
A PHYLOGENETIC ANALYSIS *Santiago Ortiz*²
OF *DICOMA* CASS. AND
RELATED GENERA
(ASTERACEAE:
CICHORIOIDEAE:
MUTISIEAE) BASED ON
MORPHOLOGICAL AND
ANATOMIC CHARACTERS¹

ABSTRACT

This study reports a phylogenetic analysis of the genus *Dicoma* and the related genera *Achyrothalamus*, *Erythrocephalum*, *Pasaccardoa*, and *Pleiotaxis* (Mutisieae, Asteraceae), which share a series of morphological characters of the corolla, ray floret epidermis, anther appendages, and style branches. A matrix of 77 morphological and anatomical characters was used for the analysis. The genera *Gochnatia* and *Oldenburgia* were used as outgroups. The topology of the resulting consensus cladogram suggests that the genus *Dicoma* appears paraphyletic. A clade including *Dicoma* and *Pasaccardoa* appears monophyletic with subgroups clearly defined by a large number of synapomorphies. These findings indicate that maintenance of *Pasaccardoa* as an independent genus implies a need to divide *Dicoma* into several genera. The genera *Pleiotaxis*, *Achyrothalamus*, and *Erythrocephalum* form a monophyletic group. Issues relating to the geographical origin of *Dicoma* (probably Madagascar or southern Africa), and to the evolution of the different species groups, are briefly discussed.

Key words: Asteraceae, cladistics, *Dicoma*, Mutisieae, phylogeny, tropical Africa.

The “*Dicoma* group” (Asteraceae, Mutisieae, Mutisinae) of Bremer (1994) is considered by this author to be one of the most difficult groups to evaluate phylogenetically within the Mutisieae. According to Bremer (1994), it is characterized by its corolla distinctly divided into a narrow tube and wide limb, its non-mutisioid ray floret epidermis pattern, its acuminate apical anther appendages, and its mostly subapically pilose style branches. It comprises *Dicoma* itself, with 50 species occurring in tropical Africa, Madagascar, and South Africa, and two species reaching Asia (*D. schimperi* (DC.) Baill. ex O. Hoffm. is present in the Arabian Peninsula, and *D. tomentosa* Cass. is present in India and Pakistan). Other genera of this group are *Erythrocephalum* Benth. with about 12 species occurring throughout tropical Africa (particularly tropical East Africa), *Achyrothalamus* O. Hoffm. with a single species from Kenya and Tanzania, *Pleiotaxis* Steetz with about 25 species occurring throughout tropical Africa, *Pasaccardoa* Kuntze with 4 species

from tropical Africa, and *Gladiopappus* Humbert with a single species, possibly extinct, from Madagascar.

Prior to Bremer’s (1994) “*Dicoma* group,” similar groupings had been proposed by Jeffrey (1967) and Grau (1980). Indeed, Jeffrey considered this group to be one of the most distinct within the Mutisieae. Hansen (1991) suggested that most of the genera of this group be moved from the Mutisieae to the tribe Cynareae (Cardueae). His support included (a) the cuticular ornamentation of corolla epidermal cells; (b) the corolla divided into a narrow tube and a broader limb; (c) bilabiate flowers with upper limb lobules short and uncoiled or absent (except in *Gladiopappus*, in which they are long and coiled; Humbert, 1963); and (d) style branches with subapical sweeping hairs. Karis et al.’s (1992) cladistic analysis of the subfamily Cichorioideae indicated that *Dicoma*, *Erythrocephalum*, and *Pleiotaxis* form a monophyletic group within the tribe Mutisieae, in accordance with traditional views (see Hoffmann, 1893a; Cabrera, 1977).

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Table 1. Section assignments of the *Dicoma* species included in the present study, following the proposals of Hoffmann (1893a) and Wilson (1923). Question marks indicate that the species in question has not been assigned previously to any section, either by Hoffmann or Wilson or by subsequent authors; for these species, the assignment shown is mine, on the basis of morphological characters.

