flower of the dichasium, i.e. here applying to the basal-most bracteoles. *M. albidum* and *M. stayneri* have 'secondary' bracteoles below the flowers of the side branches.

Flowers are generally stalked in *Machairophyllum*. The pedicel is up to 85 mm long in solitary flowers and in terminal flowers of branched inflorescences, is usually shorter on side branches, sometimes elongate in the

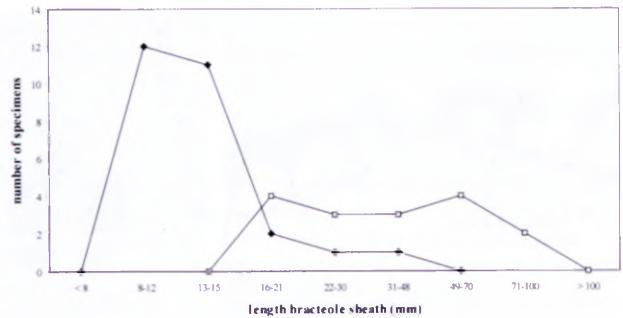


FIGURE 9.—Length of bracteole sheath in *Machairophyllum albidum*, □; and *M. bijliae*, ◆. Average measurements were used for calculation.

fruit stage, 3–6 mm thick and are smooth on the outside or have pronounced ribs. Anatomically they are rather uniform, consisting of an epidermis with a crystal sand layer, a weakly-defined hypodermis, a massive cortex followed by the vascular cylinder and a parenchymatic pith (Figure 10A, B). The vascular cylinder is a closed ring with inner xylem elements, multi-layered cambium and an outer phloem. All specimens examined have a closed collenchymatic ring on the outside of the phloem. Fibre bundles in the cortex occur occasionally.

Flower

Flowers are actinomorphic and bisexual, up to 65 mm in diameter, with few sepals, numerous petals and stamens, and up to 12 stigmas; filamentous staminodes are absent. In *M. albidum* and *M. bijliae* the number of sepals and locules is subject to slight variation (see also Bolus 1950: 229), and different numbers may even be found in different flowers on the same plant. In contrast, in *M. brevifolium* the number is constantly six. Pollination studies were not carried out, but from a functional-morphological point of view the flowers can be referred to the 'Phalaenophilous' type (Hartmann 1991: 91). A moth-pollination syndrome is suggested by the yellow flowers with a pale centre which are open in the afternoon, evening or at night.

Sepals five to eight, unequal, (Figure 11A) succulent and weakly keeled, with white, membranous margins, apically acute, acuminate or rarely somewhat obtuse, frequently with subapical mucro on the dorsal side; total length \pm 3–22 mm. Sepals of *M. albidum* tend to be wider than those of the other species, but a comparative analysis of the sizes does not allow a grouping within the genus (Figure 11B).

Petals develop as staminodes from the androecial primordium as in other Mesembryanthemaceae–Ruschioideae (Hartmann 1993); are arranged in three to seven series; are ligulate or linear-lanceolate with acute or more often obtuse apex; up to $35 \times \pm 0.3$ –2 mm; are yellow or golden yellow and often have reddish, copper-coloured or orange-coloured outsides and tips and paler bases; petal sizes as well as the ratio of the lengths of petals and sepals are largely continuous (Figure 11C, D).

Stamens remain erect during anthesis and form a cone; their bases are epipillate or only the inner ones are obscure-

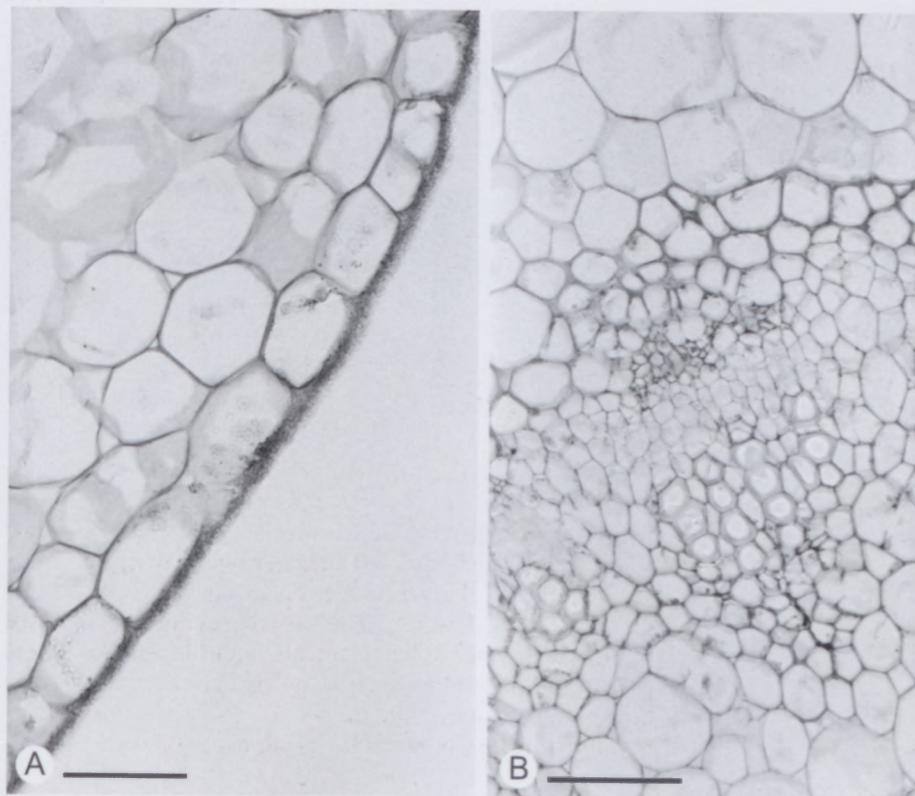


FIGURE 10.—Anatomy of flower stalk in *Machairophyllum* in *vs.* A, *M. albidum*, Kurzweil 1902, epidermis; B, *M. bijliae*, Kurzweil 1925, close-up of vascular cylinder. Scale bars: 50 µm.

ly papillate; are 5–19 mm long and generally longer in the larger-flowered *M. albidum* than in *M. bijliae*.

Nectaries are meronectaries of the lophomorphic type (Rappa 1912; Hartmann 1991), green. They appear as five to twelve \pm prominently raised portions of a ring at the inner base of the stamens opposed to the locules (Figure 12A–C). The number of nectaries is normally identical with the number of carpels/locules. Numerous modified stomata can be seen and are frequently partly blocked (Figure 12F). Crystals were occasionally also observed on these nectaries, both in transsections and SEM micrographs (Figure 12E). Their chemical nature is not known, but they are probably not simply made up of solidified nectar, as it is difficult to imagine that crystallized nectar would not have dissolved during the chemical preparation for SEM or wax embedding. In a few specimens there are also structures that resemble minute craters surrounded by a pronounced circular ridge (Figure 12D). In the past, the nectaries of *Machairophyllum* have been misinterpreted, as they have been termed distant, approximate or contiguous (Herre 1971) which is probably mainly the result of their different extent of formation.

The syncarpous ovary is epigynous and is made up of five to twelve carpels which terminate in slender, free stigmas that nearly reach the height of the stamens. Each ovary chamber contains many ovules on parietal placentae. *M. albidum* has predominantly ten to twelve stigmas, whereas most specimens of *M. bijliae* and the type of *M. stayneri* have six to eight stigmas (erroneously 7 or 8 were cited in the description of the species). The two specimens of *M. brevifolium* examined here exhibit six stigmas (Figure 13).

Unlike many other Mesembryanthemaceae, the flowers of *Machairophyllum* are afternoon-active, vespertine or nocturnal and remain closed during the day.

Fruit

Obconic, 7–15 mm in diameter when closed, loculicidal, hygrochastic capsules as in most other Mesembryanthemaceae–Ruschioideae (Hartmann 1991, 1993); their base is funnel-shaped and the top strongly raised in the centre; sutures are prominent and the high valve rims are normally reflexed (Figure 14A). Fully expanded capsules usually have the valves at right angles to the floral axis. The capsules do not clearly fall into any of the morphological fruit types distinguished by Hartmann (1988: 349) and the genus was therefore listed as a 'genus of uncertain position'. Cheslet *et al.* (2000) referred to the capsule as 'similar to that of *Cylindrophyllum* and therefore perhaps close to the *Leipoldtia* type', but with spongy tissue in the covering membranes and small closing bodies.

