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Anatomy, morphology, and cladistic analysis of monsonia L.(geraniaceae) (parte C)
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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

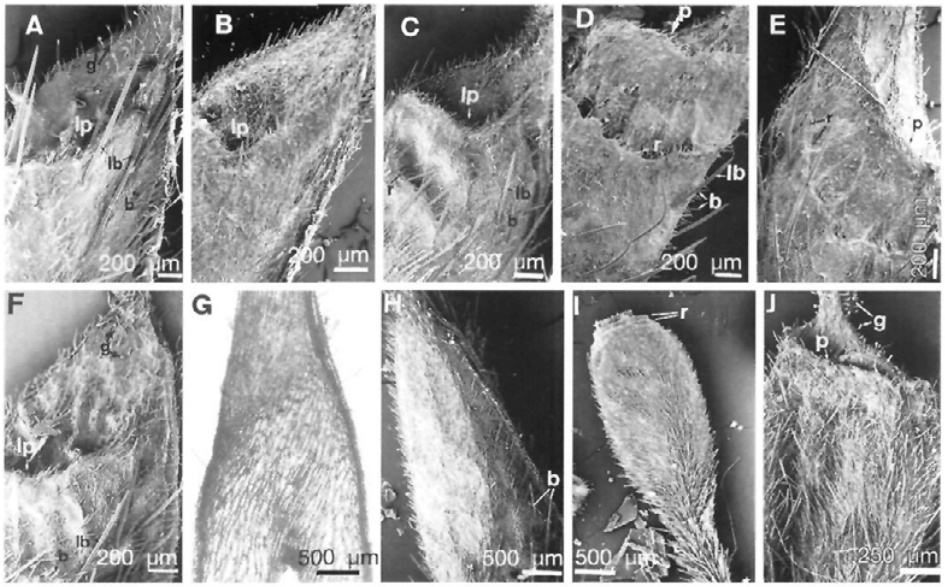

Fig. 10.–Scanning electron and light micrographs of *Monsonia* mericarps. A: SEM micrograph of a *M. brevirostrata* mericarp, with lateral pit (lp) with glandulose hairs (g) and two types of bristles: short (b) and long (lb) (*Krook 2220*, W). B: SEM micrograph of a *M. burkeana* mericarp, with lateral 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-

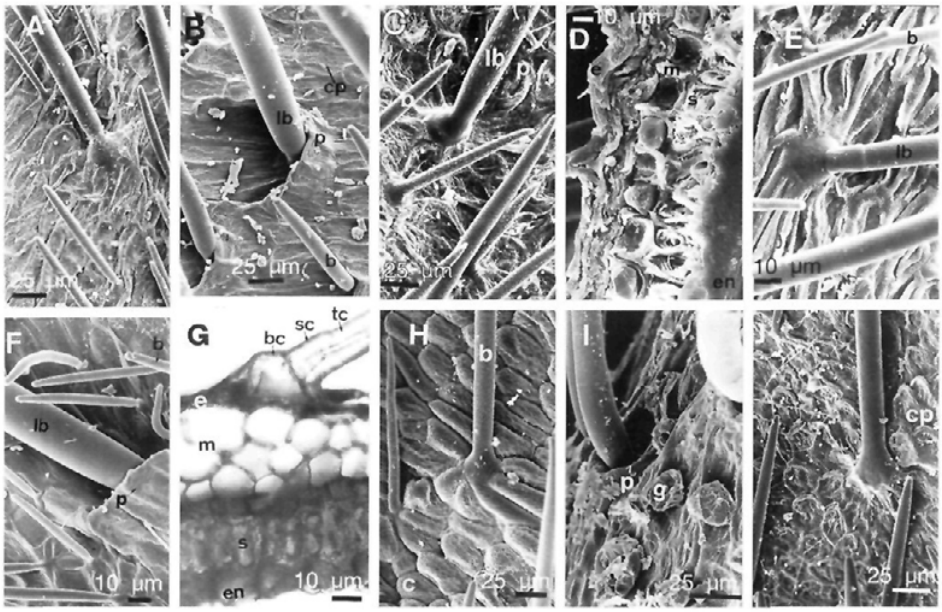

Fig. 11.–Light and scanning electron micrographs of mericarp surfaces of *Monsonia* sect. *Olopetalum*. A: SEM micrograph of mericarp surface of *M. attenuata* showing collapsed papillae and two types of bristles (*Gerrard 1431*, W). B: SEM micrograph of mericarp surface of *M. longipes* showing collapsed 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