Hoffmann (1893a)					Wilson (1923)	
	<i>Rhigiothamnus</i> (Less.) DC.	<i>Eudicoma</i> DC.	<i>Macleodium</i> (Cass.) DC.	<i>Dimorphae</i> Wilson	<i>Barbellatae</i> Wilson	<i>Plumosae</i> Wilson
<i>Steirocoma</i> DC.						
<i>D. capensis</i>	<i>D. picta</i>	<i>D. tomentosa</i>	<i>D. spinosa</i>	<i>D. tomentosa</i>	<i>D. anomala</i>	<i>D. sessiliflora</i>
<i>D. niccolifera?</i>	<i>D. fruticosa?</i>	<i>D. bangeolensis?</i>	<i>D. relhanooides</i>	<i>D. bangeolensis</i>	<i>D. elegans</i>	<i>D. zeyheri</i>
<i>D. elegans?</i>				<i>D. capensis</i>	<i>D. picta</i>	<i>D. saligna?</i>
<i>Hochstetteria</i> (DC.) O. Hoffm.				<i>D. welwitschii</i>	<i>D. nachtigalii</i>	
	<i>Psilocoma</i> Harv.	<i>Brachyachaenium</i> Baker	<i>Pterocoma</i> DC.		<i>D. spinosa</i>	
<i>D. schimperi</i>	<i>D. anomala</i>	<i>D. nachtigalii</i>			<i>D. dinteri</i>	
	<i>D. cana</i>				<i>D. cana</i>	
	<i>D. dinteri?</i>				<i>D. niccolifera?</i>	
	<i>D. aethiopica?</i>				<i>D. fruticosa?</i>	
	<i>D. grandidieri?</i>				<i>D. aethiopica?</i>	
	<i>D. montana?</i>				<i>D. grandidieri?</i>	
	<i>D. gillettii?</i>				<i>D. montana?</i>	
	<i>D. carbonaria?</i>				<i>D. gillettii?</i>	
	<i>D. oleaefolia?</i>				<i>D. carbonaria?</i>	
	<i>D. welwitschii?</i>				<i>D. oleaefolia?</i>	
					<i>D. schimperi?</i>	

Table 2. List of the species included in the study, showing voucher specimens and distribution.

