ANATOMY, MORPHOLOGY, AND CLADISTIC ANALYSIS OF *MONSONIA* L. (GERANIACEAE)

by

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Resumen

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Se exploran mediante un análisis cladístico las relaciones filogenéticas entre las 25 especies incluidas en el género *Monsonia*. Tras una detallada revisión se seleccionan 20 caracteres morfológicos y anatómicos, entre ellos algunos previamente no descritos sobre los nectarios, el androceo y los mericarpos. El análisis filogenético produjo nueve árboles más parsimoniosos. El árbol de consenso estricto muestra dos clados principales: uno, formado por las nueve especies de *Monsonia* sect. *Monsonia*, caracterizadas por las aristas plumosas y las tres de *Sarcocaulon* que se usaron como grupo externo; y el segundo, formado por las 16 especies de *Monsonia* sect. *Olopetalum*, que comparten el tipo de separación del mericarpo, la consistencia de la columela y las paredes gruesas en el mericarpo. Como consecuencia surgen nuevas dudas sobre la monofilia de *Monsonia*. Sin embargo, nuestros datos apoyan la clasificación subgenérica actual de *Monsonia* si se incluyen *M. longipes* y *M. speciosa* en la sect. *Olopetalum*. Numerosos caracteres del mericarpo están relacionados con el tipo de zoocoria, lo cual parece derivado en *Monsonia* al igual que en otras geraniáceas.

Palabras clave: anatomía, morfología, análisis cladístico, *Monsonia*, Geraniaceae.

Abstract

ALDASORO, J.J., C. NAVARRO, P. VARGAS & C. AEDO (2001). Anatomy, Morphology, and Cladistic Analysis of Monsonia L. (Geraniaceae). *Anales Jard. Bot. Madrid* 59(1): 75-100.

Phylogenetic relationships among the 25 species of the old-world genus *Monsonia* are explored by means of a cladistic analysis. After a detailed revision, 20 morphological and anatomical characters were selected, including some new ones from nectaries, androecium, and mericarps. Phylogenetic analysis yielded 9 most parsimonious trees. The strict consensus tree showed two major clades: one is formed by the 9 species of *Monsonia* sect. *Monsonia*, characterised by plumose awns, plus *Sarcocaulon*; and a second with the 16 species of *Monsonia* sect. *Olopetalum* which share the type of mericarp detaching, consistency of columella and the thick mericarp walls. Consequently, some doubts about the monophyly of *Monsonia* exists. However, the current infrageneric classification of *Monsonia* is supported after transferring *M. longipes* and *M. speciosa* to sect. *Olopetalum*. Several characters of the mericarp are related to zoochory, which seems to be a derived syndrome in *Monsonia*, as in the other Geraniaceae.

Key words: anatomy, morphology, cladistics, *Monsonia*, Geraniaceae.

INTRODUCTION

Geraniaceae comprises five genera with rostrate schizocarp: *Erodium* L'Hér., *Geranium* L., *Monsonia* L., *Sarcocaulon* (DC.) Sweet, and *Pelargonium* L'Hér. (HUTCHINSON, 1969). Two tribes are recognised: *Geranieae* with primarily actinomorphic flowers (*Erodium*, *Geranium*, *Monsonia*, and *Sarcocaulon*), and *Pelargonieae* with zygomorphic flowers (*Pelargonium*). The family is distributed worldwide and well represented in Southern Africa with four native genera: *Geranium*, *Monsonia*, *Pelargonium* and *Sarcocaulon*. *Monsonia* consists of 25 species distributed in Africa, Madagascar, and SW Asia, 18 of them being endemic to Southern Africa.

DE CANDOLLE (1824) divided *Monsonia* into three sections: sect. *Sarcocaulon*, sect. *Olopetalum*, and sect. *Odontopetalum*. SWEET (1826) raised *Monsonia* sect. *Sarcocaulon* to generic rank, a taxonomic criterion adopted in the most recent monographs (KNUTH 1912; VENTER 1979; MOFFETT 1979). BOISSIER (1867) proposed an alternative classification with only two sections, sect. *Plumosa*, characterized by long, plumose mericarp awns, and sect. *Barbata*, defined by shorter but robust awns. KNUTH (1912) divided *Monsonia* into 7 sections, based on life form and leaf and corolla shape, which was criticised by several authors (VENTER 1979; YEO 1990). VENTER (1979) and VERHOEVEN & VENTER (1986) reinstated and rearranged Boissier's classification, dividing *Monsonia* in two sections: *Monsonia* (= *Plumosa*), including plants with long plumose awns; and *Olopetalum* (= *Barbata*) including plants with shorter adhesive awns. These cited classifications are summarised in table 1.

ALBERS (1996) reconsidered the circumscription of *Sarcocaulon* and *Monsonia*, suggesting that there is no reason for maintaining both genera as separate. He based his decision on criteria such as similarity in flower structure, phenolic compounds, protein patterns and chromosome numbers. However, some of these data are still unpublished. DREYER & *al.* (1997) and MOFFET (1997) criticised Albers' proposal on the grounds that the present knowledge of the genus is not sufficient and a molecular study is needed . Besides, these authors consider that macro-morphological differences between the two genera are clear and well-defined.

Apart from the two comprehensive monographs (KNUTH 1912; VENTER 1979), partial studies of *Monsonia* were carried out on pollen morphology (VERHOEVEN & VENTER, 1986), embryology (NARAYANA & ARORA, 1963), mericarp and seed arrangement (YEO, 1990), anatomy of nectaries (LINK, 1990) and phytogeography (VENTER, 1983). A grouping analysis based on morphological features was performed by VENTER (1990), supporting his sectional treatment of *Monsonia*. KERS (1968) and VENTER (1983) assessed the geographical distribution and habitats in Monsonia. The 25 species inhabit grasslands, savannas, and deserts in Africa and Southwest Asia. The highest diversity of the genus can be found in southern Africa with 21 of the 25 species, of which 9 are endemic to South Africa and 7 to Namibia.

Previous studies in *Monsonia* show a remarkable broad range of morphological variation (VENTER 1979). Species vary in life form, root type, leaf and stipule shape, inflorescence types, sepal and gynoecium indumentum, petal size, nectary types, anther size, stamen number, exine ornamentation, stigma size and shape, fruit features, cotyledon arrangement.

A phylogenetic study of Geraniaceae using *rbc*L sequences was performed by PRICE & PALMER (1993). They found *Sarcocaulon* to be sister to *Monsonia*, with *Pelargonium* sister to the other four genera of Geraniaceae. The relationship between *Monsonia* and *Sarcocaulon* is also supported by the loss of the rpl2 intron (PRICE & *al.*, 1990; DOWNIE & PALMER, 1992).

The specific objectives of this study on *Monsonia* were to: 1) re-evaluate morphological characters used in previous monographs; 2) search for new morphological and anatomical characters; and 3) analyse phylogenetic relationships among the species using parsimony.

MATERIAL AND METHODS

This paper is based on herbarium specimens, studied in the following herbaria: B, BM, COI, G, K, LE, MA, MO, MPU, P, W and WAG. Specimens used in anatomical studies are listed in Appendix 1. In this study we follow the taxonomic treatment proposed by VENTER (1979, 1983).

Dried flowers from herbarium specimens were soaked in warm water with 1% NaOH or with 2-3 drops of liquid soap; after two hours they were transferred to water for one hour and then to 50 % ethanol. Mericarps and flowers removed from herbarium specimens were rehydrated for light photography, hand-cut sections obtained, and tissues differentially stained. Sections were made with a SLEE-MAINZ-MTC microtome, stained with Fasga mixture, which is made of Safranin and Alcyan green 2GX (Gurr Chemical Co.) (TOLIVIA & TOLIVIA, 1987), and photographed by light microscopy. Flowers and mericarps were sectioned, glued on aluminium stubs,

TABLE 1

COMPARISON OF MAIN INFRAGENERIC TREATMENTS OF *Monsonia*. SECTION (OR INFRAGENERIC RANK) NAME ARE INDICATED IN EACH COLUMN. SPECIES OF DOUBFUL ASSIGNATION ARE INDICATED BY "?"; SPECIES NOT CONSIDERED ARE INDICATED BY "-"

Species	this study	Verhoeven & Venter (1986)	Venter (1979)	Kers (1968)	Knuth (1912)	Boissier (1867)	De Candolle (1824)
M. brevirostrata	Olopetalum	Olopetalum	Barbata	–	Biflora	–	–
M. angustifolia	Olopetalum	Olopetalum	Barbata	–	Biflora	–	–
M. senegalensis	Olopetalum	Olopetalum	Barbata	Barbata	Ovata	Barbatae	–
M. natalensis	Olopetalum	Olopetalum	Barbata	–	Genistiformis	–	
M. grandifolia	Olopetalum	Olopetalum	Barbata	–	Ovata	–	–
M. emarginata	Olopetalum	Olopetalum	Barbata	–	Ovata	–	Olopetalum
M. galpinii	Olopetalum	Olopetalum	Barbata	–	Ovata	–	–
M. praemorsa	Olopetalum	Olopetalum	Barbata	–	Genistiformis	–	
M. burkeana	Olopetalum	Olopetalum	Barbata	–	Genistiformis	–	Olopetalum
M. glauca	Olopetalum	Olopetalum	Barbata	–	Ovata	–	–
M. lanuginosa	Olopetalum	Olopetalum	Barbata	–	Genistiformis	–	–
M. attenuata	Olopetalum	Olopetalum	Barbata	–	Genistiformis	–	–
M. tranvaalensis	Olopetalum	Olopetalum	Barbata	–	Genistiformis	–	–
M. longipes	Olopetalum	Monsonia	Barbata	?	Plumosa	–	–
M. ignea	Olopetalum	Olopetalum	Barbata	?	Plumosa	–	–
M. speciosa	Olopetalum	Monsonia	Barbata	Plumosa	Odontopetalum	–	Odontopetalum
M. drudeana	Monsonia	Monsonia	Plumosa	?	Rotundatae	–	–
M. deserticola	Monsonia	Monsonia	Plumosa	Plumosa	Rotundatae	–	–
M. nivea	Monsonia	Monsonia	Plumosa	Plumosa	Plumosa	Plumosa	–
M. heliotropioides	Monsonia	Monsonia	Plumosa	Plumosa	Plumosa	Plumosa	–
M. umbellata	Monsonia	Monsonia	Plumosa	Plumosa	Umbellata	–	–
M. luederitziana	Monsonia	Monsonia	Plumosa	Plumosa	Umbellata	–	–
M. parvifolia	Monsonia	Monsonia	Plumosa	Plumosa	Umbellata	–	–
M. trilobata	Monsonia	Monsonia	Plumosa	Barbata	–	–	–
M. ignorata	Monsonia	Monsonia	Plumosa	Plumosa	–	–	–

TABLE 2

THE 20 MORPHOLOGICAL CHARACTERS USED IN THE CLADISTIC ANALYSIS OF *MONSONIA*

Vegetative structures	States of characters 1. Plant perennial (0); annual (1). 2. Plant not succulent (0); plant succulent (1). 3. Stems not covered by bark (0); stems covered with waxy bark (1).
Spines and leaves	4. Spines absent (0); spines present (1). 5. Leaf veins palmate or subpalmate (0); leaf veins pinnate or subpinnate (1).
Stipules	6. Stipules plane, generally lanceolate (0); stipules subulate or acicular (1). 7. Stipules without a tuft of hairs on the top (0); stipules with a tuft of hairs on the top (1).
Inflorescence	8. Inflorescence cymose (0); inflorescence pseudoumbellate (1); solitary flowers (2).
Flower	9. Sepals not enlarged or if enlarged not forming closed pouches (0); sepals enlarged, and the floral disc expanded forming a closed cavity to keep nectar (1). 10. Nectaries axillar, situated between the base of antisepal filament and the sepal, (0); nectaries staminal, forming a more or less conspicuous protuberance at the base of staminal filament, with no tube inside (1); nectaries staminal, forming a more or less conspicuous protuberance with a pocket inside, and continued by a conic tube in the receptacle (2). 11. Anthers longer than 1.7 mm (0); anthers very small, shorter than 1 mm (1). 12. Pollen without supratectal processes (0); with supratectal processes (1).
Fruit	13. Fruit detaching upwards (0); downwards (1). 14. Columella consistency, weak (0); stout (1). 15. Awn not plumose (0); awn more or less plumose (1). 16. Mericarp gradually tapered to the awn (0); slightly tapered, or abruptely cutted by pits or ridges perpendicular to awn (1). 17. Mericarp with only one type of bristles (0); with two types of bristles, few long and many short (1). 18. Mericarp bristles without pockets (0); with pockets (1). 19. Mericarp wall narrower than 20 mm (0); wider than 30 mm (1).
Seed	20. Seed with plane cotyledons (0); moderately folded cotyledons, non conduplicate (1), clearly folded, conduplicate cotyledons (2).

coated with 40-50 nm gold, and examined in a JEOL-TSM T330A scanning electron microscope (SEM) at 20 kV.