Within the genus *Machairophyllum* the internal structure of the capsule is not uniform (Figure 14B–D). Capsules normally have 5–12 locules with the numbers 6–10 being the most common. A larger locule number of 14 or 15 was reported by Salm Dyck (1849), but this could not be confirmed. As pointed out before, the number of locules is often not stable in *Machairophyllum*. Valves are broadly to narrowly triangular, depending on the locule number, 3.0–6.6 mm long, basal width 3.5–6.0 mm, shortly and narrowly winged with the exception of *M. brevifolium*; wings taper apically with their ends drawn out into slender tips which are connate with the awns of the expanding keels; expanding keels \pm parallel at the base and close to each other and diverge to some degree in their distal part, serrate or lacerate on their inner margin, though sometimes minutely so; tips are slender awns, 1–2(–3) mm long which nearly reach the tip of the valves. These awns are generally cohering and frequently cross each other. In *M. brevifolium* the awns are shorter or hardly developed. Covering membranes

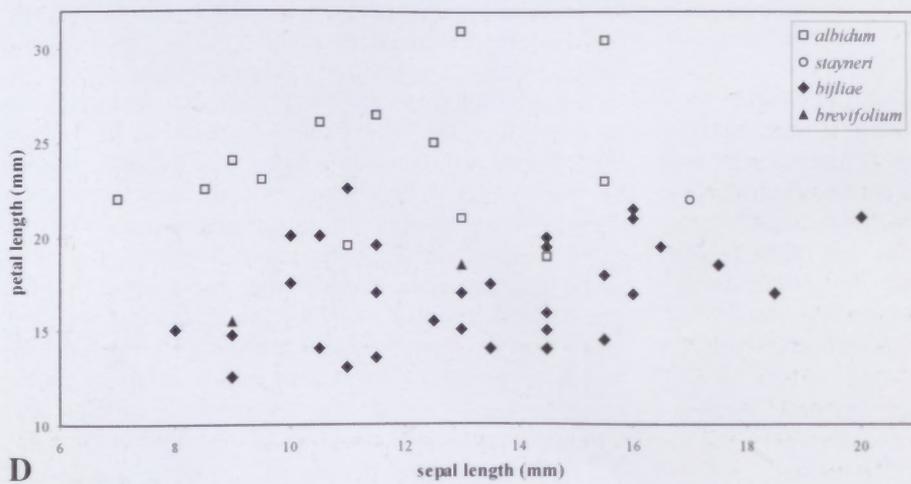
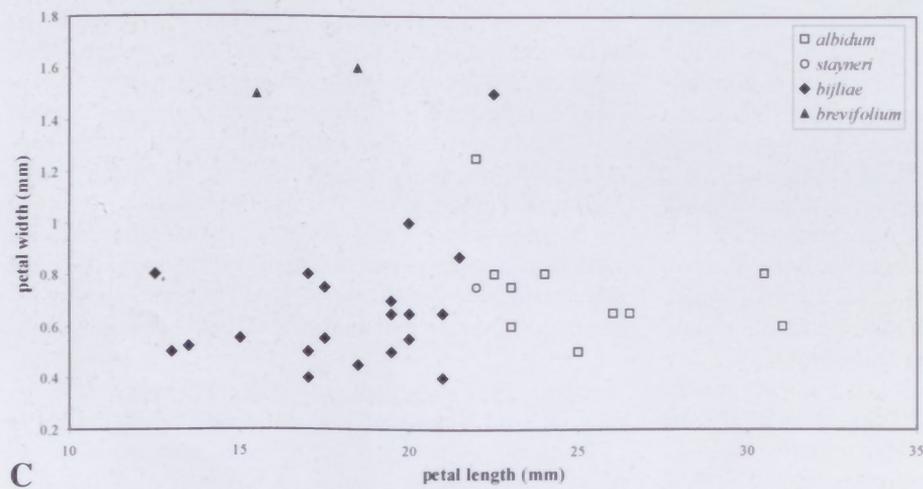
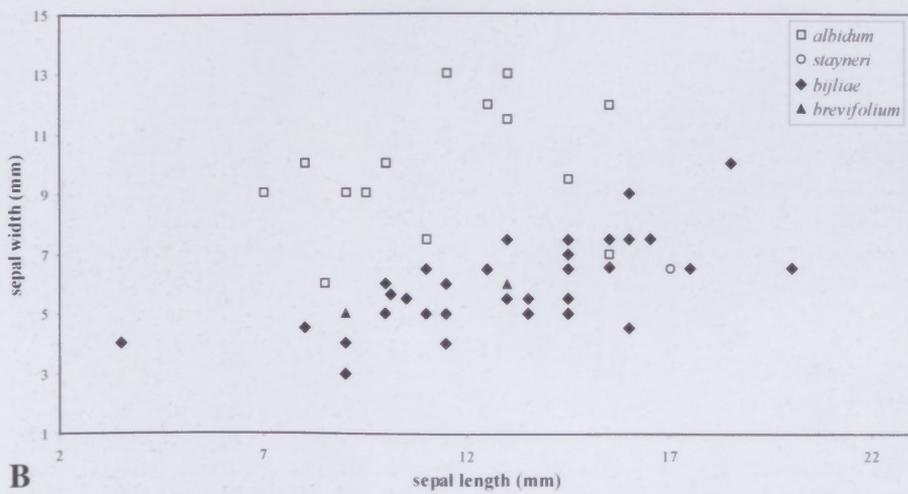
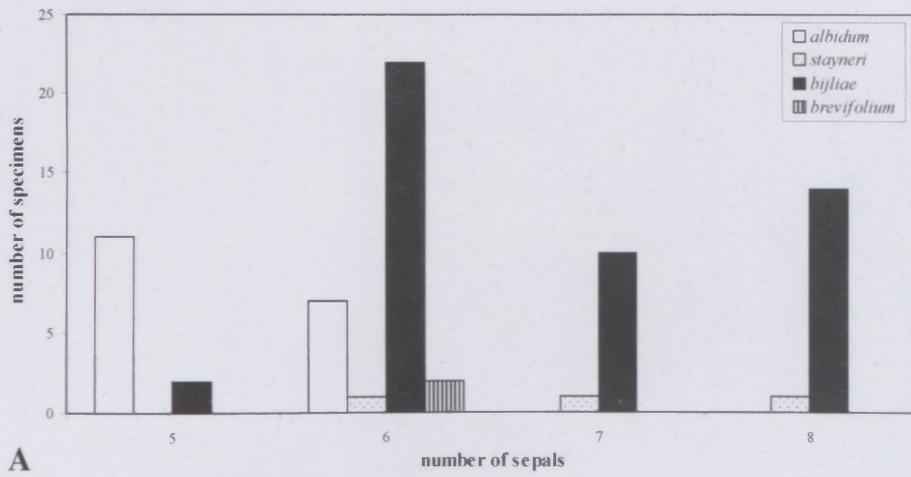


FIGURE 11.—Diagrams showing sepal and petal characters in *Machairophyllum*. Plotted measurements in B–D represent average values found in examined flowers. A, number of sepals; B, relationship of sepal length and width; C, relationship of petal length and width; D, relationship of sepal length and petal length.

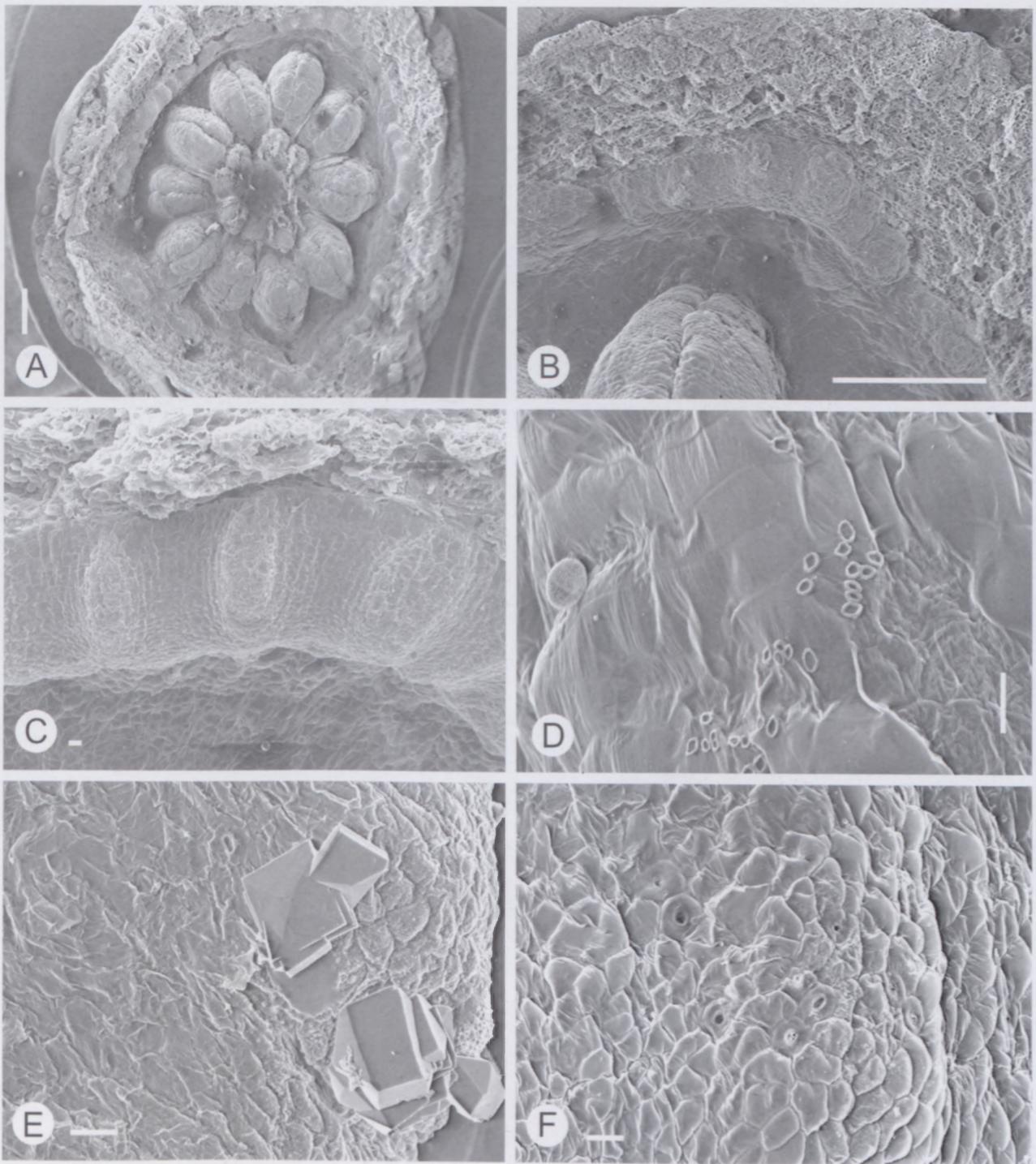


FIGURE 12.—SEM micrographs of nectaries in *Machairophyllum*. A–E, *M. albidum*: A, receptacle with sepals, petals, stamens and stigmas removed, showing ring of nectar glands; B, C, individual nectar gland; D, crater-like structures on surface of nectar gland; E, crystals. F, *M. bijliae*, modified stomata on nectary. A–C, Kurzweil 1900; D, E, Kurzweil 1902; F, Kurzweil 1919. Scale bars: A, B, 1 mm; C–E, 20 μ m.