Species	Voucher specimens	Distribution
<i>Achyrothalamus</i>		
<i>A. marginatus</i> O. Hoffm.	Faulkner 3980 (K), Pocs 88056 (K)	Kenya, Tanzania
<i>Dicoma</i> Cass.		
<i>D. aethiopica</i> S. Ortiz & Rodr. Oubiña	Gilbert, Ensermu & Vollesen 7870 (K)	Ethiopia
<i>D. anomala</i> Sond.	M. da Silva 3181 (COI), Gossweiler 4143 (COI)	Tropical Africa and southern Africa
<i>D. bangueolensis</i> Buscal. & Muschl.	Beckett 242 (K)	Somalia
<i>D. cana</i> Balf f.	Balfour 157 (K)	Socotra
<i>D. capensis</i> Less	Bryant 104 (K), Schlieben 8938 (BM)	Southern Africa
<i>D. carbonaria</i> (S. Moore) Humbert	Chauwet 359 (K), Decary 9263 (MO)	Madagascar
<i>D. dinteri</i> S. Moore	Dinter 3525 (K), Merxmüller 881 (BM)	Namibia
<i>D. elegans</i> Welw. ex O. Hoffm.	Antunes 71 (COI), Gossweiler 1822 (COI)	Angola
<i>D. fruticosa</i> Compton	Van Breda 4426 (K)	South Africa (Cape Province)
<i>D. gillettii</i> Rodr. Oubiña & S. Ortiz	Gillett & Beckett 23263 (K)	Somalia
<i>D. grandidieri</i> (Drake) Humbert	Capuron 18643-SF (K), Decary 10707 (BM)	Madagascar
<i>D. montana</i> Schweick.	L.E. Codd 8689 (K), Dyer 9169 (BM)	South Africa (Transvaal)
<i>D. nachtigalii</i> O. Hoffm.	Pearson 7642 (K)	Angola, Namibia
<i>D. niccolifera</i> Wild	Walters 2347 (K), Leach 8928 (K)	Zambia, Zimbabwe
<i>D. oleaeifolia</i> Humbert	Kaudern s.n. (K)	Madagascar
<i>D. picta</i> (Thunb.) Druce	Acocks 19004 (K)	South Africa (Cape Province)
<i>D. rehanooides</i> Less.	Acocks 5578 (S)	South Africa (Cape Province)
<i>D. saligna</i> Lawalrée	Gossweiler 11331 (COI), Exell & Mendonça 3032 (COI)	Zambia, Angola, Congo
<i>D. schimperi</i> (DC.) Baill. ex O. Hoffm.	Bally & Melville 15857 (K), Thesiger s.n. (BM)	Arabian Peninsula, Djibouti, Egypt, Sudan, Somalia
<i>D. sessiliflora</i> Harv.	Wingfield 4416 (K), Schleiben 5913 (BM)	Tropical Africa
<i>D. spinosa</i> (L.) Druce	Foucarde 2499 (K), Schlechter 9794 (BM)	South Africa (Cape Province)
<i>D. tomentosa</i> Cass.	M. da Silva 2923 (COI), Nordenstan 2454 (S)	Pakistan, India, tropical Africa, southern Africa
<i>D. welwitschii</i> O. Hoffm.	Exell & Mendonça 3069 (COI), M. da Silva 3668 (COI)	Congo, Angola
<i>D. zeyheri</i> Sond.	Mogg 16306 (K), Willms 661a (BM)	Mozambique, Swaziland, South Africa (Transvaal, Natal)
<i>Erythrocephalum</i> Benth.		
<i>E. microcephalum</i> Dandy	Burt 2699 (K), Dummer 5015 (K)	Uganda, Kenya, Tanzania
<i>E. scabrifolium</i> C. Jeffrey	H.M. Richards 4836 (K), Bullock 2344 (K)	Tanzania, Congo, Zambia, Malawi, Angola
<i>E. zambesianum</i> Oliv. & Hiern	Burt 3289 (K), Davies 367 (K)	Tanzania, Congo, Zambia, Zimbabwe, Malawi, Mozambique

Table 2. Continued.

Species	Voucher specimens	Distribution
<i>Pasaccardoia</i> Kuntze		
<i>P. baumii</i> O. Hoffm.	Monteiro & Murta 2024 (COI), Gossweiler 3017 (COI)	Angola
<i>P. grantii</i> (Benth. & Oliv.) Kuntze	Polhill 11608 (S)	Tanzania, Congo, Zambia
<i>P. jeffreyi</i> Wild	Exell & Mendonça 380 (COI), Exell & Mendonça 365 (COI)	Congo, Zambia, Angola
<i>Pleiotaxis</i> Steetz		
<i>P. pulcherrima</i> Steetz	Cardoso 87 (COI), Barbosa 11577 (COI)	Tanzania, Rwanda, Burundi, Congo, Zambia, Malawi, Angola, Mozambique
<i>P. rugosa</i> O. Hoffm.	F. Moreno 146 (COI), Gossweiler 1825 (COI)	Congo, Angola
<i>P. subpaniculata</i> Chiov.	Murta 103 (COI), B. Teixeira 298 (COI)	Congo, Angola
<i>Gochnatia</i>		
<i>G. amplexifolia</i> (Gardner) Cabrera	Hatschbach 27032 (S)	Brazil
<i>G. attenuata</i> (Britton) Jervis & Alain	Ekman 19174	Cuba
<i>G. cordata</i> Less.	Malme 899a (S)	Brazil, Paraguay, Uruguay and Argentina
<i>G. microcephala</i> (Griseb.) Jervis & Alain	Ekman 9280 (S)	Cuba
<i>G. picardae</i> (Urb.) Jiménez	Ekman 5385 (S)	Haiti
<i>Oldenburgia</i>		
<i>O. grandis</i> (Thunb.) Baill.	Bayliss 4519 (S)	South Africa
<i>O. papionum</i> DC.	Bond 1721 (S)	South Africa
<i>O. paradoxa</i> Less.	Esterhuysen 30160 (S)	South Africa