Cladistic analyses species were conducted using Fitch parsimony (as implemented in PAUP 3.0; SWOFFORD, 1993) with unordered and equal weighting all characters. Heuristic searches were replicated 100 times using random taxon entries and ACCTRAN optimization. The 25 species belonging to the two sections of *Monsonia* (9 in sect. *Monsonia* and 16 in sect. *Olopetalum*) were included as the ingroup. *Pelargonium peltatum*, was chosen as the outgroup based on previous chloroplast sequence analyses (PRICE & PALMER 1993) in which this genus is basal to the other genera of Geraniaceae: *Sarcocaulon*, *Erodium*, *Geranium*, and *Monsonia*. Other species of *Pelargonium* were also studied in order to test if some states of a character were present in all of them. To test the monophyly of *Monsonia*, three species of *Sarcocaulon* (*S. crassifolium*, *S. marlothii* and *S. mossamedense*) were also included in the analysis. MacClade version 3.04 was used to reconstruct character evolution (MADDISON & MADDISON, 1992). Reliability of clades was assessed by bootstrapping (using 100 replicates addition) (FELSENSTEIN, 1985). A total of 20 morphological and anatomical characters (tables 2, 3) were used in the cladistic analysis, two of them being quantitative (anther length and mericarp wall width). Some other characters were studied but finally excluded from the analysis because of either high instance of polymorphism or we did not observe discontinuities to define character states. The excluded characters are: presence of tuberose roots, subacaule or acaule habit, presence and length of sepal mucro, petal size, presence or absence of stalked glandular hairs on the ovary, shape of bristle tip and pits on the mericarp body, reticulate ornamentation and papillae types on the mericarp surface, and presence and distribution of glandular hairs.

RESULTS

Morphological characters

A matrix of characters with potential phylogenetic information is shown in tables 2 and 3, and discussed below.

Life form.–Most species of *Monsonia* are perennials, except for *M. senegalensis*, *M. brevirostrata* and *M. angustifolia* (tables 2 and 3, character 1). The same is true for *Pelargonium*. Three main types of roots are recognized in *Monsonia* but not used in the analysis: (1) vertical napiform roots, with finer lateral rootlets (annuals); (2) vertical branched roots, sometimes with tubers

TABLE 3

DATA MATRIX USED IN CLADISTIC ANALYSIS OF *MONSONIA*. INAPPLICABLE OR MISSING DATA ARE CODED AS "?"

	1	2	3	2	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Pelargonium peltatum	0	0	0	0	0	0	0	1	?	?	0	0	0	1	0	0	0	0	0	0
Sarcocaulon crassicaule	0	1	1	1	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1
S. marlothii	0	1	1	1	0	0	0	2	0	0	0	0	0	0	1	0	?	0	0	1
S. mossamedense	0	1	1	1	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	1
Monsonia brevirostrata	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	1	1	0	1	2
M. angustifolia	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	1	1	0	1	2
M. senegalensis	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	1	1	1	1	2
M. speciosa	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	1	0	1	1	2
M. glauca	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	2
M. lanuginosa	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	2
M. transvaalensis	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	2
M. attenuata	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	2
M. natalensis	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	0	1	2
M. grandifolia	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	0	1	2
M. emarginata	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	2
M. galpinii	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	2
M. burkeana	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	2
M. praemorsa	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	2
M. longipes	0	0	0	0	1	1	0	1	0	2	0	0	1	1	0	1	1	1	1	2
M. ignea	0	0	0	0	1	1	0	1	0	2	0	0	1	1	0	1	1	0	1	2
M. drudeana	0	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	0	0	1
M. deserticola	0	0	0	0	0	0	0	1	0	1	1	?	0	0	1	1	0	0	0	1
M. nivea	0	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	0	0	0	1
M. heliotropioides	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	1
M. umbellata	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	1	0	1
M. luederitziana	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1
M. parvifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1
M. trilobata	0	0	0	0	0	0	0	1	1	0	0	0	0	0	?	1	0	0	0	1
M. ignorata	0	0	0	0	0	0	0	1	1	0	0	0	?	0	1	1	0	0	0	1

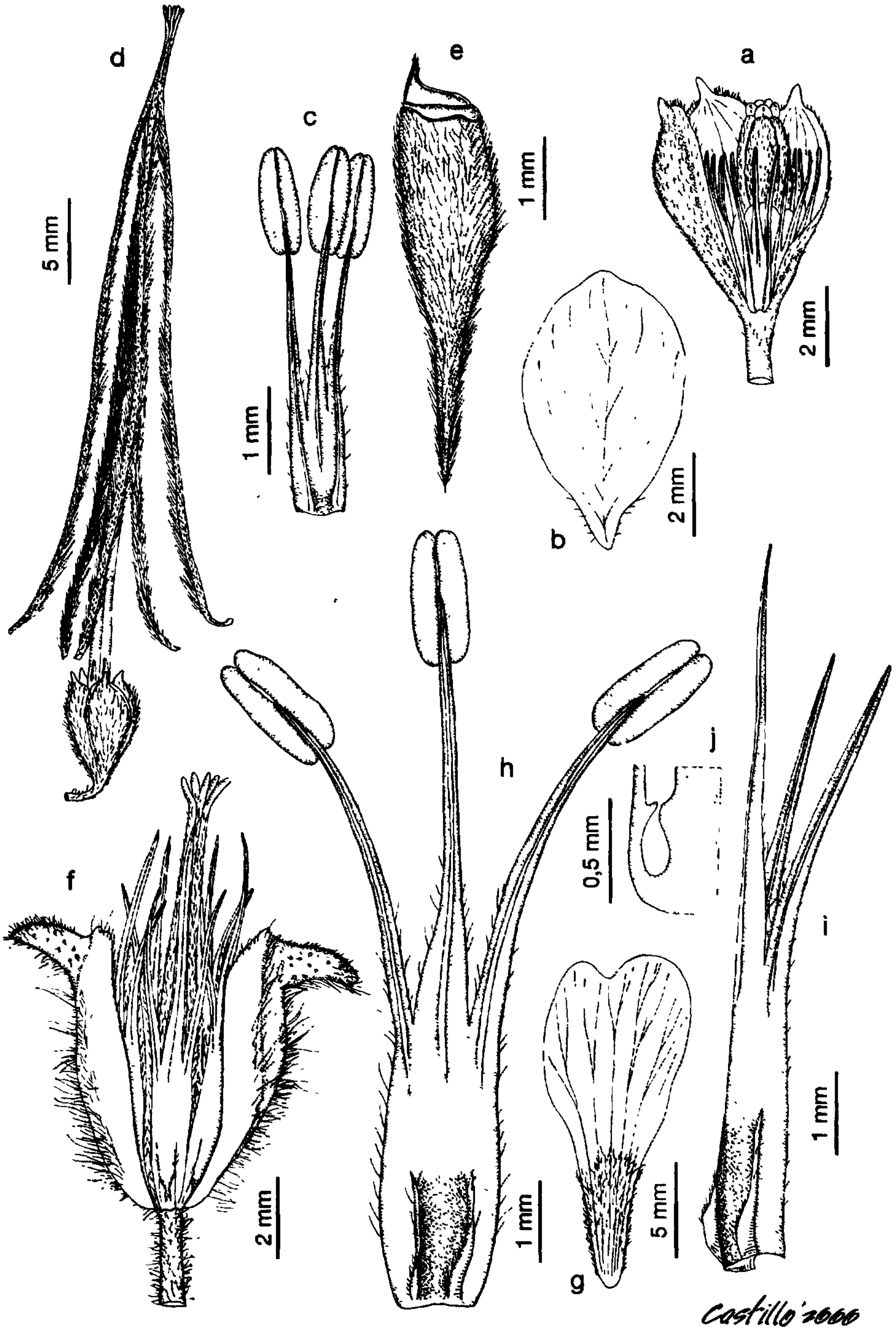

Fig. 1.–Flower and fruit structures in *Monsonia nivea* (a-e: *L. Kralik 26*, MA 628481) and *M. parvifolia* (f-j: *Schlechter s.n.*, W). a: flower; b: petal; c: group of stamens; d: schizocarp with the five awns partially separated; e: mericarp body; f: flower; g: petal; h: front view of a group of stamens; i: lateral view of a group of stamens; j: transversal section of nectary including one nectary pouch.

(perennials); and (3) horizontal, woody or stout rhizomes, often sheathed with old stipules on the base of plant, more or less branched, generally without tubers. Many of the species of *Pelargonium* have vertical branched roots, while others have tubers. Caulescence is the rule in *Monsonia*, but some species have a tendency to adopt a rosulate appearance, and the stagnation of growth makes them almost acaulous, such as *M. deserticola, M. drudeana, M. heliotropioides, M. ignorata*, and *M. nivea*. *Sarcocaulon* are fleshy shrublets covered with waxy bark (tables 2 and 3, characters 2 and 3), features which never occur in *Monsonia*. The bark is formed by a phellogen; which produces a wide phellem to the outside and several layers of phelloderm cells toward the inside (MOFFETT, 1997). Also, some species of *Pelargonium* are succulent, but none has a bark impregnate of wax and resin (Moffett, 1997). *P. peltatum* has a herbaceous habit.

Spines, leaves, leaf shape and venation.–Species of *Monsonia* lack spines, while in *Sarcocaulon* the spines are formed from the long petioles after the laminas fall off (tables 2 and 3, character 4) (Moffett, 1997). Leaves are divided only in *M. speciosa* and *M. longipes*. *Monsonia speciosa* includes lobed, palmate, palmate-lobed, and palmatifid leaves (VENTER, 1979). Two main types of leaf venation can be recognised in *Monsonia*: subpalmate to palmate, and subpinnate to pinnate, (tables 2 and 3, character 5). Only two species have palmate veins: *M. drudeana* and *M. ignorata*, while in *M. deserticola, M. heliotropioides, M. luederitziana, M. parvifolia, M. trilobata*, and *M. umbellata* veins are mostly subpalmate. Pinnate or subpinnate veins are found in all other species of *Monsonia*. Palmate or almost palmate veins occur in most species of *Pelargonium* and *Sarcocaulon*.

Stipules.–A large range of variation of stipule shapes occurs in *Monsonia*. Twelve species have oval to lanceolate stipules whereas the remaining 13 species have linear-lanceolate to subulate stipules. *Pelargonium* include both linear and lanceolate stipules (tables 2 and 3, character 6). Tuft hairs were found on the stipule apex of 15 species, whereas we did not find this character neither in the remaining 10 species nor in *Pelargonium* (tables 2 and 3, character 7).

Inflorescences.–Axillar flowering stems are found in all species, being also terminal in some of them. Development of terminal or axillar flowering stems is however not consistent within the same species. There are two significant inflorescence types: cymes and pseudoumbels. Thirteen species of *Monsonia* have cymes, while 10 species have pseudoumbels, as do most *Pelargonium* species (tables 2 and 3, character 8). Inflorescence of two *Monsonia* species bears only a single flower (*M. drudeana* and *M. speciosa*). Other than the 13 species with cymes, we have observed only monochasial inflorescences, except in *M. burkeana* and *M. emarginata* where they can be both, dichasial and monochasial. Also, all studied *Sarcocaulon* bear solitary flowers.

Flower symmetry.–All species of *Monsonia* have actinomorphic flowers (figs. 1a, 1f, 2a and 2l). On the contrary, all species of *Pelargonium* are zygomorphic except for *P. incarnatum* (STRUCK, 1997).

Sepals.–Imbricate, persistent sepals are found in all species of *Monsonia*. Concave sepals retain nectar, being sometimes connate or somewhat enlarged (figs. 1f, 3B and 3C). A group of five species have sepal enlargement at the base in such a way that an appendage encloses an axillar nectary (pouches). This pouch is limited laterally by walls that connect the sepals with the base of the staminal filaments (figs. 4A, 4B and 4C) (tables 2 and 3, character 9). The cavity is covered by hairs (figs. 4D and 4E) and has stomata on the epidermis (fig. 4F). Five representatives of sect. *Monsonia* (*M. umbellata, M. parvifolia, M. luederitziana* and *M. ignorata*) show pouches. *Pelargonium* and *Sarcocaulon* lack pouches and sepal or staminal enlargements.