are concave in *M. albidum* (Figure 14B), whereas in *M. bijliae* and *M. brevifolium* (Figure 14C, D) they are roof-like in shape, \pm translucent and rather stiff in texture. In the latter species, they do not cover the locules entirely and are somewhat short. In fact, *M. brevifolium* is quite distinct from other *Machairophyllum* species in its fruit morphology: the expanding keels are thick, without awns or wings, closing bodies are reduced to tiny knobs and the fruit is consistently six-locular. In the other species, closing bodies are small and frequently deep-set. Their shape varies from rotund to kidney-shaped. In one specimen they were found to be slightly two-lobed (Kurzweil 1919). Although fruit morphology has been considered

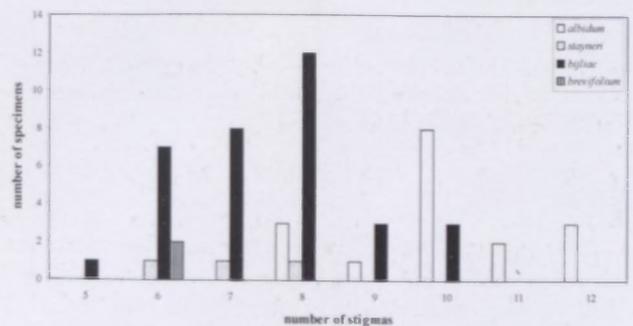


FIGURE 13.—Diagram showing number of stigmas in *Machairophyllum*.

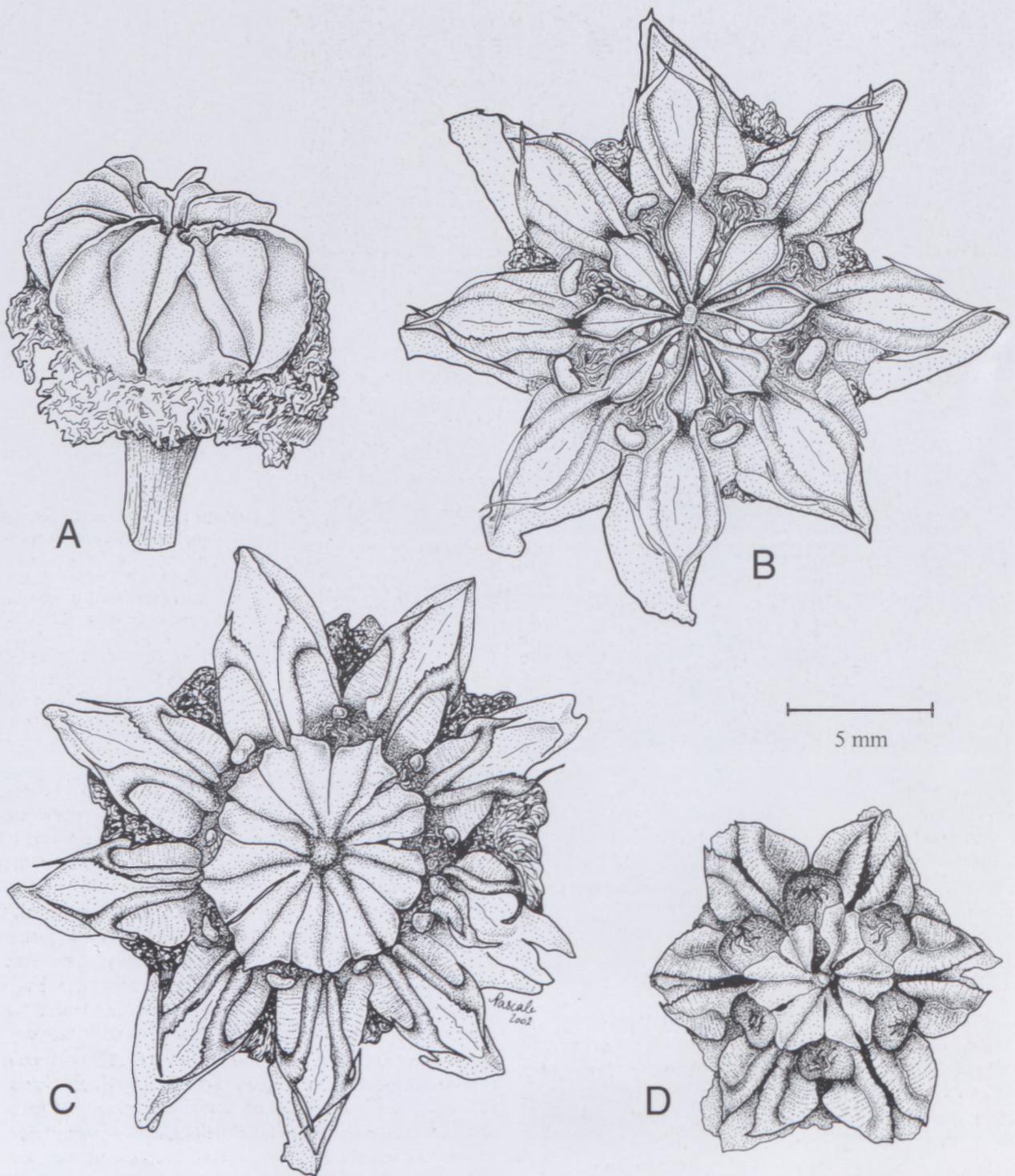


FIGURE 14.—Capsules in *Machairophyllum*: A, closed; B–D, open. A, B, *M. albidum*, Kurzweil 1900; C, *M. bijliae*, Kurzweil 1919; D, *M. brevifolium*, Kurzweil 1904. Drawn by P. Chesselet.

as the most important complex of characters for the delimitation of genera in the Mesembryanthemaceae, this does not seem to be the case in the current interpretation of the genus *Machairophyllum*.

Seeds

The micromorphology of 29 specimens was examined in the present study. Seeds are pear-shaped with a protruding micropyle which conforms with the seeds of other Mesembryanthemaceae (Figure 15A) (Hartmann & Gölling 1993), $0.87(0.73-1.00) \times 0.64(0.44-0.77)$ mm, dark brown to light yellowish brown. In the central seed

portion the testa cells are predominantly elongate with a strongly convex periclinal wall and have irregularly undulating anticlinal walls (Figure 15B–E); neighbouring cells almost touch each other. Very rarely, the anticlinal depressions between the cobblestone-like convex testa cells are rather wide. The outer periclinal wall is normally smooth to slightly verrucose. In *Desmet 2158* most of the periclinal surface is smooth but the marginal areas are rough (Figure 15D). The periclinal walls of the testa exhibit epicuticular formations of various density and shape. Epicuticular formations mostly consist of minute, loosely or densely arranged rodlets (Figure 15E–G), but flake-like epicuticular formations also occur