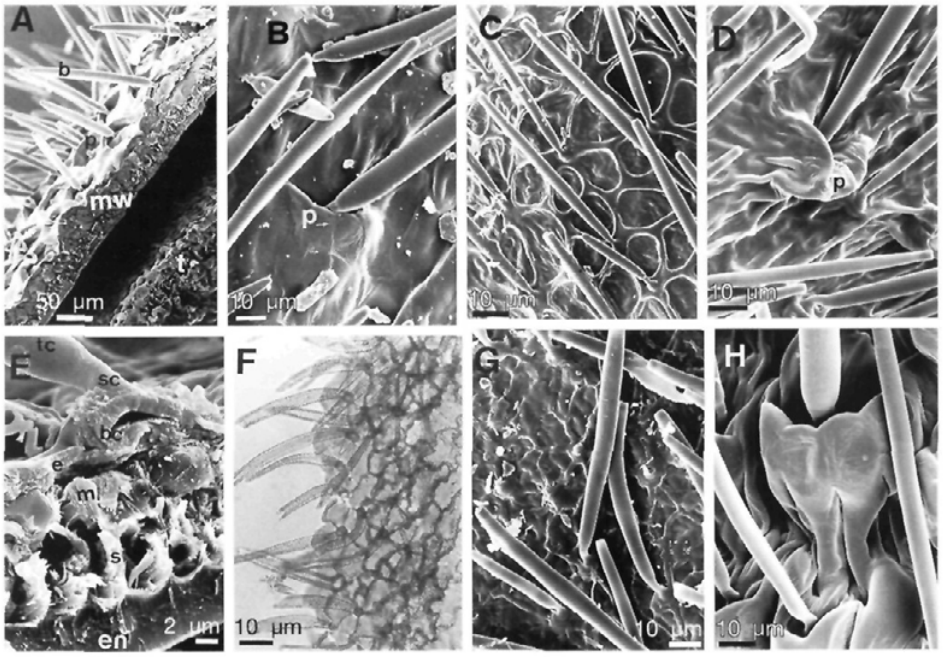

Fig. 12.–Scanning electron micrographs of mericarp surface of *Monsonia* sect. *Monsonia*. A: SEM micrograph of a section of mericarp of *M. luederitziana* showing large papillae and pockets (p) surrounding the base of bristles (b). Mericarp wall: mw, and seed testa: t (*Schlieben 8806*, W). B: SEM micrograph 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

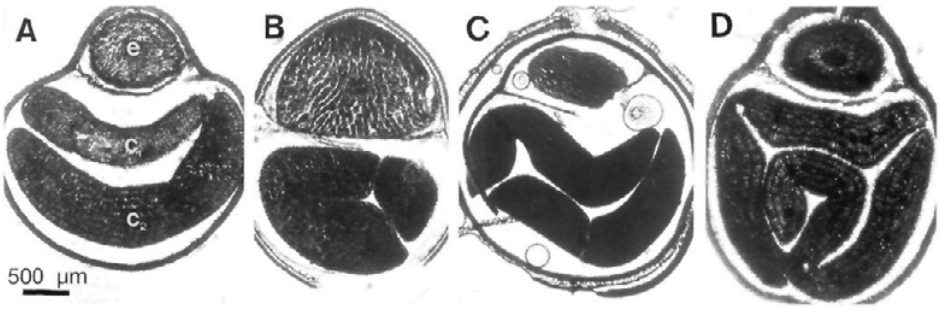

Fig. 13.–A: Light micrograph of mericarp section of *Pelargonium peltatum*, showing the embryonic axis (e) and the two unfolded, accumbent cotyledons (c1 and c2) (*Cavanilles s.n.*, MA 252520). B: Light micrograph of mericarp section of *M. umbellata*, showing the embryonic axis and the two slightly 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-