Petals.–Variation in indumentum (hair distribution), colour (white, yellow, pink, mauve, bluish) and size occur frequently within the same species (VENTER, 1979). Several shapes occur: entire, notched, or lobed

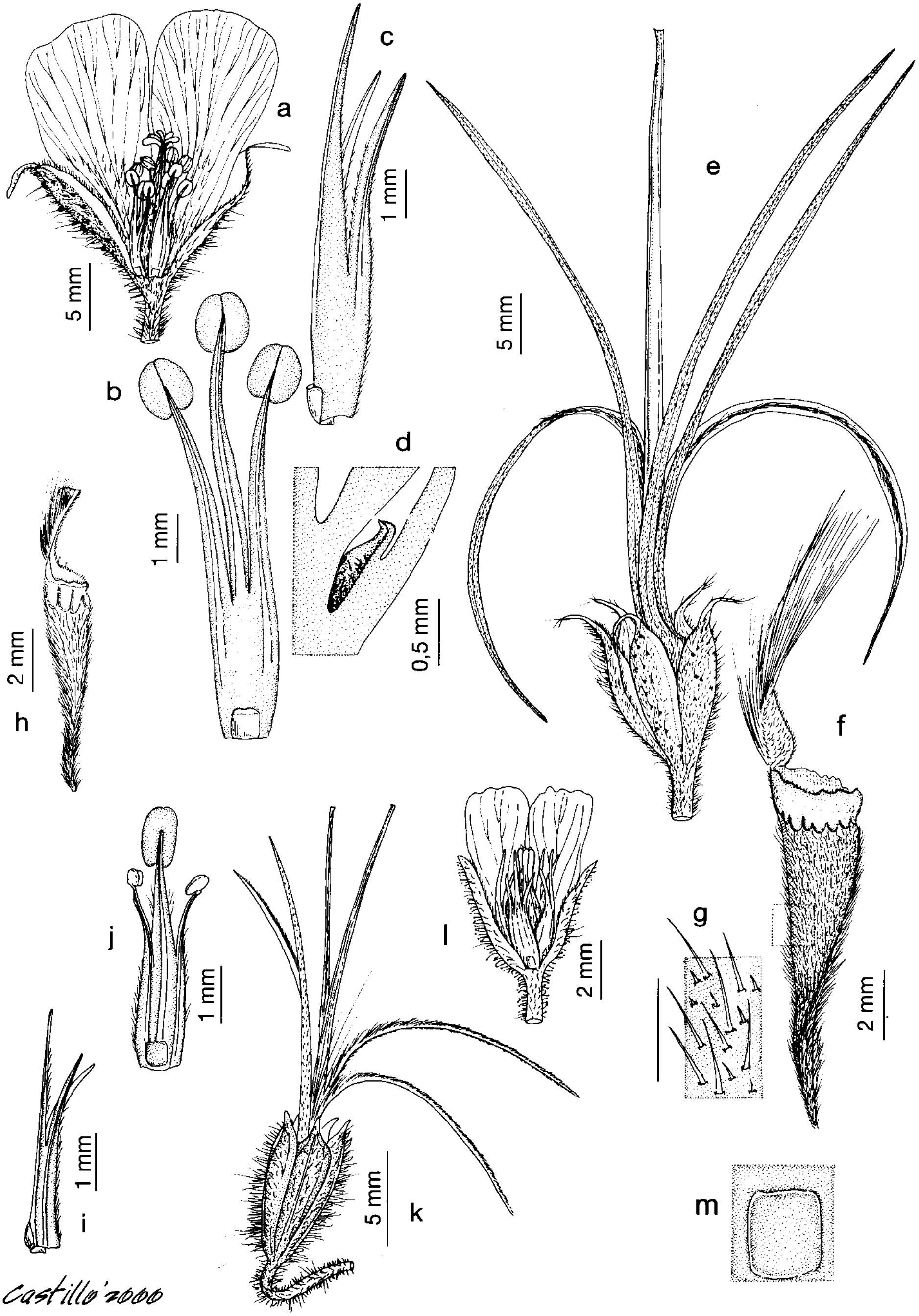

Fig. 2.–Flower and fruit structures in *Monsonia longipes* and *M. brevirostrata*. a-f: *M. longipes* (*Cufodontis 555*, W); a: flower; b: front view of a group of stamens; c: lateral view of a group of stamens; d: transversal section of nectary; e: schizocarp with the five awns partially separated; f: mericarp body; g: surface of mericarp body showing long and short bristles; h-m: *M. brevirostrata* (*Krook 2220*, W); h: mericarp body; i: front view of a group of stamens; j: lateral view of a group of stamens; k: schizocarp with the five awns partially separated; l: flower; m: nectary.

(figs 1b, 1g, 2a and 2l). Venation varies from 3, 5 or multiple veins, within different species or individuals of the same species.

Nectaries.–There are five episepal nectaries in *Monsonia*, placed on the base of each group of three joint staminal filaments. The nectaries have a secretory parenchyma with intercellular spaces inside and anomocytic stomata generally on its surface (figs 3F, 4F, 5C and 6E). They are vascularized by branches of phloematic sepal bundles. Usually, the branch that goes to sepal and stamen also reaches the nectary (figs 3E, 4B and 5E). From our anatomical studies we have coded nectaries as two main types considering the position of secretory tissue: (1) axillar nectaries, with secretory tissue at the sepal axile (fig. 3A-E); and, (2) secretory knobs, with prominent tissue (knob) on the base of each group of three joint staminal filaments. The latter type includes two subtypes, one has the secretory tissue on the outer part of the knob and has no hollow inside (fig. 5A-F), and the second has the secretory tissue on the inner part of a hollow located behind the knob, while the external part of knob has no stomata (fig. 6A-F, tables 2 and 3, character 10). The size and shape of the knobs are variable between species. All the types of nectaries are often followed by a shallow channel along the group of filaments, with two rows of hairs which serve to lead the nectar upwards (fig. 1c, 1g, 2j, 4D and 4E). The disposition of hairs, the channel and the size of nectaries are variable.

Androecium.–*Monsonia* has 15 anthers gathered in groups of three filaments, the highest number in the family (VENTER, 1979; YEO, 1990). The stamens form a tube with 5 groups of filaments fused more or less along the length. Here we report for the first time an exception to this pattern in *Monsonia* for *M. brevirostrata*, which has only 5 fertile stamens plus 10 sterile filaments. Thus, each central anther of the group is fertile, while two lateral anthers abort (fig. 2j). Anther size varies in *Monsonia*. There are seven species with small anthers (less than 1 mm) and the remaining eighteen have distinctly long anthers (tables 2 and 3, character 11). Anther size is usually related to pollen content. The pollen content per anther varies in *Monsonia*. VENTER (1986) reported a striklingly low number of pollen grains in *M. nivea* and *M. heliotropioides* (8-10 per anther), while in most other species it reaches more standard features (i.e. 740-900 grains per anther in *M. speciosa*, counted in this study).

Pollen.–Species of *Monsonia* sect. *Olopetalum* have reticulate pollen with large cells (fig. 7G-H), whereas species in *M.* sect. *Monsonia* have three types: (1) reticulate with large cells (found in 22 species) (fig. 7A-C and 7F); (2) reticulate with large cells and supratectal processes, only in *M. nivea* and *M. heliotropioides* (fig. 7E); and (3) striate pollen like in *Erodium*, which occurs only in *M. deserticola* (fig. 7D). Presence of supratectal processes was coded for the cladistic analysis (tables 2 and 3, character 12). The *Erodium*-type pollen has been found only once in *M. deserticola* and thus it was not considered in the cladistic analysis. Other details, not coded in the analysis, are the externally serrate tectum in *M. speciosa* and the slightly wavy and dense muri in *M. drudeana*, *M. luederitziana*, *M. parvifolia*, and *M. umbellata*. Pollen in *Sarcocaulon* is similar to type 1 in *Monsonia*, while in *Pelargonium* it is very variable, and in *P. peltatum* is also reticulate, but with smaller cells (STAFFORD & GIBBY, 1992). Most of these types of pollen in *Monsonia* have been reported by BORTENSCHLAGER (1967) and VERHOEVEN & VENTER (1986).

Gynoecium.–The ovary is superior, terminally beaked, 5-lobed, and 5-locular. Each carpel contains 2 axilar, campylotropous ovules, the lower being abortive (NARAYANA & ARORA, 1963; BOESEWINKEL & BEEN, 1979; BOESEWINKEL, 1997). The style is obsolete, with 5 stigmata, linear or clavate, or rarely short and ovoid or rounded (fig. 8A and 8B). The ovary base has sometimes tubular hairs with basal glands, which produce a smelling secretion. Other species have verrucate (i.e. *M. nivea*) (fig. 8D) or glandular hairs (i.e. *M. senegalensis*) (fig. 8C and 8F) on the top of the ovary. The glandular hairs can suffer a transformation or perdure until fruit maturation (fig. 8E). The tip of

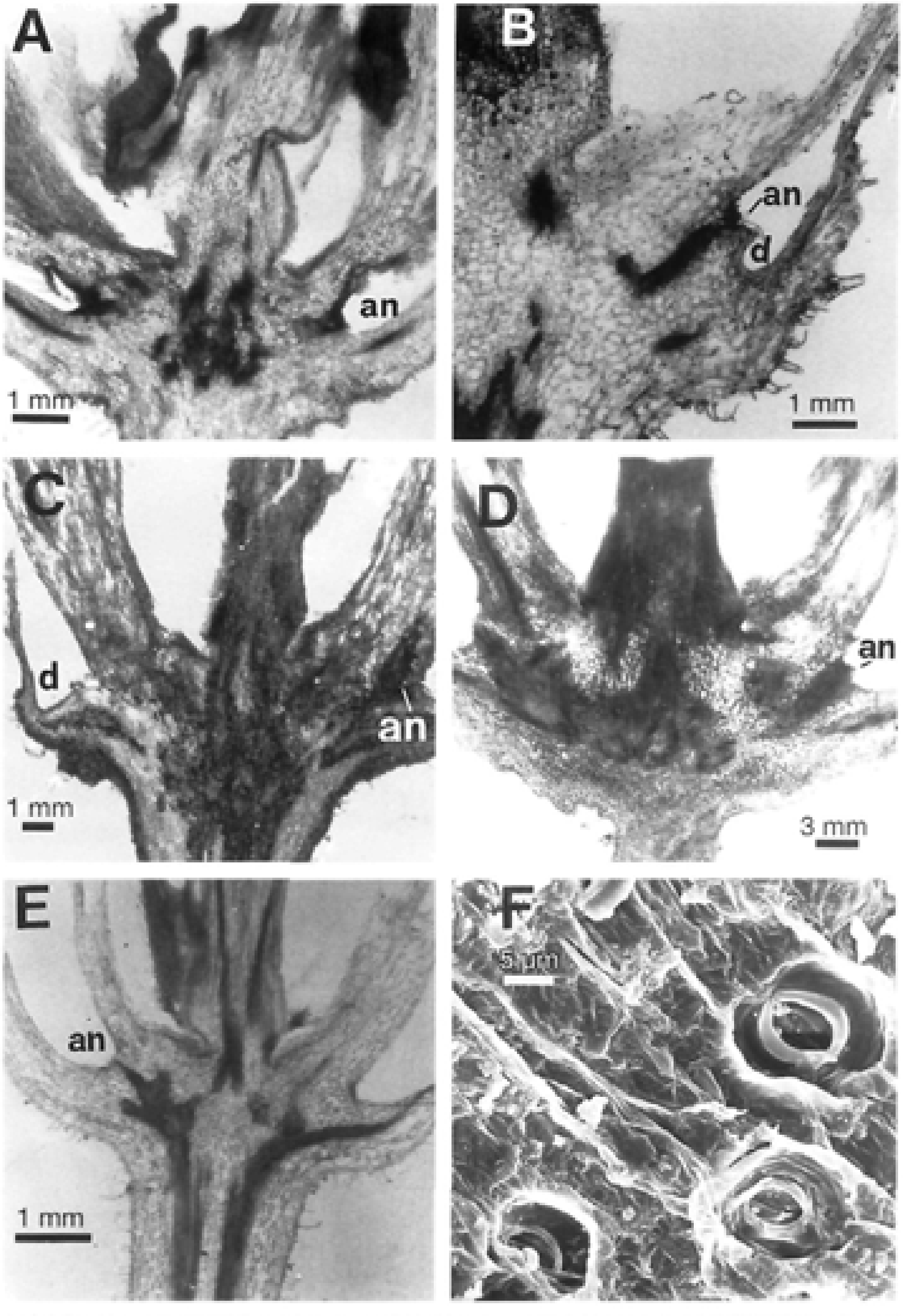

Fig. 3.–Light and SEM micrographs of axillar nectaries in the species of *Monsonia* without pouches. A: Thin-section of *M. transvaalensis* with axillar nectaries (an) (*Wendermann & Oberdieck 2155*, P). B: *M. lanuginosa* and a small depression (d) formed by the sepal (*Wendermann & Oberdieck 2155*, P). C: *M. attenuata* showing axillar nectaries (an), and cavity (d) formed by the sepal (*Gerrard 1431*, W). D: *M. speciosa* showing axillary nectaries (an) (*Marloth s.n.*, W). E: Light micrograph of *M. glauca* showing axillary nectaries (an), (*K. Dinter 5655*, P). F: SEM micrograph of nectariferous surface of *M. attenuata* showing stomata (*Gerrard 1431*, W).

glandular hairs has special structures to secrete substances (fig. 8C, 8F and 9A). Ovary ornamentation is either highly variable or typical ones are present in only a single species, which makes this character not useful for cladistic analyses.