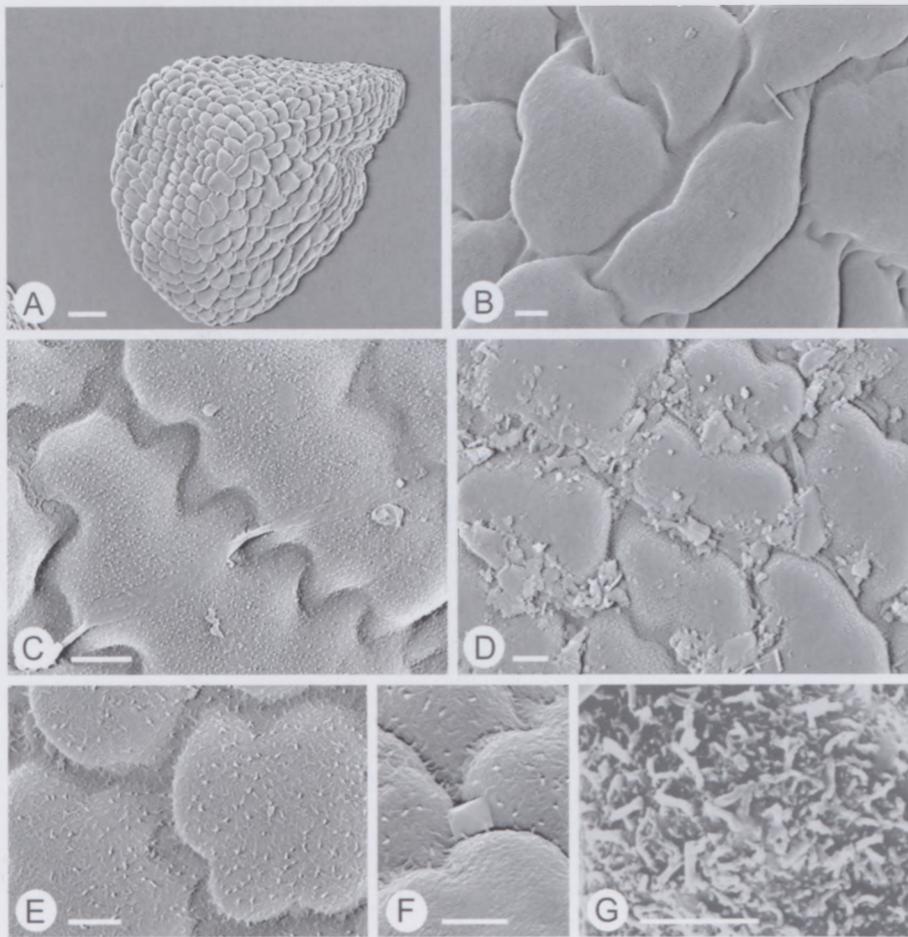


FIGURE 15.—SEM micrographs of seed morphology in *Machairophyllum*. The close-up micrographs in B–G were taken in the central seed portion. A, B, *M. cf. bijliae*, Bayer 7027; C–G, *M. bijliae*. C, Kurzweil 1898; D, Desmet 2158; E, F, Kurzweil 1916; G, Kurzweil 1925. Scale bars: A, 100 μm ; B–F, 10 μm , G, 5 μm .

(e.g. Desmet 2158; Kurzweil 1901) (Figure 15D). The occurrence of spinulose rodlets was reported in Mesembryanthemoideae and a few genera of Ruschioideae (Bittrich 1986; Ehler & Barthlott 1978). A crystal of unknown nature and function was found on the testa just above an anticlinal wall (Figure 15F).

Pollen

Pollen was examined in 33 air-dried specimens and proved to be uniform (Figure 16). Pollen grains are tricolpate which is the common condition in the family (Dupont 1977), equiaxial to strongly longiaxial, average equatorial diameter 14.80 μm ; average of the polar distance 15.36 μm . The comparatively small size observed (compare with e.g. Dupont 1977 and Chesselet *et al.* 1998) is probably the result of hydration state. The surface of the pollen grains is microspinulose as in the majority of Mesembryanthemaceae (Hartmann 1991), and the size and density of spinules is subject to slight variation in the genus. Irregular perforations through the tectum are visible in all specimens (Figure 16C). In *M. brevifolium* (Lategan 2367/36) these are rather prominent and the pollen is thus approaching a reticulate condition.

Phytogeography and ecology

All confirmed collections of *Machairophyllum* come from the southern parts of central South Africa (Western and Eastern Cape) the only area that the genus is known from with certainty (Figure 2). The distribution range is in the Little Karoo from Barrydale eastwards and in the adjacent

mountain ranges of the Swartberg in the north and the Langeberg in the south, and stretches further to Oudtshoorn, Uniondale, the Baviaanskloof and Kouga Mountains and to Salt Pans Nek (near Jansenville); it is also known from the Zuurburg (near Kirkwood north of Port Elizabeth) which is the easternmost occurrence of the genus. Unfortunately many of the older herbarium collections indicate only the district where they were found and their exact locality is therefore unknown. Populations are rather localized within the distribution range, but in some areas this may be the result of the lack of suitable habitats or of low collecting activity. Specimens referred to *Machairophyllum* were also collected in Port Elizabeth, near Mossel Bay, in De Hoop Nature Reserve near Bredasdorp and near Laingsburg, but these were later correctly identified as belonging to different genera. In addition, there is also a record from the Richtersveld of Northern Cape but this isolated occurrence needs confirmation (Figure 2). This spectacular collection was made near Lekkersing about 10 years ago (*Viviers s.n.*, NBG, hort.)—some 600 km from the well-known distribution area of the genus and also in an area where the preferred habitat of *Machairophyllum* is scarce. No plants were later found despite an extensive search in the area (E. van Jaarsveld pers. comm.). The unbranched inflorescences, the short bracteole sheaths, as well as the number of sepals and locules suggest that the plant belongs to *M. bijliae*. Another locality in Northern Cape, situated in the Vanrhynsdorp District, was shown on the distribution map of *Machairophyllum* presented in Herre (1971: 198) but no comment on the origin of the information was made (Figure 2). However, the occurrence of *Machairophyllum* in Northern Cape would not be too surprising, as up to the 1930s 'Little Namaqualand' was thought to be the distribution area of *M. albidum* (see below).

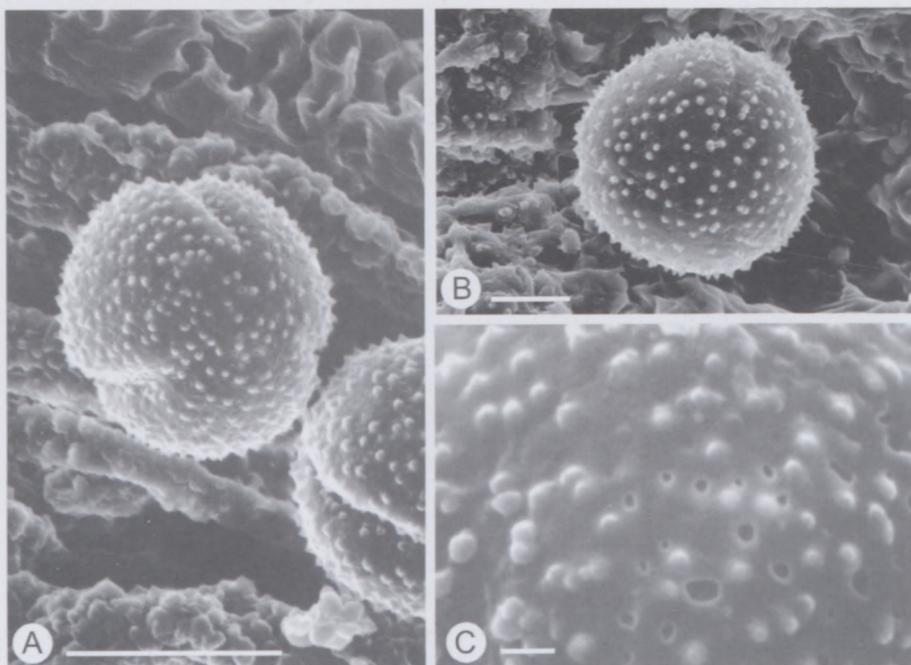


FIGURE 16.—SEM micrographs of pollen morphology and surface ornamentation in *Machairophyllum bijliae*. A, B, pollen grains; C, surface ornamentation. A, *Fourcade NBG424/24*; B, *Holland NBG1697/36*; C, *Baxter NBG3166/14*. Scale bars: A, B, 10 μ m; C, 1 μ m.

Machairophyllum albidum occurs in the western part of the distribution area of the genus, ranging from Barrydale to around Oudtshoorn. An outlying locality is known near Klaarstroom in the eastern Swartberg. The widespread *M. bijliae* is known from the George and Oudtshoorn Divisions eastwards to the Zuurberg. The distribution areas of these two species overlap in the Oudtshoorn District. *M. brevifolium* has so far only been recorded in the red conglomerate hills between Oudtshoorn and De Rust, and *M. stayneri* is only known from the Zuurberg.

In the past there was considerable confusion around the distribution of *Machairophyllum*. Linnaeus (1762), when describing *Mesembryanthemum albidum* (now *Machairophyllum albidum*) gave its locality as 'Habitat in Aethiopia' which merely implied that the plants came from Africa. Sonder (1894), in his account in *Flora capensis*, quoted Namaqualand as the distribution area of the sole *Machairophyllum* species known at the time, *M. albidum* (as *Mesembryanthemum albidum*). Sonder cited two collections, one made by A. Wyley and the other by Drège. The former collection was examined by Mrs L. Bolus who provisionally referred it to the genus *Cheiridopsis* (Bolus 1960: 156 [in the footnote]). The latter could not be traced in the present study, and therefore it cannot be ruled out entirely that it is indeed a species of *Machairophyllum*. Several subsequent authors quoted the distribution 'Namaqualand' for *M. albidum* or the entire genus *Machairophyllum* (e.g. Berger 1908; Jacobsen 1935). However, both Berger and Jacobsen probably merely adopted the distribution given by Sonder. All subsequent collections of *Machairophyllum* were only made in the southern part of central South Africa, and therefore the occurrence of *Machairophyllum* in Northern Cape was increasingly doubted (Schwantes 1957: 93).