Table 3. Characters and states used in phylogenetic analysis.

1. Woody (0) / herbaceous (1).
2. Plant erect (0) / spreading to prostrate (1).
3. Stem with conical pluricellular trichomes (0) / without pluricellular trichomes (1).
4. Leaf ovate to lanceolate (0) / obovate to oblanceolate (1).
5. Leaf herbaceous (0) / coriaceous (1).
6. Leaf margin not revolute (0) / conspicuously revolute (1).
7. Leaf not conduplicate (0) / conduplicate (1).
8. Stem without subtending leaves (0) / with subtending leaves (1).
9. Capitulum > 20 mm wide (0) / capitulum ≤ 20 mm wide (1).
10. Involucre campanulate (0) / obconic (1).
11. Outer phyllaries erect-patent to erect (0) / patent to reflexed (1).
12. Phyllary midrib inconspicuous (0) / conspicuous (1).
13. Phyllaries without longitudinal dark stripes (0) / with dark stripes running along the phyllaries (1).
14. Phyllary sclerenchymal fibers in a ± continuous tissue (0) / in distinct bundles surrounded by parenchymal tissue (1) / concentrated on the abaxial face (2) / concentrated on the adaxial face (3).
15. Resin ducts in phyllaries at the abaxial face (0) / reduced or absent (1) (see Fig. 1).
16. Phyllaries acute to acuminate-pungent (0) / subacute to obtuse (1).
17. Innermost phyllaries with scarious margins (0) / ± entirely scarious (1).
18. Innermost phyllaries longer than the rest (0) / shorter than the contiguous outer series (1).
19. Phyllary glabrescent to hairy (0) / completely glabrous (1).
20. Receptacle epaleate (0) / paleate (1).
21. Florets in capitula actinomorphic (0) / marginal florets bilabiate and disc florets actinomorphic (1) / zygomorphic (transitional between actinomorphic and ligulate) (2) / marginal florets "true-ray" (Karis et al., 1992) and disc florets actinomorphic (3).
22. Marginal florets hermaphroditic (0) / neuter (1).
23. Corollas ± as long as or only slightly longer than the involucre (0) / much longer than the involucre (1).
24. Disc corolla tube gradually dilates into limb (0) / abruptly dilates into limb (1).
25. Disc corolla lobes erect to erect-patent (0) / recurved at the apex (1).
26. Disc floret epidermal cell cuticle ornamentation: mutisoid (0) / slightly transversely undulate-striate to nearly smooth (1) / conspicuously longitudinally striate and transversely undulate ("intestine-like") (2) / senecioid (3).
27. Disc corolla margins not sclerified (0) / sclerified (1).
28. Disc corolla without long twin glandular hairs (0) / with long twin glandular hairs (1).
29. Disc corolla without simple hairs (0) / with simple hairs (1).

Table 3. Continued.