Fruit.–It is a rostrate schizocarp with 5 mericarps. The mericarps are tailed on the top, the awn being as long as the schizocarp beak. When the mericarp is ready to be dispersed the tail detaches from the central axis (columella) (YEO, 1984, 1990). We have coded this character into two states depending on awn detaching: (1) in *Monsonia* sect. *Olopetalum*, the upper part of the tail separates along the columella and then the mericarp body (fig. 2e); (2) alternatively, in *Monsonia* sect. *Monsonia* the distal part of the awn remains attached to the columella while the mericarp body detachs (fig. 1d) as in *Sarcocaulon* and *Pelargonium* (tables 2 and 3, character 13). After mericarp detachment, the awn becomes twisted and some hairs become visible on the internal surface to facilitate the mericarp dispersal by the wind or other means. The columella in sect. *Olopetalum* is short and stout while in sect. *Monsonia* is very long and weak (tables 2 and 3, character 14). Although one of the outgroups (*Sarcocaulon*) has long and weak columella, *Pelargonium peltatum* has a stout columella. This character needs a detailed study in *Pelargonium.*

Awn.–All representatives of Geraniaceae have hairs on the inner part of the awn. These hairs are similarly long on both the lower and upper parts in sect. *Monsonia* (plumose awns of Boissier's sect. *Plumosae*), whereas they are long on the lower part but short on the upper in sect. *Olopetalum* (not plumosae awns of Boissier's sect. *Barbatae*; table 1). *Monsonia trilobata* (sect. *Monsonia*) is an exception because it has not plumose awns (tables 2 and 3, character 15). Most species of *Pelargonium* are not plumose, while all studied *Sarcocaulon* are plumose. Awn fibres suffer changes in length when moist, causing mericarp rotation that helps to bury the mericarp (fig. 9C and 9F; COBELLI, 1892).

Mericarp body.–There is an abscission point where the mericarp body and the awn are detached in maturity (fig. 9D and 9F). The mericarp body has two morphologies: ± conic, tapered to the awn in a group of four species (*M. emarginata*, *M. galpinii*, *M. natalensis*, and *M. grandifolia*) (fig. 10 G-H), and abruptly narrowed into the awn in the rest (fig. 1e, 2h, 2f, 10A-F, and 10I-J; tables 2 and 3, character 16). The mericarp is tapered in *Sarcocaulon crassifolium*, *S. marlothii* and *Pelargonium peltatum.*

There are two types of structures on the mericarp near the abscission point: ridges and pits (figs. 9D, 9F-G, 10A-F and 10J). Pits are concavities situated symmetrically on both sides of the upper part of mericarp, that have glands or other secretory devices (figs. 10A, 10F and 10J). Pits are formed by collapsing several layers of developed exocarp cells (fig. 9F, G). The pit is obscure or absent in some species of *Monsonia* sect. *Monsonia*, such as in *M. deserticola*, *M. heliotropioides*, *M. ignorata*, and *M. nivea* (fig. 9D and 10I). One or two transverse ridges may or not be present on the upper part of the mericarp body (figs. 9D, 10C-E). These characters were not used due to high variability observed in both pits and ridges in *Monsonia.*

Indumentum.–Mericarp indumentum is formed by many types of hairs. A comprehensive classification of them was reported by Venter (1990). There are four main types: (1) gland based hairs (fig. 9B); (2) stalked glands (= gland-tipped hairs; fig. 8C, 8E and 9A), which can be columnar, straight acicular and curved acicular; (3) sessile or punctate glands (fig. 11 I); and eglandular hairs (fig. 9C, 11A-J, 12A-H). The eglandular hairs are uni- or pluricellular. An important type of stout pluricellular hairs is the bristle. This has a basal bulb, a narrowed cell, and a long cylindrical cell (figs. 11G and 12E). Its surface can be smooth, striate or granulate; granulate bristles could increase mericarp adherence (figs. 11B-C, 11F, 11H). The bristle tip is acute, rounded or truncate (figs. 11C, 12B, 12G). Thirty species have long bristles of similar length (fig. 12A-D, 12F-H), whereas the remaining species have short and long bristles on the mericarp (fig. 11E-F) (tables 2 and 3, character 17). Similar, long bristles cover the meri-

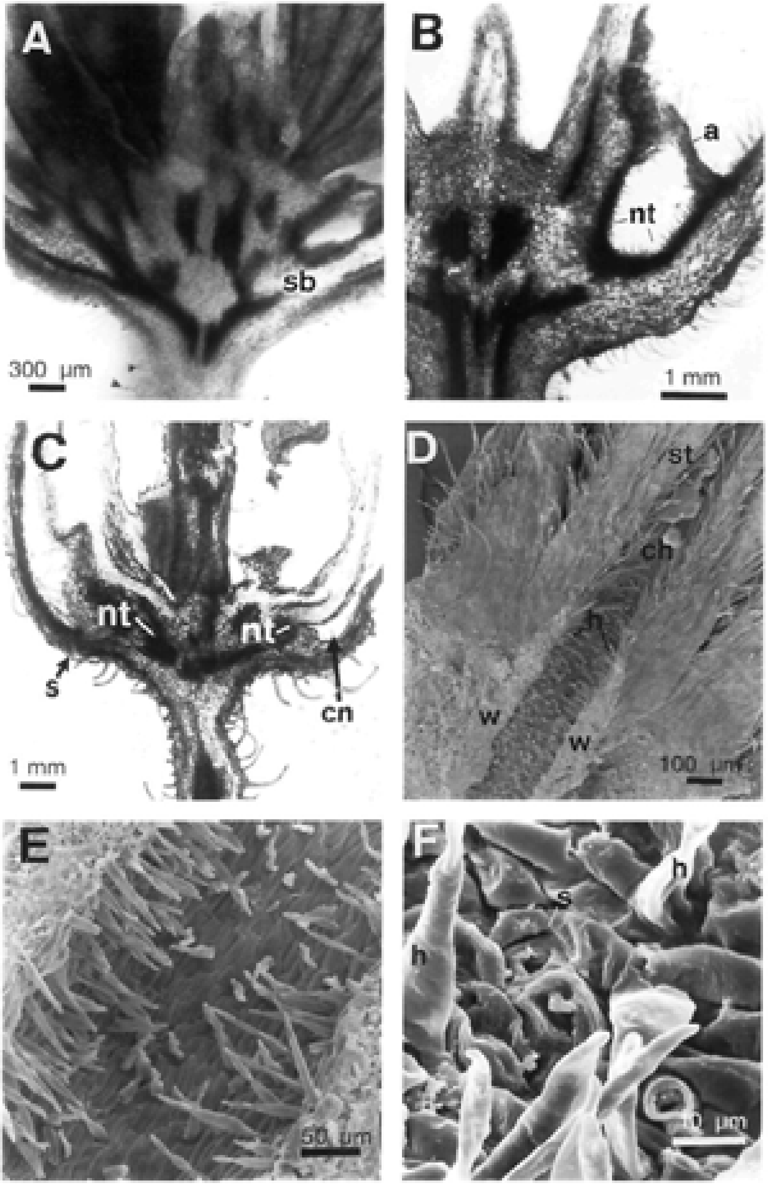

Fig. 4.–Light and SEM micrographs of axillar nectaries with the sepals and the receptacle enlarged forming a pouch. A: Thin-section of *Monsonia umbellata* flower showing the cavity formed by sepals and receptacle. The sepal bundle (sb) progress close below the nectary (*L. W. Carisso & F. Sousa 243*, COI). B: Thin-section of *M. luederitziana* flower showing the cavity formed by sepals and receptacle formed by enlarged sepals which have an appendage to close it (a); the nectariferous tissue (nt) is stained in the surface of the cavity. It is covered by hairs and connected with the sepal bundle (*Schlieben 8806*, W). C: Thin-section of *M. parvifolia* flower showing the cavity formed by sepals (s) and receptacle (cn) and the nectariferous tissue (nt) (*Schlechter s.n.*, W). D: SEM micrograph of nectary of *M. parvifolia* showing the cavity formed between the base of a stamens group (st) and the sepals; two walls (w) connect the stamen filaments with the sepals and close the cavity. The nectary is followed by a channel (ch) along the group of filaments, with two rows of hairs (h), which lead the nectar upwards. E: SEM micrograph of nectary of *M. parvifolia* showing this cavity covered with hairs. F: SEM micrograph of surface of *M. parvifolia* nectary showing one stoma (s) and hairs (h) (*Schlechter s.n.*, W).

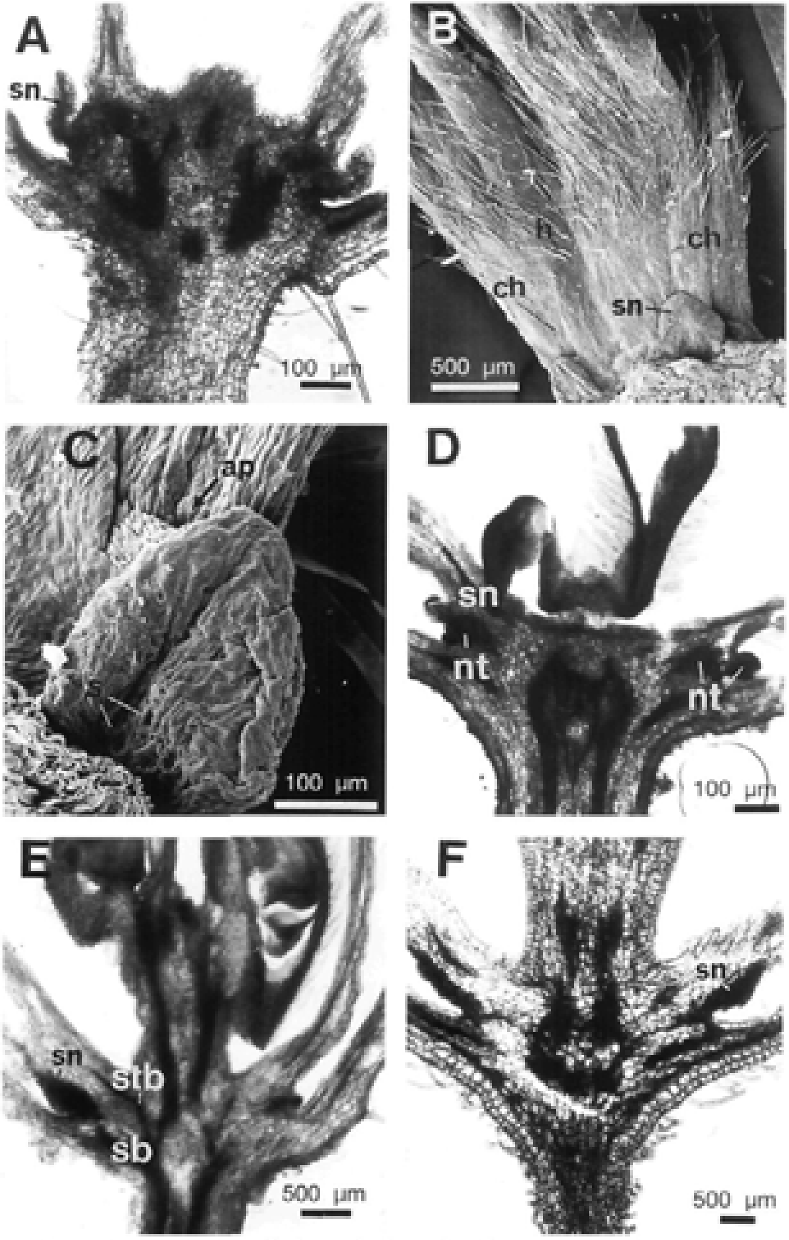

Fig. 5.–Light and SEM micrographs of staminal nectaries in species of *Monsonia* showing nectary protuberance without nectariferous tube. A: Thin-section of *M. grandifolia* flower; the nectaries form a long protuberance with the secretory tissue in all the surface (sn) (*H. Rudatis 1342*, W s.n.). B: SEM micrograph of base of stamen filaments and nectary of *M. natalensis*. The nectary form a protuberance at the base of each stamen group (sn) which has a channel (ch) where the nectar rise, being latter retained on the hairs (*Kuntze s.n.*, P). C: SEM micrograph of antisepal side of *M. natalensis* nectary, showing aperture on the nectary top (ap), nectariferous tissue is only on the antisepal side. The base contains most of stomata; the interior has no stomata (s) serving to retain nectar (*Kuntze s.n.*, P). D: Light micrograph of *M. emarginata* showing staminal nectaries (sn) and the nectariferous tissue (nt) (*Penther 2174*, W). E: Light micrograph of *M. brevirostrata* showing staminal nectaries (sn) and the bundles of stamen (stb) and sepal (sb) (*Krook 2220*, W). F: Light micrograph of *M. nivea* showing staminal nectaries (sn) (*L. Kralik 26*, MA 628481).