Machairophyllum albidum and *M. bijliae* are most commonly found on rocky outcrops (Figure 1A, B), on bare rock on N-exposed slopes and on rocky ridges in mesic to dry fynbos or in renosterveld, commonly also

where fynbos and renosterveld meet. On one herbarium collection a fynbos–valley bushveld mix is also given. The occurrence of *Machairophyllum* in comparatively moist fynbos is rather atypical in the family, as most Mesembryanthemaceae are found in arid or semi-arid areas in southern Africa, although this unusual habitat is also that of a few other genera (e.g. *Erepsia*, *Carpobrotus*). The few accurate collector's notes available indicate that the species grow in rocky soil and bedrock derived from TMS. The plants rarely occupy grassy habitats amongst rocks over deeper soils (mainly in Eastern Cape) and are then nearly hidden in tall vegetation (Figure 1C). No accurate ecological information is given on the type sheet of *M. stayneri*, but the area where the species was collected generally falls in the Savanna Biome (Rutherford & Westfall 1994) although fynbos and renosterveld occur at higher altitudes in this area. *M. brevifolium* is only known from the red conglomerate hills near Oudtshoorn where it grows in fields of pebbles interspersed with small shrubs.

Altitudes for the genus range from 330 m in the Little Karoo to just below 1 600 m in the Swartberg. *M. albidum* is usually found at low altitudes ranging from 330 to 600 m. *M. bijliae* is very much a high-altitude species, with almost all collections made between 800 m and 1 560 m (top of Swartberg Pass). The only exception is a collection of this species made at 570 m near Joubertina (*Fourcade* 2384; BOL). The type locality of *M. brevifolium* is between 550 and 600 m.

Flowering in *Machairophyllum albidum* and *M. bijliae* is often stimulated by burning of the habitat, which has been observed during the present study and has also been reported before (J. Vlok pers. comm.; notes on a herbarium sheet of *M. albidum*, *Blackburn s.n.*, BOL63638). The fact that veld fires have a profound effect on the flowering of plants in the Cape Floristic Region is well documented in other families (e.g. *Amaryllidaceae*, *Iridaceae*, *Orchidaceae*), but is not known in *Mesembryanthemaceae*. However, other effects of veld fires on mesembs have been reported (e.g. the rapid

spreading of *Erepsia* species in response to burning: Liede 1989, 1990; Hartmann 2001). Plants of *Machairophyllum* are normally not seriously damaged by veld fires. Most plants grow in rocky sites where the fire intensity is low. Dense clump formation ensures that only the outer leaves are singed during the burning and most adult individuals therefore survive the fire. Furthermore, the seeds of the previous season are well protected by the comparatively hard and robust capsules, and plenty of seed is therefore available in the post-fire environment. Flowering in *M. brevifolium* is apparently not stimulated by burning.

Phylogeny

Machairophyllum in its current delimitation is fairly uniform in vegetative, floral and several capsule features which seems to suggest that it is indeed a natural group. At present, the genus can be diagnosed according to the following characters: clump-forming habit without visible stems; smooth and dotless and often waxy leaves of a green or whitish green colour; large yellow flowers which are open in the afternoon, evening or at night; absence of filamentous staminodes; long filiform stigmas; capsules with raised sutures and reflexed valve rims; covering membranes present; closing bodies small; expanding keels serrate or lacerate and apically \pm awned. However, in a strict sense the morphological and anatomical data obtained here are considered insufficient as a basis for a sound phylogenetic analysis, as a definite synapomorphy for the genus cannot be identified at this stage. We therefore suggest that further data be obtained for the entire *Bergeranthus* group, including molecular ones, to resolve the phylogeny of *Machairophyllum*. While *M. albidum* and *M. bijliae* are fairly similar in details of the internal capsule structure (valve wings present; covering membranes complete; high and variable number of locules), *M. brevifolium* deviates somewhat (valve wings absent; covering membranes incomplete; low and stable number of locules) thus leaving doubt regarding its systematic position. Nevertheless, until new data become available, *Machairophyllum* is retained in its current delimitation for practical reasons despite the distinctness of *M. brevifolium* and we consider it premature to require that genera in the mesembs be defined on the basis of synapomorphies.

TAXONOMY

Machairophyllum Schwantes in Möllers Deutsche Gärtner-Zeitung 42: 187 (1927); Bolus: 155–158 (1960) (synopsis). Type species: *Machairophyllum albidum* (L.) Schwantes.

Perissolobus N.E.Br.: 278 (1930); N.E.Br.: 294 (1931). Type species: *Perissolobus bijlii* N.E.Br.

Nearly stemless and tuft-like perennial herbs, entirely glabrous, basally branched with age, sometimes forming mats of up to 1.2 m diam. Leaves succulent and trigonous, decussate, simple and entire, sessile, stipulate, crowded, linear-lanceolate ('sabre-shaped', 'dagger-shaped') or rarely subrhomboid, 10–145 \times 8–26 mm

and up to $\frac{3}{4}$ as deep, base of a leaf pair connate to form a sheath 5–18 mm long, leaf apex acute or acuminate; surface smooth and dotless, waxy in appearance, whitish green to green, often with a reddish tinge; old leaves persisting on plant for several years and turning black; stomata superficial to slightly sunken, outer epidermal wall with well-developed crystal sand layer, epicuticular wax mostly in the form of a solid and smooth layer, rarely breaking up into platelets, local wax projections mainly in form of rodlets, rarely granules or flakes. Inflorescences unbranched with a solitary flower or dichasially branched with up to seven flowers, rarely monochasial due to loss of one side branch, bracteolate; bracteoles leaf-like, 7–130 \times \pm 5–10 mm, bases connate for (5–)10–70(–100) mm. Flowers actinomorphic and bisexual, large, showy, up to 65 mm diam., open in afternoon, evening or at night, on 12–100 mm long pedicels; pedicels sometimes elongating in fruit. Sepals 5–8, triangular-lanceolate, green with purplish tinge, with whitish membranous margins, (3–)8–18(–22) \times (3–)4–16 mm, unequal, acute, acuminate or rarely obtuse, outside often apically keeled and mucronate. Petals (petaloid staminodes) numerous, densely 3–7-seriate, linear or lorate, (8–)15–35 \times 0.3–2.0 mm, obtuse or acute, yellow or golden and frequently orange-red or copper-coloured on outside and near tip, often paler near base. Filamentous staminodes absent. Stamens erect, forming a cone; filaments epapillate or only inner ones inconspicuously papillate at base, (5–)7–15(–19) mm long, whitish; anthers dehiscing with longitudinal slits, anther and pollen yellow. Ovary usually obconic, syncarpous, 5–12(–15?)-carpellate, placentation parietal, with many ovules per chamber. Nectar glands 5–12, apparent as \pm raised portions on a ring. Stigmas (5)6–12(–15?), slender or filiform, usually slightly shorter than stamens, (4–)8–15(–16) mm long. Fruit a hydrochastic loculicidal capsule, 5–12(–15?) locular, base funnel-shaped with slightly concave sides, sutures on top strongly compressed, valve rims high and usually reflexed, valves mostly shortly and narrowly winged, wings basally broader and tapering into fine awns distally, which are connate with awns of expanding keels, expanding keels at first parallel and close to each other, but diverging above, serrate or lacerate and mostly terminating in slender awns which are directed towards median axis of valve (often crossing each other), nearly as long as valves, loculi with complete or almost complete translucent to whitish covering membranes, closing bodies small and frequently deeply set, no additional closing devices present. Seeds \pm pyriform, \pm (0.7–)0.8–1.0 mm long. Flowering occurs from spring to early summer.

Key to species

- 1a Inflorescence branched; bracteole sheath mostly longer than 25 mm:
 2a Sepals 5 or 6; stigmas 8–12; widespread 1. *M. albidum*
 2b Sepals and stigmas 6–8; only Zuurberg 2. *M. stayneri*
 1b Inflorescence unbranched; bracteole sheath mostly shorter than 25 mm:
 3a Leaves (20–)32–70(–85) \times 8–15(–18) mm; sepals 5–8; stigmas 5–10; widespread 3. *M. bijliae*
 3b Leaves 10–30 \times 10–26 mm; sepals and stigmas 6; currently only known in red conglomerate hills to east of Oudtshoorn 4. *M. brevifolium*

1. *Machairophyllum albidum* (L.) Schwantes in Möllers Deutsche Gärtner-Zeitung 42: 187 (1927). *Mesembryanthemum albidum* L.: 699 (1762). *Bergeranthus albidus* (L.) Schwantes: 180 (1926). *Carruanthus albidus* (L.) Schwantes: 181 (1926) nom. inval. Iconotype: Dillenius, Hortus Elthamensis: 243, t. 189, fig. 232 (1732).

Mesembryanthemum cookii L.Bolus: 2 (1925). *Bergeranthus cookii* (L.Bolus) Schwantes: 180 (1926). *Carruanthus cookii* (L.Bolus) Schwantes: 181 (1926) nom. inval. *Machairophyllum cookii* (L.Bolus) Schwantes: 187 (1927). Type: Western Cape, 3320DC, Barrydale and 15 miles west, October, Compton & Cook NBG1995/23 (BOL, holo.).