30. Star-shaped calcium oxalate crystals in disc corolla subepidermal cells absent (0) / present (1) (see Fig. 2).
31. Vascular tissue in disc corolla bifurcate at the lobe sinuses (0) / bifurcate well below the sinuses (1) / bifurcate at the corolla base (2).
32. Marginal vascular tissue in the disc corolla broad (0) / narrow (1).
33. Marginal vascular tissue in disc corolla conspicuously submarginal (see Fig. 3-3 and 3-4 (0) / ± marginal (Fig. 3-1 and 3-2) (1).
34. Accessory vascular strands in the disc corolla lobes absent (0) / present (1).
35. Apex of the disc corolla lobes with thick-bundled veins (0) / without thick-bundled veins (1).
36. Stamen insertion in disc corolla: at the tube/throat junction (0) / near the corolla base (1).
37. Star-shaped calcium oxalate crystals in stamen filaments absent (0) / present (1).
38. Stamen filament collar inconspicuous (0) / conspicuous and not swollen (1) / conspicuous and swollen at the apical part.
39. Stamen filament collar < 0.8 mm long (0) / > 1.5 mm long (1).
40. Anther not protruding beyond the corolla (0) / protruding beyond the corolla (1).
41. Anther appendage apiculate (0) / acute to slightly acuminate (1).
42. Anther tails calcarate (0) / ecalcarate (1).
43. Anther tails long tapering (0) / with subacute to subrounded apex (1).
44. Contiguous anther tails free (0) / joined (1).
45. Anther tail apices with antrorse ramifications (0) / without ramifications (1).
46. Apex of the anther tail ramifications obtuse (0) (Fig. 5-3) / acute (1) (Figs. 5-1 and 5-2).
47. Sporoderm thick (0) / thin (1).
48. Pollen smooth to slightly granulate (0) / echinate (1).
49. Style with two veins (0) / four veins (1).
50. Star-shaped crystals in styles absent (0) / present (1).
51. Style branches adjacent (0) / style branches separate (1).
52. Style branches straight (0) / conspicuously curved (1).
53. Style branches short (0) (Figs. 6-1 and 6-2) / long (1) (Figs. 6-3 and 6-4).
54. Styler sweeping hairs absent (0) / reaching or almost reaching the bifurcation (1) (Figs. 6-1 and 6-2) / in a long group not reaching the bifurcation (2) (Figs. 6-4) / in a subapical tuft (3) (Fig. 6-3).
55. Styler sweeping hairs of similar length (0) (Fig. 6-1) / with a sub-basal group slightly longer than the rest (1) (Fig. 6-2) / with a sub-basal group conspicuously longer than the rest (2) (Figs. 6-3 and 6-4).
56. Style branch vascular tissue narrow (0) / very thick (1).
57. Cypsela carpopodium present (0) / absent (1).
58. Disc floret cypsela ellipsoid (0) / obovoid to obconic (1).

Table 3. Continued.

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59. Cypsela of marginal florets without rostrum (0) / with rostrum (1).
60. Cypsela \pm smooth (0) / conspicuously ribbed (1).
61. Star-shaped crystals in the cypsela pericarp absent (0) / present (1).
62. Superficial cypsela glands absent (0) / in a continuous layer (1) / on the ribs (2) / in the intercostal grooves (3).
63. Cypsela twin hairs simple (0) / twin hairs bifurcate (1) / absent (2).
64. Twin hairs all around the cypsela (0) (Fig. 7-2) / between ribs (1) (Fig. 7-1 and 7-3).
65. Twin-hair bases not bulbous-glandular (0) / conspicuously bulbous-glandular (1).
66. Twin hairs of the cypsela base similar to those of the other parts of the cypsela (0) / conspicuously enlarged (1).
67. Cypsela with biseriate glands (0) / without biseriate glands (1).
68. Immature testa with similar proportion of needle crystals and square to short-rectangular non-oriented crystals (0) / with long-rectangular crystals oriented in the same direction (1).
69. Mature testa pattern: *Gochnatia* type (0) / *Erythrocephalum* type (1) / *Dicoma* type (2) / *Dicoma welwitschii* type (3).
70. Testa epidermal cells with the lateral and basal walls strengthened (0) / only the basal walls strengthened (1).
71. Pappus of bristles (0) / scales (1) / bristles and scales (2) / absent (3).
72. Pappus bristles scabrid to barbellate (0) / plumose (1).
73. Pappus element persistent (0) / caducous (1).
74. Pappus elements of one row (0) / several rows (1).
75. Pappus and involucre of the same length (0) / pappus overtopping the involucre (1).
76. Pappus erect to erect-patent after fruiting (0) / patent after fruiting (1).
77. All the pappi of the capitulum florets of similar length (0) / pappi of marginal florets much longer than those of disc florets (1) / internal pappus bristles of marginal florets as long as pappus of disc florets, and external pappus bristles of marginal florets much longer than pappus of disc florets (2).
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While studying African taxa of the Mutisieae (Asteraceae), particularly *Dicoma* Cass. (see Ortiz & Rodríguez-Oubiña, 1994, 1996, 1997; Ortiz et al., 1998; Rodríguez-Oubiña & Ortiz, 1995, 1997), I investigated phylogenetic relationships within *Dicoma*, and between this genus and related taxa.