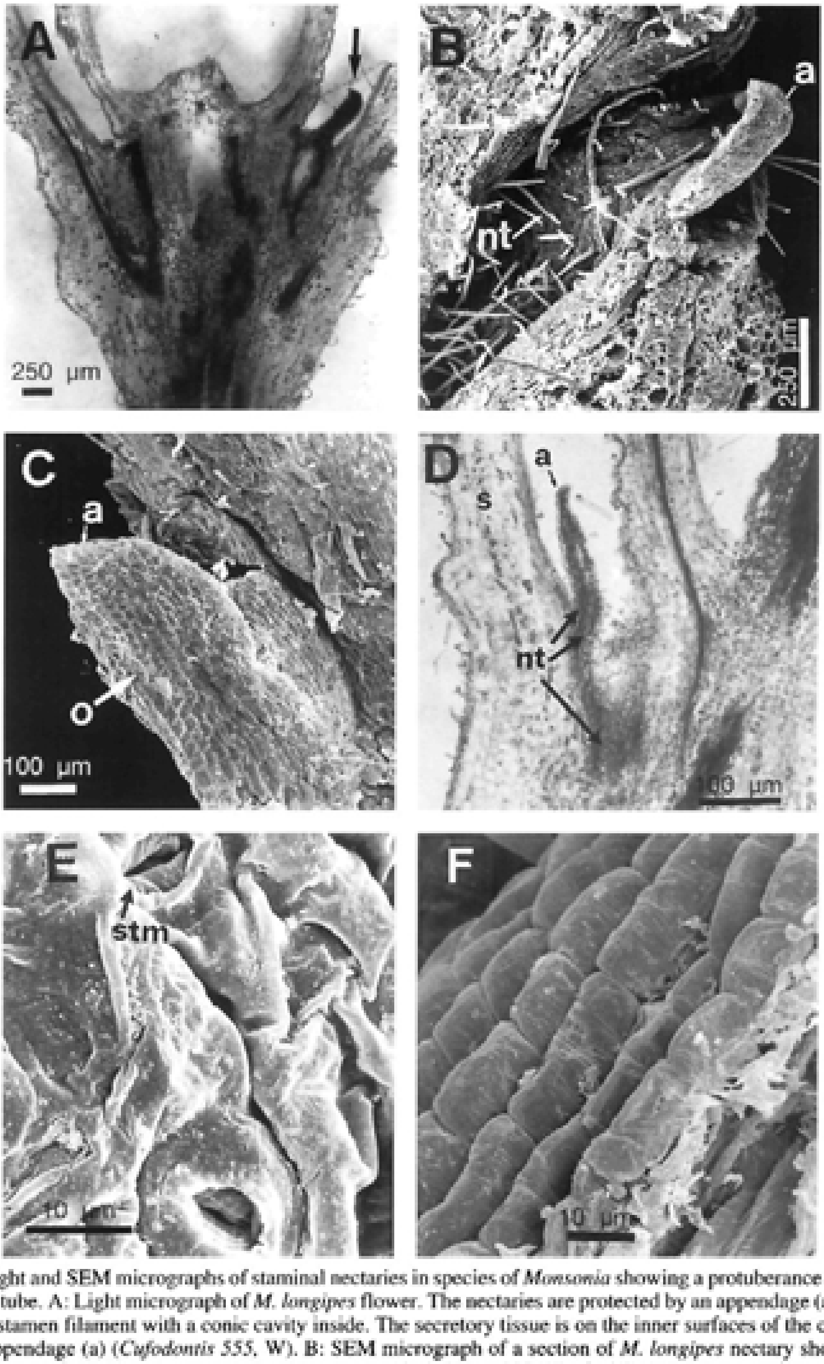

Fig. 6.–Light and SEM micrographs of staminal nectaries in species of *Monsonia* showing a protuberance with nectariferous tube. A: Light micrograph of *M. longipes* flower. The nectaries are protected by an appendage (arrow) attached to stamen filament with a conic cavity inside. The secretory tissue is on the inner surfaces of the cavity (nt) and the appendage (a) (*Cufodontis 555*, W). B: SEM micrograph of a section of *M. longipes* nectary showing the nectariferous surface (nt) and the sepal appendage (a) (*Cufodontis 555*, W). C: SEM micrograph of appendage of *M. longipes* nectary (a) showing the outer surface (o) of sepal appendage (a) (*Cufodontis 555*, W). D: Light micrograph of a section of *M. longipes* nectary showing the secretory tissue on the basal surfaces of the cavity (nt), and the appendage. E: SEM micrograph of inner surface of nectary, which has stomata (stm) (*Cufodontis 555*, W). F: SEM micrograph of outer surface of nectary, which has no stomata (*Cufodontis 555*, W).

carp body in all species of *Pelargonium* and *Sarcocaulon*.

Ornamentation.–Mericarp surface includes two ornamentation types: reticulate in which polygonal exocarpic cells form a net (i.e. *Monsonia deserticola* and *M. nivea*) (fig. 12C and 12F); and non-reticulate ornamentation with ± irregular cells (*M. luederitziana* and *M. emarginata*) (fig. 11J and 12H). In both cases, periclinal cell walls vary from concave to convex or papillary, including sloped or globose papillae (fig. 11H, 12H). Conversely, the anticlinal walls are often wavy (fig. 12F). Sometimes, exocarp cells collapse giving a planate surface, but the papilla outline remains visible (figs. 11A, 11B, 11J). Mericarps with sloped papillae have bristles surrounded by semicircular rims called "pockets", which are formed by fusion of these papillae and show a wide morphological variation (figs. 11B, 11F, 11I, 12A, 12B, 12D, 12H) (tables 2 and 3, character 18). These pockets prevent the bristle from returning. All tested species of *Pelargonium* and *Sarcocaulon* lack these pockets.

Mericarp wall.–Two types of mericarp wall exist in *Monsonia*: the widest walls (about 40-70 mm wide) were found in sect. *Olopetalum*, having a sclerenchymatose part (15-30mm wide) of 3-5 layers of cells (fig. 11D, 11G), while sect. *Monsonia* and *Pelargonium* have narrower walls (20-30 mm wide), with a sclerenchymatose region (2-10 mm wide) of usually 1-3 cell layers (fig. 12A, 12E; tables 2 and 3, character 19). The mesocarp layer is also wider in sect. *Olopetalum* (figs. 9E, 9H, 11D, 11G, 12A, 12E).

Seeds.–Cotyledons are flat and incumbent in *Pelargonium* (fig. 13A) while they are folded and accumbent in *Monsonia* (Fig. 13B-D) (HEGELMAIER, 1899; YEO, 1990). However, the degree of cotyledon folding di-

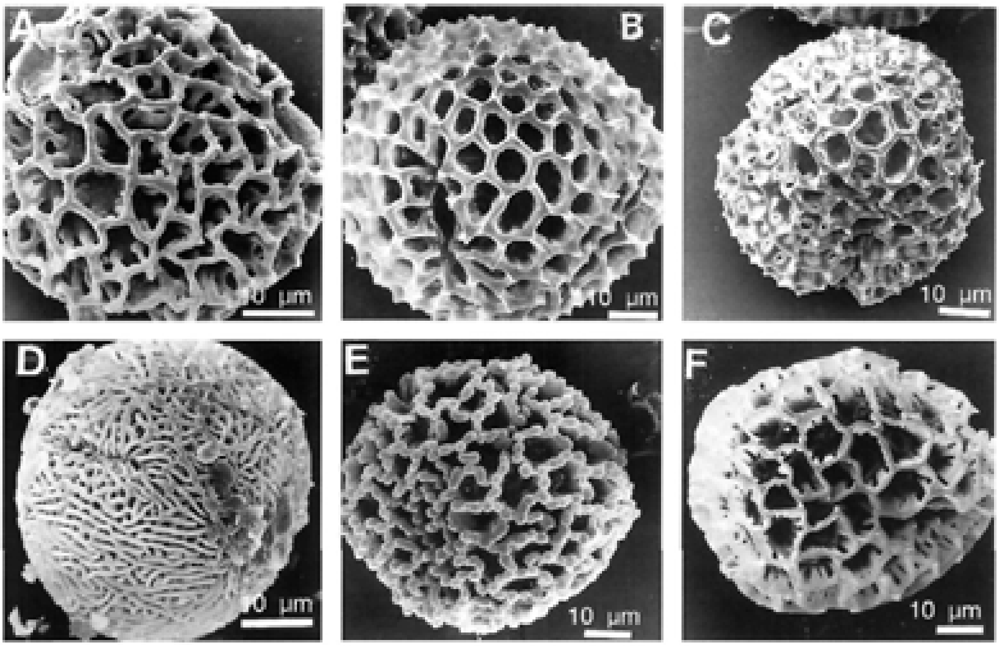

Fig. 7.–Scanning electron micrographs of *Monsonia* pollen. A: Pollen of *M. transvaalensis*, reticulate with large cells (6-10 mm of diameter) (*Wendermann & Oberdieck 2155*, P). B: Pollen of *M. speciosa*, reticulate with large cells (6-10 mm of diameter) (*Marloth s.n.*, W). C: Pollen of *M. ignorata*, reticulate with large cells (10-16 mm of diameter) (*Lavranos & Pehlemann 19639*, MO s.n.). D: Pollen of *M. deserticola*, striate, similar to pollen of *Erodium* (*Dinter 6611*, P). E: Pollen of *M. nivea*, reticulate with large cells (8-11 mm of diameter) and supratectal processes (*L. Kralik 26*, MA 628481). F: Pollen of *M. luederitziana*, reticulate with large cells (9-14 mm of diameter) (*Schlieben 8806*, W).

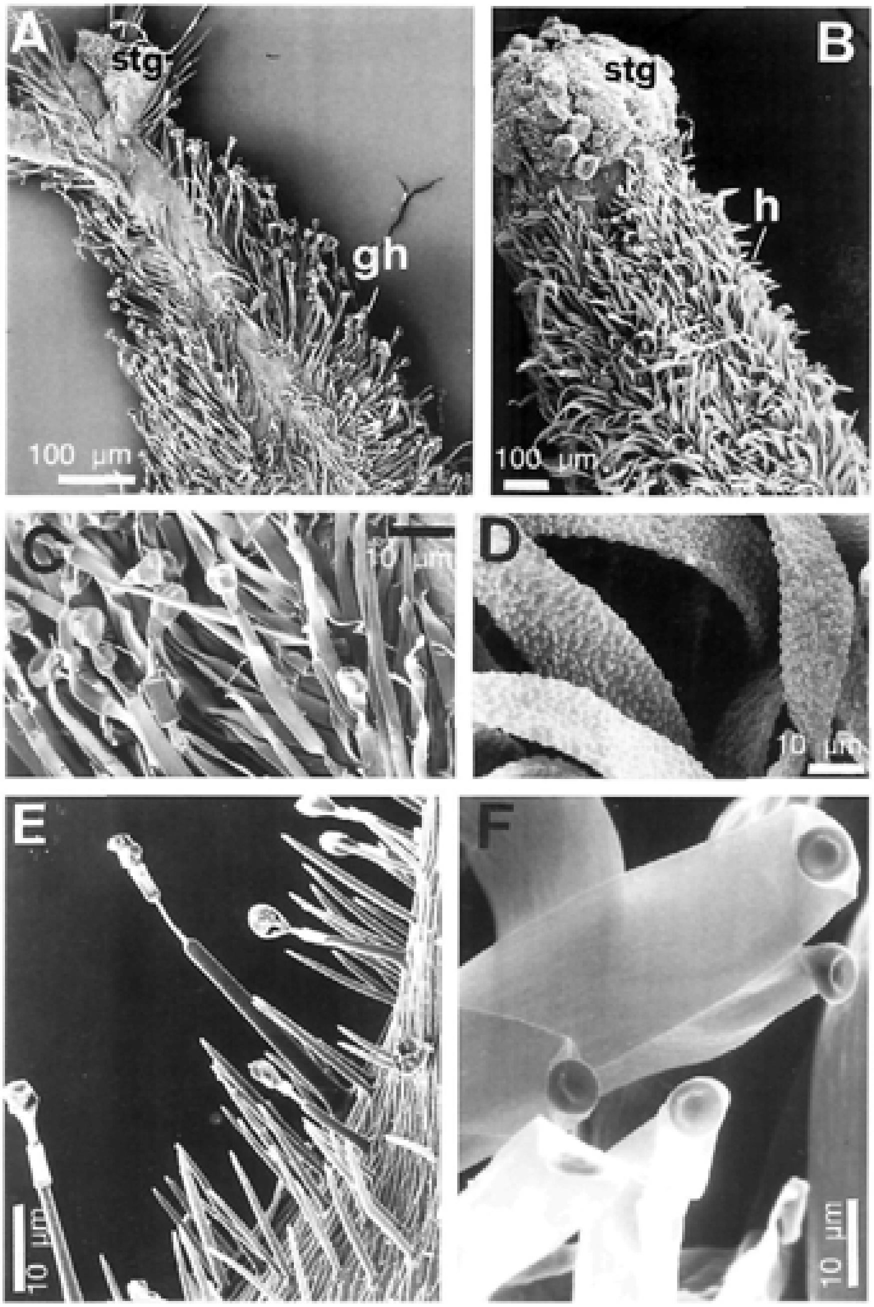

Fig. 8.–Scanning electron and light micrographs of hairs on gynoecia of *Monsonia* . A: SEM micrograph of *M. senegalensis* gynoecium, which has clavate stigmata (stg) and long glandulose hairs (gh) (*G. Cardoso de Matos 6269*, MA 498297). B: Micrograph of *M. heliotropioides* gynoecium, with short, ovate stigmata (stg) and short hairs (h) (*Rechinger 27633*, W). C: SEM micrograph of glandulose hairs of *M. senegalensis* gynoecium. D: Micrograph of verrucate hairs (vh) of *M. heliotropioides* gynoecium. E: SEM micrograph of glandulose hairs on the top of *M. brevirostrata* mericarp (*Krook 2220*, W). F: SEM micrograph of gynoecium hairs of *M. angustifolia*, showing the umbilicate tip structure (*Penther 2218*, W).