Compact, tufted and nearly stemless, succulent herb, entirely glabrous, basally branched with age. *Leaves* trigonous, linear-lanceolate, entire, sessile, 40–145 × 9–20 mm and up to $\frac{3}{4}$ as deep, apically acute to acuminate, connate sheath 7–17 mm long, surface smooth and waxy in appearance, whitish green or green. *Inflorescence* branched, up to 170 mm tall, with 2–7 flowers; bracteoles leaf-like, (25–)50–130 × 5–8 mm, with a connate sheath (17–)42–80(–100) mm long. *Flowers* large and showy, 45–65 mm diam., vespertine, nocturnal or open from 15h00 onwards and often closing again in the evening; pedicels up to 100 mm long. *Sepals* 5 or 6, triangular-lanceolate, 6–20 × 5–16 mm, unequal, green with a purplish tinge, with whitish membranous margins, apically ± acute. *Petals* ± 400, linear or lorate, 18–35 × (0.3–)0.6–1.0(–1.5) mm, inside yellow, frequently orange-red or copper-coloured on outside and near tip. *Stamens* numerous, erect and forming cone, 10–15(–19) mm long; filaments white; anthers yellow. *Ovary* obconic, (8–)10–12(–15?)-carpellate, placentation parietal, with many ovules per chamber. *Nectar glands* as ± raised portions on whitish ring, (8–)10–12, green. *Stigmas* (8–)10–12(–15?), slender, 8–15(–16) mm long. *Fruit* a loculicidal capsule 12–15 mm diam., base funnel-shaped, sutures on top compressed, valve rims high and diverging; with (8–)10–12(–15?) locules, valves 4.0–5.6 × 3.2–3.5 mm in size, narrowly winged; covering membranes complete; closing bodies small; expanding keels lacerate, parallel and adjacent at base, but soon diverging, apically awned. *Flowering time*: mainly November and December.

Distribution, habitat and biology

The species is mainly known in the Little Karoo from Barrydale to the George and Oudtshoorn Divisions which is the western part of the distribution area of the genus. On Cloetespas near Herbertsdale, the species extends over the coastal mountain range. *M. albidum* has also been collected near Klaarstroom in the eastern part of the Swartberg (*Burger* BOL38796, BOL) which is an outlying occurrence of the species (Figure 2). *M. albidum* grows in fynbos and renosterveld, mostly associated with rocky habitats, from 330–600 m.

Similar species

Vegetatively *Machairophyllum bijliae* is largely identical to *M. albidum* which also occurs in the same type of habitat although *M. bijliae* frequently has shorter leaves. In the flowering stage the difference is immediately obvious, as *M. bijliae* consistently has solitary flowers,

whereas inflorescences of *M. albidum* are branched. On average *M. bijliae* has also slightly smaller flowers with shorter petals. *M. bijliae* differs further by mostly having shorter bracteole sheaths, a higher number of sepals, and ovaries with fewer locules. While the centre of distribution of *M. bijliae* is further east, the distribution areas of the two species overlap in the Oudtshoorn area. *M. bijliae* is always found above 800 m, whereas *M. albidum* is generally a low-altitude species.

Vouchers: Compton & Cook NBG1995/23 (BOL); Hall BOL32083 (BOL); Kurzweil 1890, 1900 (NBG); Muir 3937 (K).

2. *Machairophyllum stayneri* L.Bolus in Journal of South African Botany 26: 155 (1960). Type: Eastern Cape, 3325BC, summit of Zuurberg Pass, October 1958, Stayner KG196/59 (BOL, holo.).

Densely compact, nearly stemless, entirely glabrous, basally branched with age, sometimes forming mats up to 1.2 m diam. *Leaves* trigonous, entire, linear-lanceolate, 70–80(–100?) × 13–16 mm and up to $\frac{3}{4}$ as deep, apex acute or acuminate, basal sheath 10–15 mm long; surface smooth and waxy. *Inflorescence* branched, up to 150 mm tall, lateral buds develop 'tardily' (*vide* Bolus 1960); bracteoles up to 52 mm long, basally connate for ± 15 mm (*vide* Bolus 1960). *Flowers* nocturnal, 50–62 mm diam.; pedicels up to 33 mm. *Sepals* 6–8, long-acuminate, 14–20 × 5–8 mm. *Petals* in 5 or 6 series, 17–27 × 0.5–1.0 mm, yellow to golden and orange to pink on outside, basally paler. *Stamens* 13–17 mm. *Nectar glands* 6–8. *Stigmas* 6–8, thick-filiform, 12–14 mm long. *Fruit* a loculicidal capsule with 6–8 locules. *Flowering time*: October.

Distribution, habitat and biology

The species is known only from the type collection which was made on the Zuurberg in the Eastern Cape (Figure 2). No ecological information was given on the type sheet.

Note

The only collection of this species, consisting of a complete plant and several loose fragments, was made over forty years ago. Despite an extensive search by the first author, no plants could be located. The number of sepals and locules associated with short bracteole sheaths and branched inflorescences suggest that the species is distinct. The branched inflorescence seems to point to a close relationship with *Machairophyllum albidum*. Alternatively, the short bracteole sheaths as well as floral characters may indicate affinities to *M. bijliae*.

If the species is recollected, future studies based on more material may well suggest that *Machairophyllum stayneri* is merely a form of one of the other species. It must be noted that all characters except the branched inflorescence are well within the range of variation of *M. bijliae* which also shares a similar distribution. Thus it cannot be ruled out entirely that the specimen in question is an abnormal plant of *M. bijliae*.

Voucher: Stayner KG196/59 (BOL).

3. ***Machairophyllum bijliae*** (N.E.Br.) L.Bolus, Notes on *Mesembryanthemum* and allied genera 3: 135 (1938), as *bijlii*. *Perissolobus bijliae* N.E.Br. 294 (1931), as *bijlii*. Type: Eastern Cape, Somerset East Div., no date, *Van der Bijl 93* (K, holo.-NBG, photo!).

Machairophyllum stenopetalum L.Bolus: 303 (1931). Type: Eastern Cape, near Willowmore, August 1931, *Brauns SUG8030* (BOL, holo.!).

M. acuminatum L.Bolus: 485 (1935). Type: Eastern Cape, near Humansdorp, October 1934, *Fourcade NBG424/24* (BOL, holo.!).

M. baxteri L.Bolus: 486 (1935). Type: Western Cape, near George, October 1934, *Baxter NBG3166/14* (BOL, holo.!).

M. vanbredai L.Bolus: 238 (1964). Type: Eastern Cape, 3325BC, Witwater Farm, Somerset East Div., August 1962, *Van Breda 1749/62* (BOL, holo.!).

Plants compact, nearly stemless, entirely glabrous, basally branched with age. *Leaves* trigonous, linear-lanceolate, entire, (20–)32–70(–88) × 8–15(–20) mm and up to $\frac{3}{4}$ as deep, connate for (5–)8–13(–18) mm, apex acute or acuminate; surface smooth, waxy in appearance, whitish green to green, often with reddish tinge. *Inflorescence* unbranched; bracteoles leaf-like, (18–)25–40(–60) × 5–8(–10) mm, connate for 7–18(–42) mm. *Flowers* solitary, 30–55 mm diam.; pedicels (13.5–)30.0–70.0(–100.0) mm and up to 38 mm diam., elongating up to 130 mm in fruit; flowers mainly nocturnal (opening late afternoon or evening and staying open all night). *Sepals* (5)6–8, unequal, leaf-like, triangular-lanceolate, (3–)8–22 × 3–8(–11) mm, apex acute, acuminate or rarely obtuse, green with purplish tinge, with whitish membranous margins. *Petals* numerous, linear to lorate, (8–)15–25(–28) × 0.3–1.0(–2.0) mm, yellow, outsides often orange-yellow to copper-coloured, base pale yellow. *Stamens* erect, forming cone, (5–)7–14(–15) mm long; filaments without significant papillae, white; anthers yellow. *Ovary* obconic, (5)6–8(–10)-carpellate, with many ovules per chamber. *Nectar glands* as (5)6–8(–10) ± raised portions on ring, green. *Stigmas* (5)6–8(–10), filiform, (4–)7–14 mm long. *Fruit* a loculicidal capsule, up to 13 mm diam., up to 24 mm when expanded, base funnel-shaped, sutures on top compressed, valve rims high and diverging, capsule with (5)6–8(–10) locules, valves 4.0–5.3 × 3.8–5.8 mm with narrow wings with terminal awns; expanding keels serrate to lacerate, parallel and adjacent at base, but soon diverging, with terminal awns; covering membranes complete, translucent to whitish; closing bodies small. *Seeds* brown, ± 1 mm long. *Flowering time*: mainly between August and November.

Distribution, habitat and biology

This is the most widespread *Machairophyllum* species. It is known from many collections which were made in a broad band from the Oudtshoorn Division, the Swartberg Mountains, the Willowmore District, the Baviaanskloof and Kouga Mountains and Jansenville to the Zuurberg near Kirkwood in Eastern Cape (Figure 2). *M. bijliae* grows in fynbos and renosterveld, mostly associated with rocky habitats. Most collections were made at altitudes of between 800 and 1 300 m, but one collection has been made near Joubertina at 570 m (*Fourcade 2384*; BOL). The highest record comes from near the top of Swartberg Pass at 1 560 m.

Similar species

Machairophyllum bijliae vegetatively resembles *M. albidum*. Differences are given under this species.

Note

The original spelling 'bijlii' is a mistake in gender because the species was named after Mrs D. van der Bijl.