The principal aims of the work reported here were to investigate the relationships between *Dicoma* and other genera and the phylogenetic rela-

tionships within *Dicoma*, with the aims of identifying generic and infrageneric subdivisions and of assessing the validity of the subdivisions previously proposed by Lessing (1830, 1832), De Candolle (1838), Harvey (1865), Hoffmann (1893a), Wilson (1923), and Pope (1991) (see Table 1). Another objective was to obtain preliminary information about the geographical origin and evolution of different species groups within *Dicoma*.

MATERIALS AND METHODS

The phylogenetic analysis was based on morphological and anatomical study of specimens from the BM, COI, K, MO, and S herbaria. A number of species of *Dicoma* were selected as representative of the various morphological types present within this heterogeneous genus as follows. First, the seven species of the group I denominate the "*D. sessiflora* group" (see Results) are representative of a morphological type observed in a total of 19 species, including *D. auriculata* Hutch. & B. L. Burtt, *D. elliptica* G. V. Pope, and *D. gossweileri* S. Moore. Second, the species *D. niccolifera* Wild. and *D. capensis* Less. are representative of a morphological type observed in 7 species, including *D. macrocephala* DC., *D. cuneneënsis* Wild., and *D. schinzii* O. Hoffm. Finally, *D. anomala* Sond., *D. aethiopica* S. Ortiz & Rodr. Oubiña, and *D. montana* Schwick. are representative of a morphological type observed in some 10 species not considered in the present analysis, including *D. galpinii* Wilson, *D. popeana* S. Ortiz & Rodr. Oubiña, and *D. somalense* S. Moore. In addition, and with the aim of covering as much morphological variability as possible, we included species from all the known sections of the genus (see Table 1).

A total of 34 species were included in the study: the single species of *Achyrothalamus*, 24 species of *Dicoma*, 3 species of *Erythrocephalum*, 3 species of *Pasaccardoa*, and 3 species of *Pleiotaxis* (see Table 2). I also studied *Dicoma anomala* Sond., *D. zeyheri* Sond., and *D. capensis* Less. in the field in South Africa. *Gladiopappus vernonioides* Humbert was not included, since I was unable to obtain material of this taxon.

A total of 77 morphological characters were studied (see Table 3). For microscopic examination, floral parts were first boiled in water with a surfactant, then mounted in Hoyer's solution (Anderson, 1954). Phyllary and achene sections were cut by hand with razor blades. Some characters initially considered were excluded from the analysis because they were the same in all species including outgroups, such as endothelial cell wall thickening organization