vides *Monsonia* into two groups: sect. *Monsonia* contains 9 species with folded, non-conduplicated cotyledons (fig. 13B-C), and sect. *Olopetalum* includes 16 species with conduplicate cotyledons, one half of each cotyledon lying on the primary fold of the opposite cotyledon (fig. 13D) (tables 2 and 3, character 20). In *Sarcocaulon* cotyledons are folded, in a similar fashion to *Monsonia* sect. *Monsonia*

Chromosome number.–There are few chromosome counts in *Monsonia*, most of them reported by WARBURG (1938) and HAIFA & JOUMENA (1991). The somatic numbers are 22 for *M. senegalensis* (sect. *Olopetalum*) (WARBURG, 1938), 26 for *M. nivea*, and 18 for *M. heliotropioides* (sect. *Monsonia*) (HAIFA & JOUMENA, 1991). According to ALBERS (1996), *Monsonia* has $x = 8, 9, 10, 11, 12$, but he did not indicate which species were studied. In *Sarcocaulon* base number is $x = 11$ (ALBERS, 1990).

Cladistic analysis

The cladistic analysis using *Pelargonium* and *Sarcocaulon* as outgroups, yielded 9 minimal length cladograms consisting of 37 steps, a consistency index (CI) of 0.621, a retention index (RI) of 0.913, a rescaled consis-

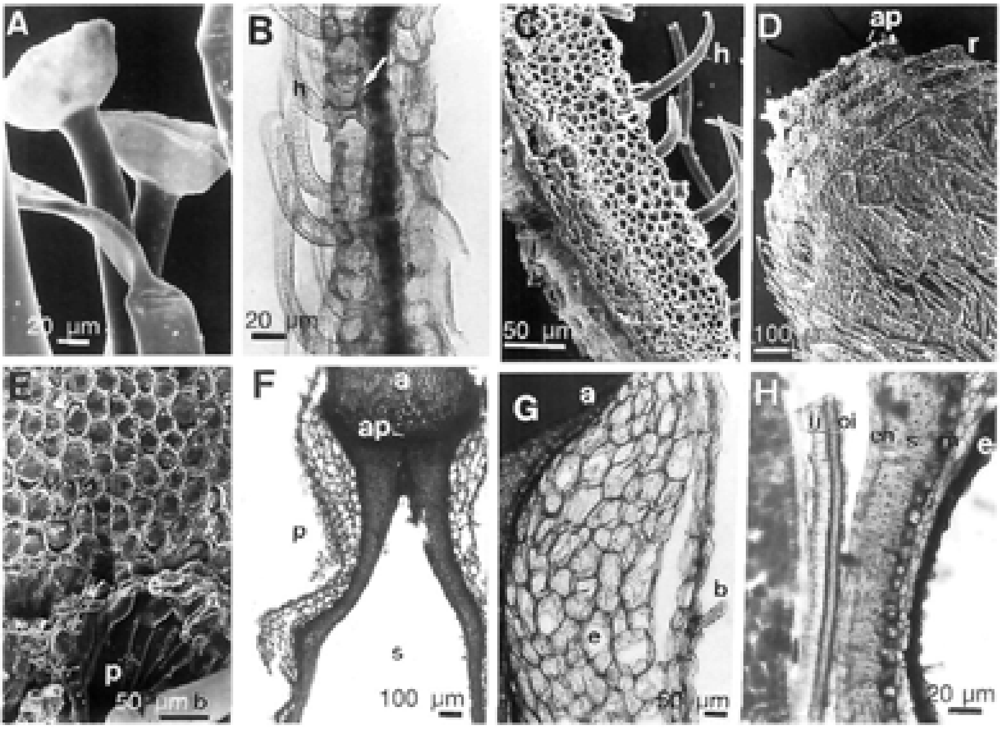

Fig. 9.–Light and scanning electron micrographs of glands and mericarps of *Monsonia* sect *Olopetalum*. A: SEM micrograph of glandular hairs on the surface of a pedicel of *M. angustifolia (Penther 2218)*. B: Light micrograph of mericarp wall of *M. nivea* (*L. Kralik 26*, MA 628481). C: SEM micrograph of a section of the awn of *M. burkeana* showing fibres inside, which are hygroscopic (h: hairs) (*T. T. Heany 23*, COI). D: SEM micrograph of a mericarp of *M. nivea* with ridges (r) and the abscission point of the awn (ap) (*L. Kralik 26*, MA 628481). E: SEM micrograph of mesocarp cells of *M. deserticola* after separation of the exocarp (p: pocket, b: bristle). F: Light micrograph of a section of *M. brevirostrata* mericarp (a: awn, ap: abscission point of the awn) (s: seed space; p: pit) (*Krook 2220*, W). G: Light micrograph of a section of *M. brevirostrata* mericarp; e: cells of exocarp on the pit; b: bristle. H: Light micrograph of a section of the mericarp wall and seed testa in *M. attenuata* (en: endocarp; s: schlerenchima; m: mesocarp; e: exocarp; ii: inner integument of testa; oi: outer integument of testa) (*Gerrard 1431*, W).

tency index (RC) of 0.567, and a homoplasy index (HI) of 0.378. The strict consensus tree recovers two major clades (fig. 14), one of these clades includes some of the outgroups (*Sarcocaulon*). The first major clade consists of all species of *M.* sect. *Olopetalum* and is defined by three synapomorphic characters from the mericarp: mode of detaching (character 13), wall width (character 17), and cotyledon folding (character 20). This clade is supported by 85 % bootstrap. *Monsonia speciosa* is sister to the rest of the species of *M.* sect. *Olopetalum* (88 % bootstrap) (subclade I), as a result of one synapomorphy (plane stipules, character 6).

A terminal, well-supported subclade (87 % bootstrap) (subclade IV) is formed by the three annual species (*M. brevirostrata*, *M. angustifolia*, *M. senegalensis*). Three weakly supported subclades are also found within the sect. *Olopetalum*: one formed by *M. brevirostrata-M. senegalensis-M. angustifolia-M. natalensis-M. grandifolia-M. emarginata-M. galpinii-M. praemorsa-M. burkeana-M. glauca-M. lanuginosa-M. atenuatta-M. transvaalensis* (78 % bootstrap) (subclade II) which have a tuft of hairs on the stipules (character 7). *Monsonia longipes*, and M. *ignea* (66 % bootstrap) (subclade III), are defined by staminal knob-like nectaries, with a conic tube

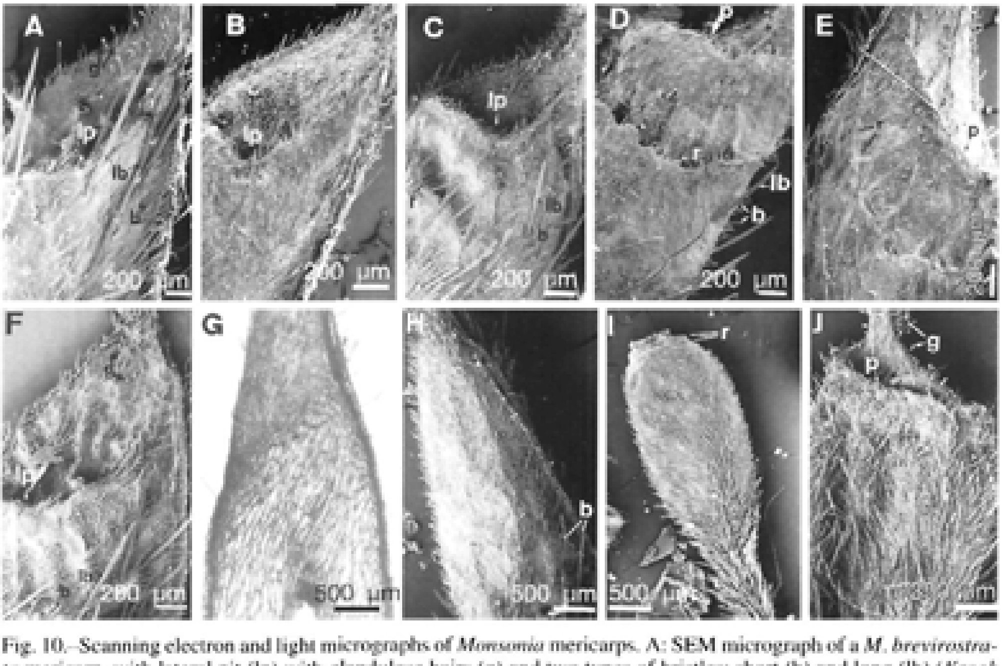

Fig. 10.–Scanning electron and light micrographs of *Monsonia* mericarps. A: SEM micrograph of a *M. brevirostrata* mericarp, with lateral pit (lp) with glandulose hairs (g) and two types of bristles: short (b) and long (lb) (*Krook 2220*, W). B: SEM micrograph of a *M. burkeana* mericarp, with lateral pit (lp) with glandulose hairs and two types of bristles: short (b) and long (lb) (*T. T. Heany 23*, COI). C: SEM micrograph of a *M. lanuginosa* mericarp, with a lateral pit (lp) with sparse glandulose hairs, one slight lateral ridge (r) and two types of bristles: short (b) and long (lb) (*Slechter 1308*, COI). D: SEM micrograph of a *M. angustifolia* mericarp, with a perpendicular pit (p) with no visible glandulose hairs, one lateral ridge (r) and two types of bristles: short (b) and long (lb) (*Penther 2218*, W). E: SEM micrograph of a *M. longipes* mericarp, with a nearly perpendicular pit (p) with not visible glandulose hairs, one lateral ridge (r) and two types of bristles: short (b) and long (lb) (*Cufodontis 555*, W). F: SEM micrograph of a *M. ignea* mericarp, with a lateral pit (lp), glandulose hairs (g), wavy mericarp surface and two types of bristles: short (b) and long (lb) (*Puccioni & Stefanini 959*, P). G: Light micrograph of a thin section of a gradually tapered mericarp in *M. emarginata* (*Penther 2174*, W). H:. SEM micrograph of mericarp in *M. emarginata* with only short bristles (*Penther 2174*, W). I: SEM micrograph of a mericarp in *M. nivea* which has two ridges (r) beside the awn (*L. Kralik 26*, MA 628481). J: SEM micrograph of a mericarp in *M. umbellata* which has a glandulose pit (p) and awn insertion (g) (*L.W. Carisso & F. Sousa 243*, COI).

(character 10). *Monsonia natalensis*, *M. grandifolia*, *M. emarginata*, *M. galpinii* (59 % bootstrap) form subclade V, nested in subclade II and characterised by tapered mericarps (character 16).

The second major clade (76 % bootstrap) includes the species of sect. *Monsonia* and the three species of *Sarcocaulon* forming a politomy. The clade is defined by two synapomorphies: folded, but non-conduplicated cotyledons (character 20) and plumose awns (character 15). There is also a weakly supported subclade formed by *M. deserticola*- *M. nivea*- *M. heliotropioides* (subclade VI) supported by an non-synapomorphic change (anthers very small, shorter than 1 mm, character 11). The three species of *Sarcocaulon* form a clade (96 % bootstrap) defined by three synapomorphies: stems fleshy and covered with waxy bark (characters 2 and 3) and spines formed from petioles of long leaves (character 4).