Vouchers: *Baxter 3166/14* (BOL); *Desmet 2158* (NBG); *Taylor NBG1556/33* (BOL); *Van Breda 1761/61* (BOL).

4. ***Machairophyllum brevifolium*** L.Bolus, Notes on *Mesembryanthemum* and allied genera 3: 126 (1938). Type: Western Cape, 3322CB, near Oudtshoorn, August–September 1937, *Lategan NBG2369/36* (BOL, holo.!).

Machairophyllum latifolium L.Bolus: 126 (1938). Type: Western Cape, near Oudtshoorn, February 1938 (hort?), *Lategan NBG2367/36* (BOL, holo.!).

Plants nearly stemless, compact, sometimes forming mats with age, entirely glabrous. *Leaves* trigonous, lanceolate or subrhomboid, entire, 10–30 × 10–26 mm, 12–15 mm deep, apically acute, connate for ± 8–10 mm; surface smooth, waxy in appearance, whitish green to green. *Inflorescences* unbranched; bracteoles 7–23 mm long, connate for ± 5–10 mm. *Flowers* solitary on a pedicel 12–15 mm long, open in the afternoon or vespertine, 30–45 mm diam. *Sepals* 6, unequal, broadly triangular-lanceolate, 8–14 × 4–8 mm. *Petals* numerous, lorate, 3 or 4-seriate, 13–20 × 1–2 mm, yellow. *Stamens* 9–10 mm long; filaments without conspicuous papillae at base; anther and pollen yellow. *Ovary* 6-carpellate, with many ovules per chamber. *Nectar glands* 6. *Stigmas* 6, filiform, 10–12 mm long. *Fruit* a loculicidal capsule with 6 locules, base funnel-shaped, sutures on top compressed, valve rims diverging; valves ± 3 × 4 mm, without wings; expanding keels lacerate, basally parallel and adjacent to each other but soon diverging, acute, but without awns; loculi largely covered by translucent covering membranes; closing bodies very small. *Seeds* brown, ± 1 mm long. *Flowering time*: August and September.

Distribution, habitat and biology

The species is known from only three collections made at or near the type localities of *Machairophyllum brevifolium* and the conspecific *M. latifolium* in the red conglomerate hills between Oudtshoorn and De Rust (Figure 2). In the population which was visited by the first author (at the Farm 'Skuinpad') ± 50 plants grew among small pebbles in rather open shrub vegetation next to the edge of a cliff. The type locality of *M. brevifolium* is at ± 500–600 m altitude. A few collections of this species were also made elsewhere, but their identity is doubtful.

Note

Bolus (1938: 126) pointed out the striking resemblance of this species to the genus *Faucaria*, referring to it as a possible 'connecting link'. This does not necessarily imply a close affinity in a phylogenetical sense although a relationship of the two genera would not be

very unlikely (J. Vlok pers. comm.). *Machairophyllum* and *Faucaria* were not considered as being related in the preliminary grouping presented by Hartmann (1991). However, in the new classification of Chesselet *et al.* (2002) they are grouped together in the Delospermeae.

Vouchers: *Lategan NBG2367/36, NBG2369/36* (BOL).

Unknown species

Three names, '*Machairophyllum minor* L.B.' ('L.B.' probably stands for L.Bolus; *Nel SUG8313*; BOL), '*M. minus*' (*Tugwell & Levenson NBG2634/14*; BOL) and *M. uniondalensis* (Hammer 1991), could not be traced and have never been validly described.

NOTES ON SOME PRESUMABLY RELATED GENERA (TABLE 2)

Bijlia and *Carruanthus*

Bijlia N.E.Br is a genus of two species known from around the Great Karoo town of Prince Albert and from kloofs on the northern slope of the Swartberg to the west of it. A detailed explanation of the complicated nomenclature of the then sole species *B. dilatata* H.E.K.Hartmann was presented by Hartmann (1992). A second species, *B. tugwelliae* (L.Bolus) S.A.Hammer was added later (Hammer 1995). The genus *Carruanthus* (Schwantes), from the Karoo near Willowmore, comprises two species, *C. ringens* (L.) Boom and *C. peersii* L.Bolus. The latter species was placed in the monotypic genus

Tischleria Schwantes on account of having a slightly different capsule structure, but is now also included in *Carruanthus* (Herre 1971; Dyer 1975; Smith *et al.* 1998; Chesselet *et al.* 2000; Hartmann 2001).

Plants of *Bijlia* and *Carruanthus* are compact and glabrous herbs like *Machairophyllum*, and have trigonous leaves. In their morphology, the leaves of *Carruanthus* are similar to those of *Machairophyllum* but differ by having prominent teeth on the margins. Anatomically the leaves of *Bijlia* and *Carruanthus* are very similar to those of *Machairophyllum*. Their surface has a solid wax cover which breaks up to form platelets (Figure 17A, B). Local wax projections in the form of rodlets, granules or flakes (common in *Machairophyllum*) appear to be scarce in *Bijlia* and *Carruanthus*.

Flowers of *Bijlia* and *Carruanthus* are solitary or are arranged in few-flowered cymes, the short peduncles usually hidden among the leaves. Pedicels of *Bijlia* are up to 10 mm long and those of *Carruanthus* up to 100 mm long. Both genera have five subequal to unequal sepals, linear-lanceolate petals and numerous stamens. Filamentous staminodes are absent. In *Bijlia tugwelliae* the nectaries are visible as raised portions of a ring (Figure 17D–F) which is also the situation in *Machairophyllum*. Capsules of *Bijlia* and *Carruanthus* are five-locular, and have strongly raised sutures. In *Carruanthus* these have reflexed valve rims which is shared with *Machairophyllum*. In contrast, the rims are erect and straight in *Bijlia*. While the capsule opens up, in *Bijlia* the valves separate only slightly from each other, where-

TABLE 2.—Various features in the genera *Machairophyllum*, *Carruanthus*, *Bijlia* and *Cerochlamys*

Feature	<i>Machairophyllum</i>	<i>Carruanthus</i>	<i>Bijlia</i>	<i>Cerochlamys</i>
Leaf teeth	absent	present	absent	absent
Leaf anatomy, main bundle	collateral, entire	collateral, slightly two-lobed	collateral, slightly two-lobed	mainly concentric in <i>C. pachyphylla</i> (Kurzwil 1905)
Leaf surface, wax layer	mostly smooth and with local projections in the form of rodlets	breaking up into platelets	breaking up into platelets	breaking up into platelets
Inflorescence, length in relation to the leaves	longer	longer	shorter	shorter
Flowers colour	yellow	yellow	yellow	pink, white
Flowers, time of the day	afternoon till morning	afternoon till evening	afternoon	all day
Flowers, filamentous staminodes	absent	absent	absent	present
Capsule, diameter	7–15 mm	6–9 mm	6–10 mm	6–11 mm in <i>C. trigona</i> and <i>C. pachyphylla</i>
Capsule, sutures	raised, valve rims mostly strongly reflexed	raised, valve rims mostly strongly reflexed	raised and straight valve rims	raised and valve rims straight in <i>C. gemina</i> and <i>C. pachyphylla</i>
Capsule, locules	5–12(–15?)	5	5	5 or 6
Capsule, opening	fully	fully	only slightly	valves erect when expanded
Capsule, expanding keels	parallel at the base, diverging above	more or less parallel	slightly diverging at the base, strongly above	diverging from the base
Capsule, expanding keels	serrate or lacerate	very finely serrate	finely serrate	smooth in <i>C. pachyphylla</i>
Capsule, awns of expanding keels	0–2(–3) mm	0–1 mm	0.5–1 mm	0–1 mm
Capsule, valve wings	mostly short and narrow, rarely absent	short and narrow	absent	absent
Capsule, covering membranes	mostly complete	complete in <i>C. ringens</i> , narrow brim in <i>C. peersii</i>	complete	complete
Capsule, closing bodies	minute or small and deeply set	small or absent	large, white	absent, but placenta often with terminal knob
Seeds	cells convex	cells convex	cells papillate	cells papillate
Seeds, epicuticular formations	mostly rodlets	rodlets	granules	unknown