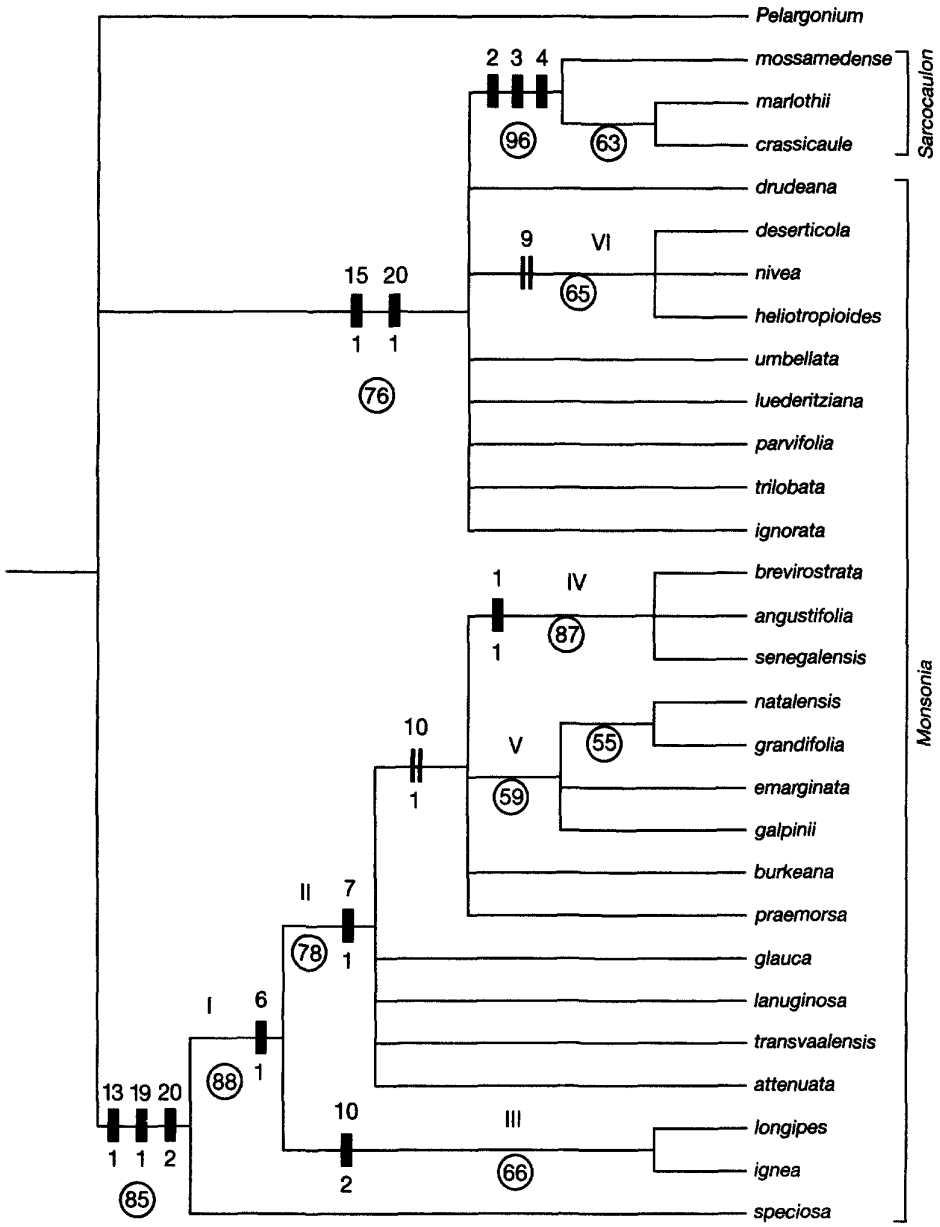

Fig. 14.–Strict consensus tree of 9 most parsimonious trees of *Monsonia* obtained from the analysis of 20 morphological and anatomical characters. Circled numbers indicate bootstrap values from 100 replicates. Solid bars are unambiguous synapomorphies, parallel lines are parallelisms; roman numbers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