Discussion

Monophyly of Monsonia

Monophyly of *Monsonia* is challenged by the inclusion of *Sarcocaulon* in a clada togeth-

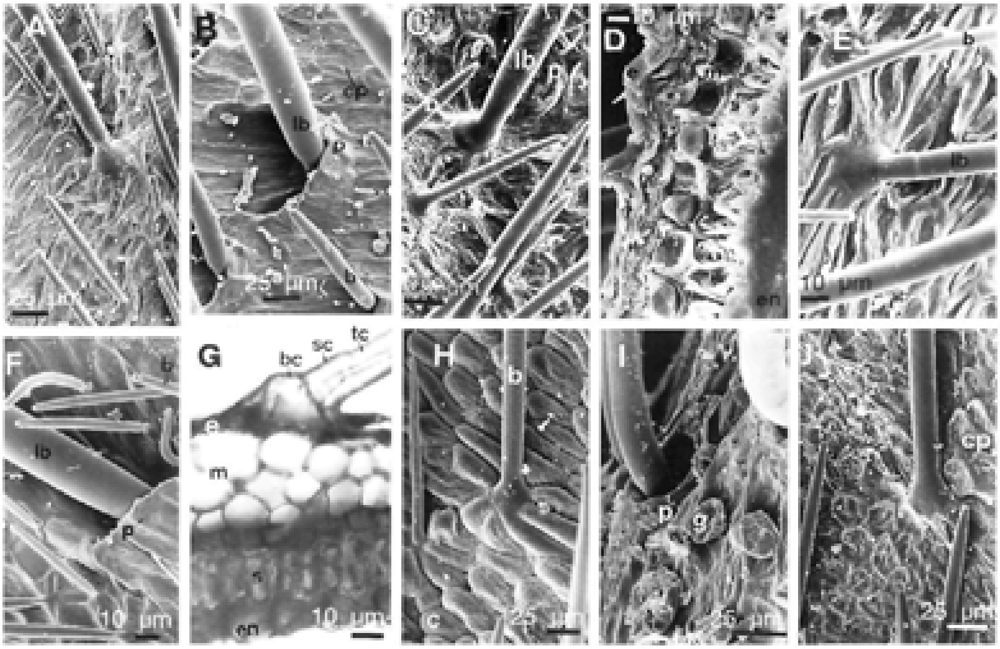

Fig. 11.–Light and scanning electron micrographs of mericarp surfaces of *Monsonia* sect. *Olopetalum*. A: SEM micrograph of mericarp surface of *M. attenuata* showing collapsed papillae and two types of bristles (*Gerrard 1431*, W). B: SEM micrograph of mericarp surface of *M. longipes* showing collapsed papillae (cp), pockets rounding the base of bristles (p) and two types of bristles, short (b) and long (lb) (*Cufodontis 555*, W). C: SEM micrograph of mericarp surface of *M. burkeana* showing collapsed papilles (p), and short (b) and long (lb) bristles with granulate surface and without pockets (*Dinter 6611*, P). D: SEM micrograph of mericarp wall section in *M. brevirostrata*, showing exocarp (e), mesocarp (m), schlerenchima region (s) and endocarp (en) (*Krook 2220*, W). E: SEM micrograph of mericarp surface of *M. brevirostrata*, showing a reticulate pattern (without pockets), covered by wax and with two types of bristles: short (b) and long (lb). F: SEM micrograph of mericarp surface of *M. senegalensis* showing pockets (p) only at the base of long bristles (lb), lacking in short bristles (b) (*G. Cardoso de Matos 6269*, MA 498297). G: Light micrograph of a mericarp wall section of *M. emarginata* showing exocarp (*e*), schlerenchima region (s), endocarp (en), basal cell of the bristle (bc), second cell of the bristle (sc) and tubular cell of the bristle (tc) (*Penther 2174*, W). H: SEM micrograph of *M. emarginata* showing a reticulate pattern with convex cells (c) and a single type of bristles without pockets (b) (*Penther 2174*, W). I: SEM micrograph of mericarp surface of *M. speciosa* showing small glands (g), and bristles with pockets (p) (*Marloth s.n.*, W). J: SEM micrograph of mericarp surface of *M. lanuginosa* showing collapsed papillae (cp) (*Slechter 1308*, COI).

er with *Monsonia* sect. *Monsonia*. Thus, ALBERS' (1996) criterion that *Sarcocaulon* should be included in *Monsonia* is supported by our analysis based on morphological characters. However, according to MOFFETT (1997) these changes could be premature and cause nomenclatural instability. At the present status of knowledge we prefer to maintain *Sarcocaulon* as a separate genus, until more independent evidence is available.

Cladistic Analysis and Classification of Monsonia

The results obtained from the cladistic analysis are in agreement with the division of *Monsonia* into two groups: *M.* sect. *Olopetalum* (= *Barbata*) and *M.* sect. *Monsonia* (= *Plumosa*) (Venter, 1979) (table 1). Two species (*M. longipes* and *M. speciosa*) were placed in sect. *Monsonia* by VENTER (1990) and VERHOEVEN & VENTER (1986) based on a cluster analysis of morphological characters. However, these two species share the three synapomorphies of *M.* sect. *Olopetalum* (mode of detaching, wall width, columella consistency, and cotyledon folding), and thus fail within the clade of this section. (tables 2 and 3).

In contrast, *M.* sect. *Monsonia* is only defined by two synapomorphies: folded, but

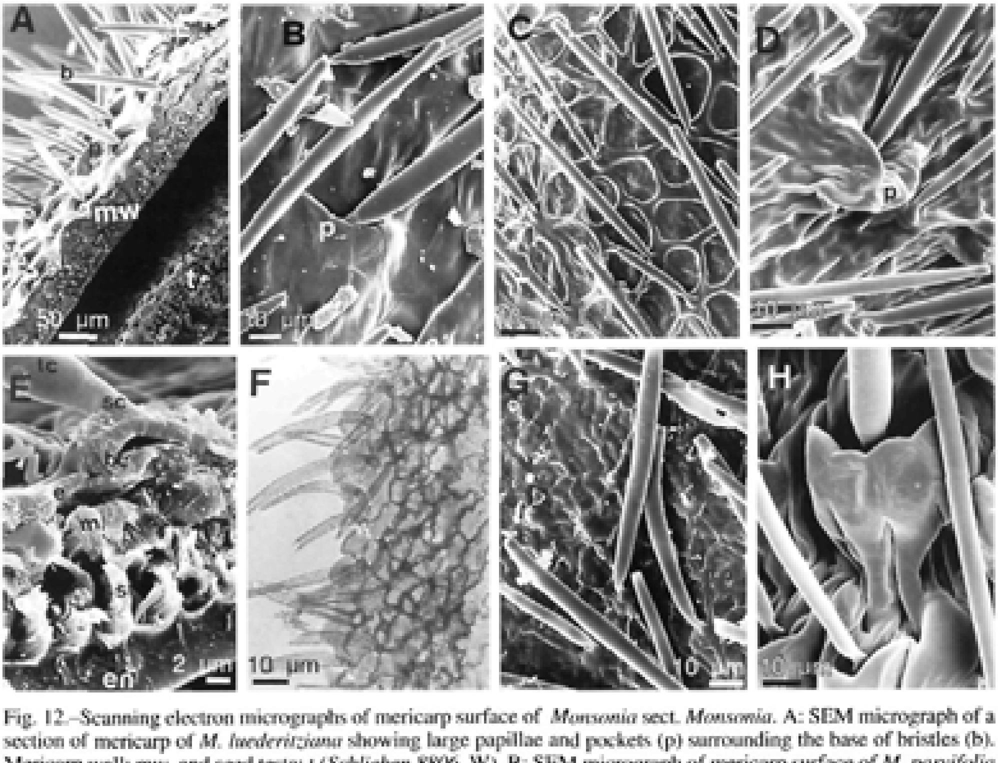

Fig. 12.–Scanning electron micrographs of mericarp surface of *Monsonia* sect. *Monsonia*. A: SEM micrograph of a section of mericarp of *M. luederitziana* showing large papillae and pockets (p) surrounding the base of bristles (b). Mericarp wall: mw, and seed testa: t (*Schlieben 8806*, W). B: SEM micrograph of mericarp surface of *M. parvifolia* showing pockets rounding the base of bristles (p) (*Schlechter s.n.*, W). C: SEM micrograph of mericarp surface of *M. deserticola* showing a reticulate pattern with concave cells, and bristles without pockets. (*Dinter 6611*, P). D: SEM micrograph of mericarp surface of *M. heliotropioides*, showing pockets (p) rounding the base of bristles (*Rechinger 27633*, W). E: SEM micrograph of a mericarp wall section with a bristle insertion in *M. nivea*, showing exocarp (e), schlerenchima region (s), endocarp (en), basal cell of the bristle (bc), second cell of the bristle (sc) and tubular cell of the bristle (tc) (*Kralik 26*, MA 628481). F: Light micrograph of separate exocarp layer of *M. nivea* fruit showing wavy cells and the bristle insertion. G: SEM micrograph of mericarp surface of *M. nivea* showing a single type of bristles wich have a truncate tip. H: SEM micrograph of mericarp surface of *M. luederitziana* showing pockets surrounding the bristles base (*Schlieben 8806*, W).

non-conduplicated cotyledons and plumose awn.

In the analytic classification proposed by Knuth (1912) (table 1) there are some natural groups; although we do not consider any taxonomic status for sect. *Biflora*, two species (*M. brevirostrata*, *M. angustifolia*) included in that section by Knuth form a natural group together with *M. senegalensis* in our analysis (subclade IV, fig. 14). Otherwise, Knuth´s sections were not supported in the cladogram: *Umbellatae*, *Ovata*, *Genistiformis*, and *Rotundatae*.

Sarcocaulon is monophyletic. The three synapomorphies supporting its clade are also shared by the species not included in this analysis: succulent stems (character 2), stems covered by wax (character 3), and spines formed from leaf petioles (character 4).

Character differentiation and evolution

Most characters analysed in this study were already discussed by Venter (1979). We have revisited all of them and searched for additional taxonomic information.

The annual life span seems to have arisen only once in *Monsonia*. The three annual species (*M. angustifolia*, *M. senegalensis*, *M. brevirostrata*) are usually colonizers. Two of them are distributed in a wide range of distribution and altitude, whereas *M. brevirostrata* occurs on mountainous bare ground (Venter 1979). Although most annuals are derived in Geraniaceae (incl. *Monsonia)*, there are several instances in *Pelargonium* (Bakker & *al.* 1998) and *Geranium* (Yeo 1973) where perennials derived from annuals.

Leaf characters appear to have followed two different evolutionary patterns. Pinnate leaves have appeared twice, once involving most species of sect. *Olopetalum* and, independently, in *M. nivea* (sect. *Monsonia*). In contrast, subulate stipules and hair tufts occured once within sect. *Olopetalum*.

According to Yeo (1990) pseudoumbels are considered an advanced feature in Geraniaceae due to suppression of bracts and internodes. Our cladistic analysis suggests that pseudoumbels in *Monsonia* are primitive while cymose inflorescences are derived.

Nectary features were already described in the literature (Narayana & Arora, 1963; Al-Nowaihi & Khalifa, 1973; Kumar, 1976; Link, 1990; Vogel, 1998). It is commonly accepted that they are derived from hydathodes in Geraniaceae (Link, 1990; Vogel, 1998). Link (1990) published a schematic and comprehensive classification of Geraniaceae nectaries, with three types: cryptothetic-staminal, phanerothetic-discoid, and cryptothetic-hypanthial. In *Monsonia* we have re-interpreted Link´s classification considering three types: axillar, staminal with a protuberance, and staminal with a tube. In general, Link's

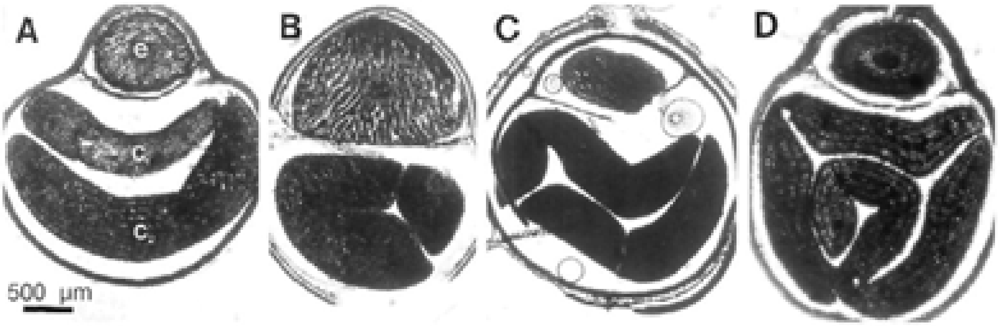

Fig. 13.–A: Light micrograph of mericarp section of *Pelargonium peltatum*, showing the embryonic axis (e) and the two unfolded, accumbent cotyledons (c_1 and c_2)(*Cavanilles s.n.*, MA 252520). B: Light micrograph of mericarp section of *M. umbellata*, showing the embryonic axis and the two slightly folded cotyledons (*L.W. Carisso & F. Sousa 243*, COI). C: Light micrograph of mericarp section of *M. luederitziana*, showing the embryonic axis and the two slightly folded cotyledons (*Schlieben 8806*, W). D: Light micrograph of mericarp section of *M. emarginata* showing the embryonic axis and the two clearly folded cotyledons (*Penther 2174*, W).

cryptothetic-staminal are axillar and Link's phanerothetic-discoid are staminal with a protuberance. However, part of Link's cryptothetic-hypanthial nectaries are actually axillar, while the rest are staminal with a tube. A second character is found in a sepal structure related to nectar protection from desiccation: an enlargement at the sepal base, which encloses the nectary in pouches and is related to part of axillary nectaries. This structure was interpreted by Link as part of cryptothetic-hypanthial nectaries. Staminal nectaries with a protuberance have occurred twice, once involving some of species of sect. *Olopetalum* (subclades IV and V plus *M. burkeana* and *M. praemorsa*) and, independently, in part of sect. *Monsonia* (subclade VI). In contrast, staminal nectaries with a tube occurred only once within sect. *Olopetalum.* (subclade III). Additionally, sepals with pouches have appeared once within *Monsonia*, defining subclade VII.