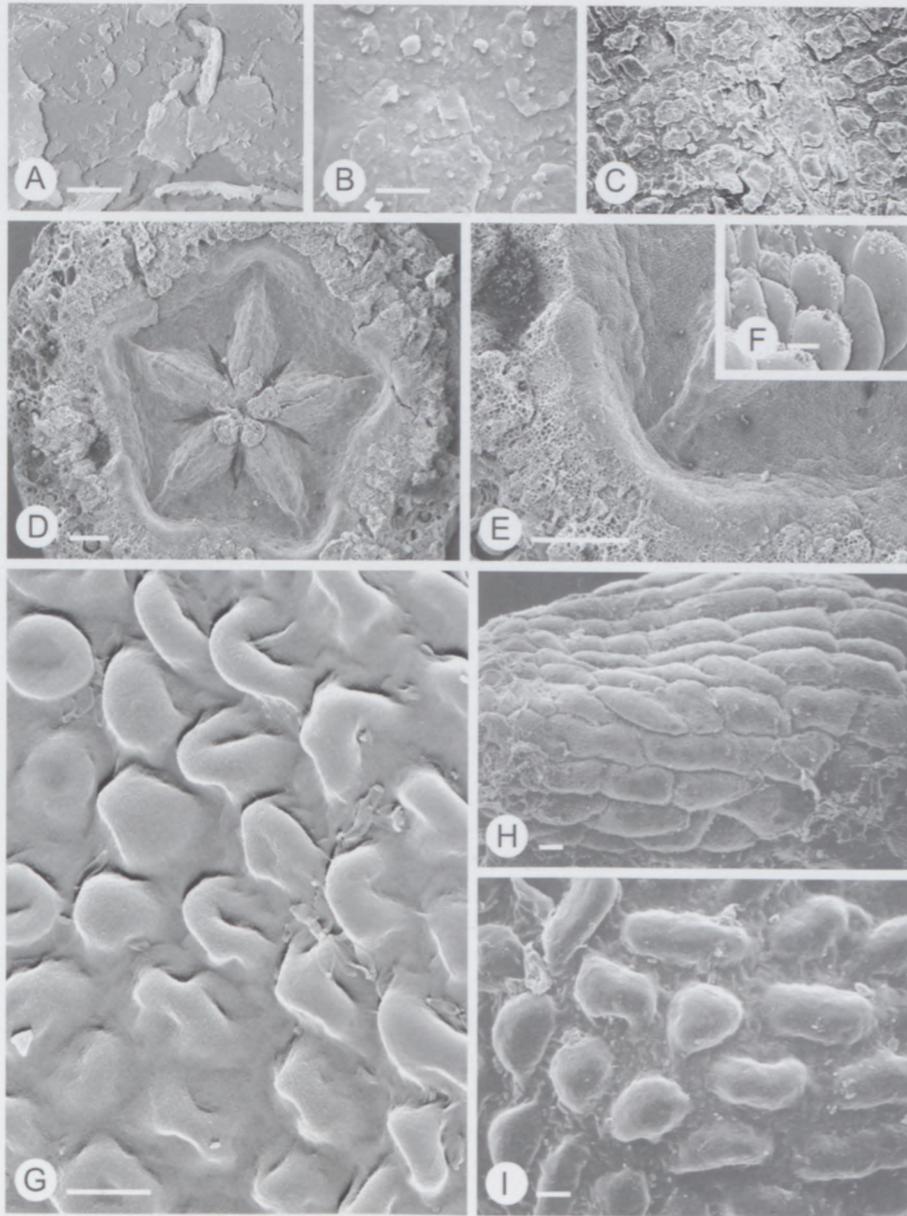


FIGURE 17.—SEM micrographs of various features in *Bijlia*, *Carruanthus* and *Cerochlamys*. A–C, leaf surface: A, *Bijlia tugwelliae*, Kurzweil 1927; B, *Carruanthus peersii*; C, *Cerochlamys pachyphylla*. D–F, nectaries of *Bijlia tugwelliae*, NBG702/86. G–I, seed surface: G, *Bijlia dilatata*, NBG526/68; H, *Carruanthus peersii*; I, *Cerochlamys pachyphylla*. B, H, Kurzweil 1926; C, I, Kurzweil 1905. Scale bars: A–C, F–I, 20 μ m; D, E, 500 μ m.

as they are fully or largely spreading in *Carruanthus*. Valve wings are absent in *Bijlia* but are developed as short and narrow flaps in *Carruanthus*. The covering membranes are complete in *Bijlia* and *Carruanthus ringens* but are only developed as a small limb in *C. peersii*. Closing bodies are large, white bulges in *Bijlia* but are small or absent in *Carruanthus*. The general shape of the seeds of *Bijlia* and *Carruanthus* does not differ markedly from that of *Machairophyllum*. Seeds are ovoid to pear-shaped and \pm 0.6–0.9 mm long. In both *Bijlia* species the testa cells are extended into papillae (Figure 17G), and have epicuticular formations in the form of granules. Seeds of *Carruanthus* are very similar to those of *Machairophyllum* in that they have elongate and strongly convex testa cells with coarsely undulate anticlinal walls (Figure 17H). Epicuticular formations in *Carruanthus* are also very similar and mainly take the shape of rodlets.

Concluding remarks: a similar leaf shape and anatomy, elongate-pedicelled flowers, capsules with raised sutures with reflexed valve rims and short and narrow valve wings, as well as a strikingly similar seed ultrastructure mark clear affinities of the genera *Carruanthus*

and *Machairophyllum* and suggest that the two are sister groups. The small size or absence of closing bodies in both *Carruanthus* species and the lack of a complete covering membrane in one (*C. peersii*) is probably the result of reduction.

Cerochlamys

Cerochlamys N.E.Br comprises three species in the Swellendam, Oudtshoorn and Laingsburg Districts in Western Cape. A fourth species was recognized by Hartmann (1998b) but was referred to the genus *Acrodon* N.E.Br (Burgoyne 1998). The following brief comments refer to the actual examination of *C. pachyphylla* (L.Bolus) L.Bolus, while information on the other species was largely obtained from the literature (mainly Hartmann 1998b).

All three species are compact and nearly stemless succulents with smooth, clavate or trigonous leaves. The leaf surface of *Cerochlamys pachyphylla* and *C. gemina* (L.Bolus) H.E.K.Hartmann has a solid wax cover which breaks up to form platelets (Figure 17C) which also occurs in *C. trigona* N.E.Br (Hartmann 1998b). In *C. pachy-*

phylla (Kurzweil 1905) the main leaf vascular bundles was found to be strongly curved or concentric with collenchymatic sheaths.

The short-pedicelled flowers of *Cerochlamys* are solitary or arranged in few-flowered cymes. Flowers are pink, purple or white, and are open during the day. *Cerochlamys* has mostly five subequal to unequal sepals (except six in *C. gemina*), linear-lanceolate petals and numerous erect stamens in a cone. All species have white filamentous staminodes. Nectaries were reported as separate (Herre 1971) and as '... very broad, touching each other, sometimes apparently in a ring' (Hartmann 1998b: 53). The stigmas of the three species are comparatively short. Capsules are five-locular in *C. pachyphylla* and *C. trigona*, but six-locular in *C. gemina*. In *C. pachyphylla* the sutures on top of the capsule are strongly raised, and have straight valve rims. Valves are erect in the opened position and lack wings. The roof-shaped covering membranes are complete. Expanding keels are diverging and terminate in long awns. Closing bodies are absent in *Cerochlamys* although the placenta ends are often knob-shaped (Hartmann 1998b). Seeds are ovoid to pear-shaped and \pm 0.6–0.9 mm long. The isodiametric to elongate testa cells are extended into papillae (Figure 17I).

Concluding remarks: floral and fruit characters of *Cerochlamys*, particularly, the filamentous staminodes, the short stigmas, its flowering phenology with diurnal pink, purple or white flowers are very unusual in the *Bergeranthus* group suggesting that the genus may not be correctly placed here. While resolving the correct taxonomic position of *Cerochlamys* is obviously beyond the scope of the present paper, the genus is here not considered as part of the *Machairophyllum* complex.

SPECIMENS EXAMINED

Herbarium abbreviations in accordance with the latest version of Index Herbariorum, BOL* = Pickle collection at BOL; NBG = National Botanic Garden Kirstenbosch, SUG = Stellenbosch University Garden.

Acocks 15999 (3) BOL.

Baxter NBG3166/14 (3) BOL. *Bean* 1091 (3) BOL. *Blackburn* 2, BOL63638 (1) BOL. *Brauns* SUG8030 (3) BOL. *Burger* BOL38796 (1) BOL.

Cilliers SUG10742 (3) BOL. *Clarke* NBG930/20 (3) BOL. *Compton & Cook* NBG1995/23 (1) BOL.

Desmet 2076, 2147, 2158 (3) NBG.

Esterhuysen 16231, 24894 (3) BOL.

Fourcade 2384, NBG424/24 (3) BOL.

Hall BOL25194, BOL32083, NBG477/53, NBG522/52 (1) BOL; NBG223/68 (1) NBG; *Herre* SUG12178 (3) BOL. *Holland* NBG1697/36 (3) BOL.

Kurzweil 1890, 1900, 1902 (1) BOL*, NBG; 1896, 1898, 1899, 1901, 1913, 1916, 1918, 1925 (3) BOL*; 1919 (3) BOL*, NBG; 1904 (4) BOL*.

Lategan NBG2367/36, NBG2369/36 (4) BOL.

Markoetter SUG10661 (3) BOL. *Muir* 3937 (1) K.

Nel SUG8313 (3) BOL.

Peers BOL32084 (3) BOL. *Pillans* 915, NBG496/16 (1) BOL. *Pocock* NBG627/26 (3) BOL. *S.* 246 = NBG661/28 (3) BOL.

Stayner KG196/59 (2) BOL; NBG177/88 (3) hort. 'student' SUG10041 (3) BOL.

Taylor BOL32085, BOL63637, NBG1556/33 (3) BOL; NBG858/30 (1) BOL. *Tugwell & Levenson* NBG2634/14 (3) BOL.

Van Breda 1196, 1749/62, 1761/61 (3) BOL. *Van Jaarsveld* 07082 = NBG 769/83 (3) NBG; 07264 = NBG 806/83 (3) hort. *Van der Bijl* NBG1465/33 (1) BOL. *Viviers s.n.* (3) hort.

Wisura 2159 (3) NBG. Without collector: 467b, SUG8274 (3) BOL; SUG 8984 (1) BOL.

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