The androecium in *Monsonia* consists of 15 anthers, except for *M. brevirostrata* which has a reduction to 5 fertile stamens plus 10 sterile filaments. Fertile stamen reduction has been observed in other genera of Geraniaceae such as in *Pelargonium* (VAN DER WALT, 1990), *Geranium pusillum* and *G. biuncinatum* (AEDO & *al.* 1998, and unpublished data). Reduction in anther length (< 1 mm) has occurred once within sect. *Olopetalum* (subclade IV) and twice in sect. *Monsonia* (*M. deserticola*, *M. nivea* plus *M. heliotropioides*; and *M. umbellata*), being likely associated with a shift to autogamy that has brought also a reduction in the number of pollen grains (as few as 8 in each anther of *M. heliotropioides*) and petal size (1.5 mm in *M. nivea*).

Supratectal processes define a clade of two species (*M. nivea* and *M. heliotropioides*) within sect. *Monsonia*. Similar processes are present in many species of *Geranium* and *Erodium*, whereas *Sarcocaulon* and *Pelargonium* lack this character.

Four of the seven fruit characters considered in the cladistic analysis define the two sections of *Monsonia*. Mericarp detaching, consistency of columella, and mericarp wall thickness support the monophyly of sect. *Olopetalum*, while plumose awn characterises sect. *Monsonia*. The two types of mericarp detaching were first found by PICARD (1837) and revisited by YEO (1990) in Geraniaceae, which also serve in our analysis to define the two sections. Mericarps separate upwards in sect. *Monsonia*, while in sect. *Olopetalum* they separate downwards (see also ZOHARY, 1972, figures 332, 345 and 350). Robustness of columella and mericarp are very variable characters in Geraniaceae (unpublished data) and may be related to dormancy (AEDO & *al.* 1998). Plumose awn has been considered in the past a significant character to outline infrageneric groups in *Monsonia* and *Erodium* (BOISSIER, 1867).

The awn aids both seed dispersal and establishment in the soil (COBELLI, 1892; YEO 1990), as occurs in sect. *Olopetalum*. Additionally, mericarp devices contribute to mericarp burying in the following aspects: (1) the hygroscopic awn rotates and plants the mericarp; (2) the ridges on the top of mericarp are directed upwards and serve to enable penetration or retention of the mericarp underground; (3) the mericarp bristles are directed upwards, helping retain te mericarp underground; (4) the fusiform mericarp has a sharp callus on its bottom, to enable penetration of the soill. In contrast, plumose awns of sect. *Monsonia* do not aid to bury the mericarp because they are not sufficiently robust to penetrate in the soil nor do they aid rotation through humidity changes.

A shift from wind dispersal to adhesive dispersal by animals is suggested by phylogenetic reconstructions of Geraniaceae. Phylogenetic analysis of rbcL (PRICE & PALMER 1993) and trnL-F (unpublished data) sequences suggests that the primarily wind-dispersed *Pelargonium* is sister group to the rest of Geraniaceae. Two main wind-dispersed mechanisms can be envisaged in Geraniaceae. One is present in most *Pelargonium* mericarps having a tuft of hairs from the basal to medial zone of the tails (similar to a pappus). The other is found in *Monsonia*, *Sarcocaulon* and *Erodium* and consists of a plumose awn. Mericarp structure associated with zoochory mode (SØRENSON, 1986, STEB-

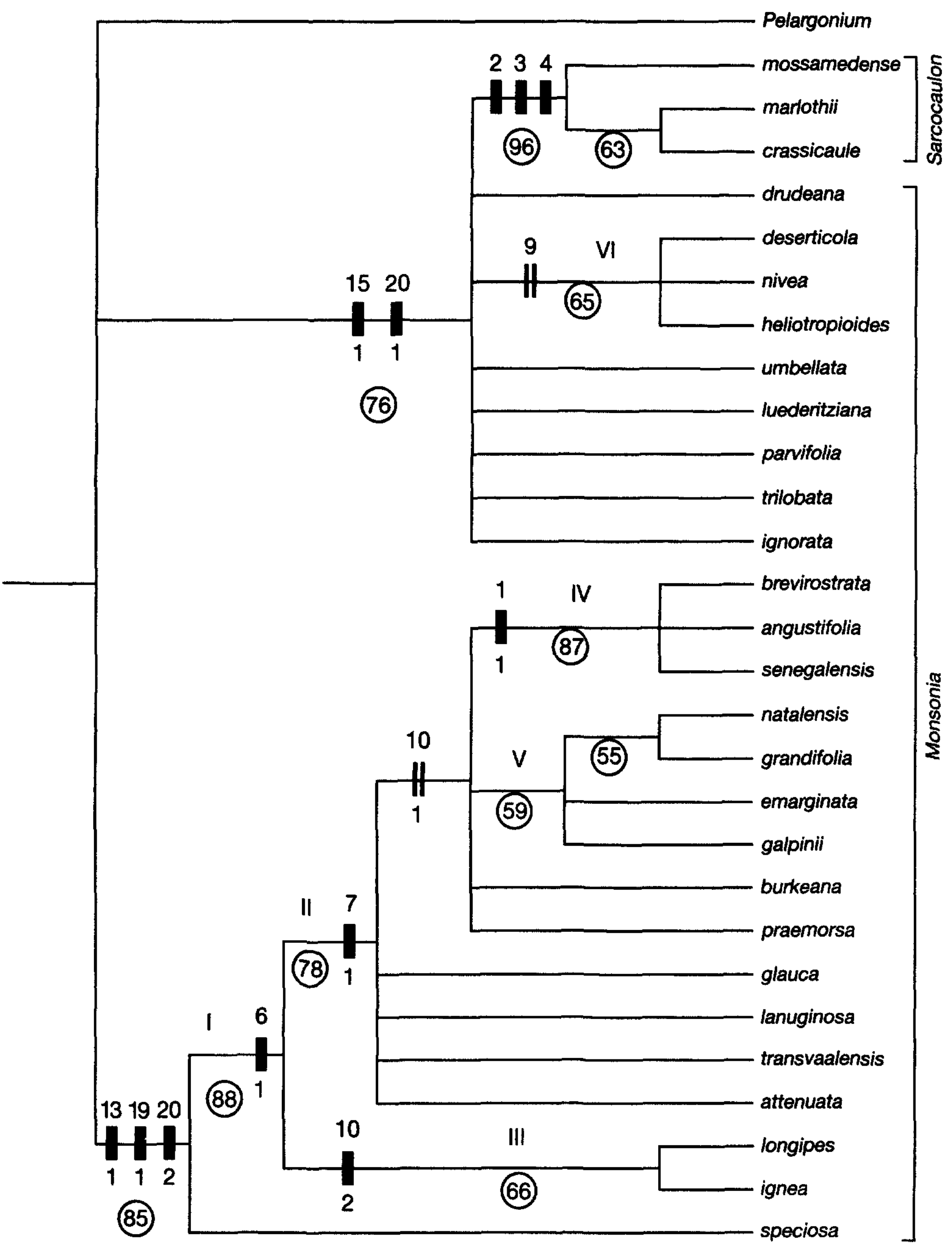

Fig. 14.–Strict consensus tree of 9 most parsimonious trees of *Monsonia* obtained from the analysis of 20 morphological and anatomical characters. Circled numbers indicate bootstrap values from 100 replicates. Solid bars are unambiguous synapomorphies, parallel lines are parallelisms; roman numbers designate clades referred to in the text.

BINS, 1974) seems to be an advanced adaptation that occur independently in Geraniaceae, including sect. *Olopetalum*. Besides, animal dispersed mericarps are usually larger in Geraniaceae than those of the wind dispersed ones (LEISHMAN & WESTOBY, 1994; GAJEWSKI 1959, 1963), and this is the case of sect. *Olopetalum*.

There is a pattern for cotyledon evolution in which a flat cotyledon has increasingly been folded to conduplicate cotyledons in sect. *Olopetalum* (YEO 1990). Cotyledon conduplication is also found in *Erodium* and *Geranium*, which might have occurred independently. Molecular phylogenetic studies, already in progress, may shed further light on this and depict a far more robust picture of morphological evolution in *Monsonia* and Geraniaceae as a whole.

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Appendix 1

List of selected specimens used for the morphological and anatomical studies.

M. angustifolia A. Richard: *Penther 2218* (W); *Dinter 458* (COI); *Lebrun 7919* (P).

M. attenuata Harvey: *Gerrard 1431* (W); *Schlechter 6827* (LE); *Codd 8271* (K); *Davidse 6725* (MO).

M. brevirostrata Knuth: *Krook 2220* (W); *Schlechter 6573* (LE); *Van Wick 3925* (MO).

M. burkeana Harvey: *Dinter 6611* (P); *Heany 23* (COI); *Schlechter 3581* (LE); *Miller 2002* (K); *Westfall 1587* (MO).

M. deserticola Knuth: *Dinter 6611* (P); *Kers s.n.* (MO); *Giess & al. 5312* (MO); *Giess & al. 5461* (MO)

M. drudeana Schinz: *Giess 14605* (K); *Schenk 33* (P); *Giess & al. 5304* (MO).

M. emarginata (L. f.) L'Hér.: *Penther 2174* (W); *Ecklon 440* (LE); *Van Wick & Vorster 2265* (MO).

M. galpinii Knuth: *Hilner 165* (P).

M. glauca Knuth: *Dinter 5655* (P); *Bruce 61* (MO); *Pearson 7897* (K); *Bayliss 6377* (MO); *Smith 3258* (MO).

M. grandifolia Knuth: *Rudatis 1342* (W); *Medley Wood 6724* (LE); *Hilliard 5468* (MO); *Hilliard 8890* (MO); *Haygatte 834* (MO); *Edwards 106* (MO).

M. heliotropioides (Cav.) Boiss.: *Rechinger 27633* (W); *Schimper 306* (LE); *Duthie s.n.* (LE); *Guinet & Sauvage 232* (MPU).

M. ignea Schinz: *Puccioni & Stefanini 959* (P); *Keller 50* (K); *Ellis 184* (K).

M. ignorata Merxmüller & Schreiber: *Lavranos & Pehlemann 19639* (MO); *Lavranos & Bleck 23760* (MO); *Puff 780804* (W); *Dinter 6019* (K); *Giess 13423* (MO)

M. lanuginosa Knuth: *Slechter 1308* (COI, LE, W); *Nelson 536* (K).

M. longipes Knuth: *De Wilde 6013* (MO); *Ndegwa 745* (MO); *Cufodontis 555* (W); *Ndegwa 496* (MO); *Amshof 6691* (MO).

M. luederitziana Focke & Schinz: *Schlieben 8806* (W); *Pearson 9755* (K); *Leistner 2265* (K); *Isaac 215* (MO).

M. natalensis Knuth: *Kuntze s.n.* (P; K); *Mc Clean 336* (K).

M. nivea (Decaisne) Webb: *Kralik 26* (MA-628481); *Rechinger 27272* (W); *Radcliffe 3739* (K).

M. parvifolia Schinz: *Schlechter s.n.* (W,LE); *Schlechter s.n.* (LE); *Leach 13084* (K); *Burger 3925* (MO)

M. praemorsa Knuth: *Gerrard 388* (W); *Gueinzius 452* (G).

M. senegalensis Guillemin & Perrottet: *Cardoso de Matos 6269* (MA-498297); *Sauvage 75* (MPU); *Kotschy 95* (W); *Gillett 20125* (MO).

M. speciosa L.: *Marloth s.n.* (LE, W, P); *Penther 2147* (W).

M. transvaalensis Knuth: *Wilms 96* (K); *Werdermann & Oberdieck 2155* (P); *Munday 2430* (MO).

M. trilobata Kers: *de Winter 3548* (K); *Theron 1960* (B).

M. umbellata Harvey: *Carisso & Sousa 243* (COI); *Seydel 2947* (COI); *Giess 3417* (W); *Acocks 24551* (MO).

Pelargonium peltatum (L.) L'Her.: *Cavanilles s.n.* (MA-252520).

Sarcocaulon crassicaule Rehm.: *Puff 780811* (W).

S. marlothii Engl.: *Seydel 1126* (COI).

S. mossamedense (Welw. ex Oliv.) Hiern.: *Exell & Mendonça 2175* (COI).

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