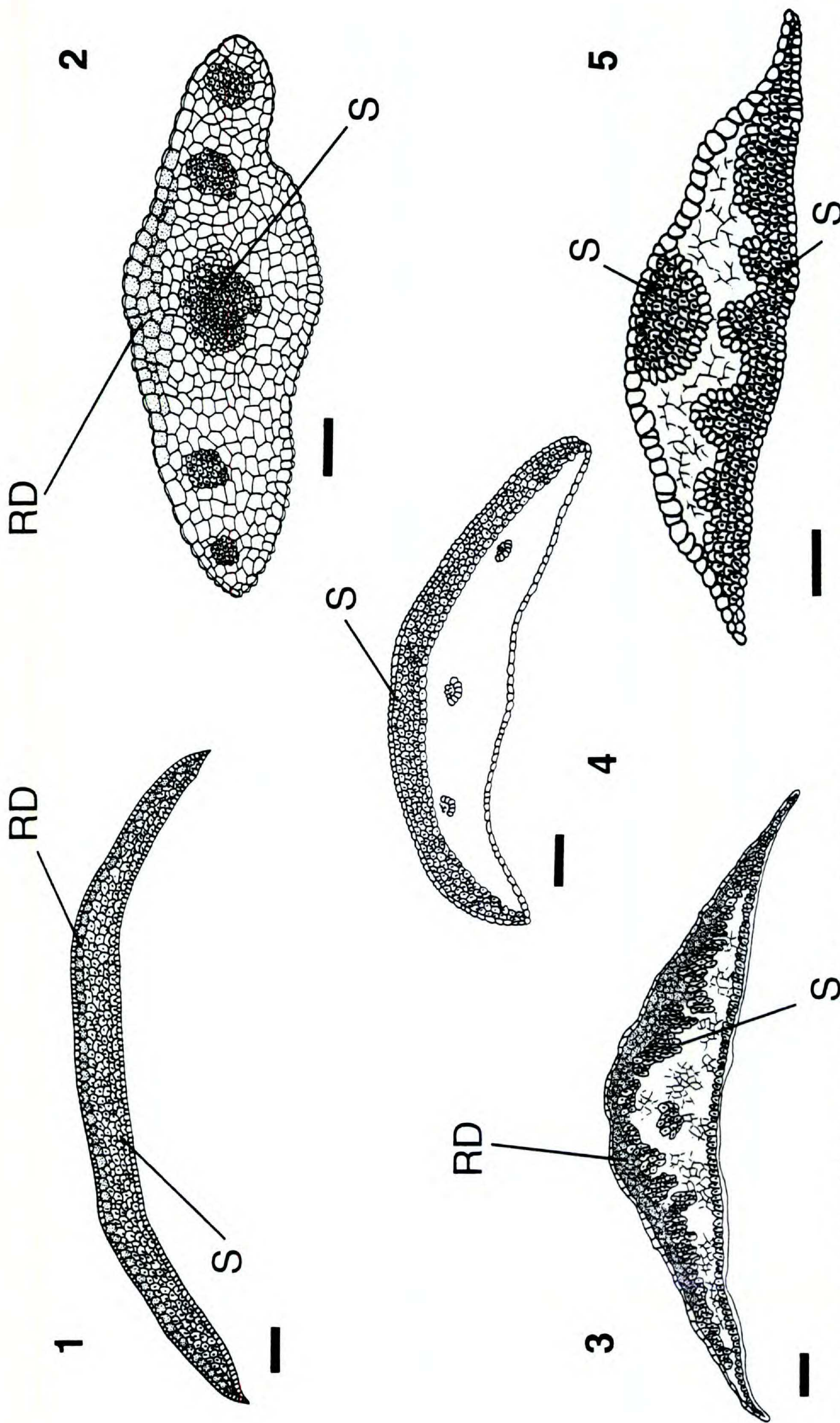


Figure 1. Anatomy of the phyllaries (cross section). —1. Sclerenchymal fibers form a more or less continuous mass occupying the inner part of the phyllary (*Gochnatia picardae* (Urb.) Jimenez, *Ekman* 9280 (S)). —2. The sclerenchymal fibers, though likewise situated in the central part of the phyllary, form clearly distinct groups separated by a very lax parenchyma, which appears to be of aeriferous type (*Oldenburgia grandis* (Thunb.) Baill., *Bayliss* 4519 (S)). —3, 4. The sclerenchymal fibers are concentrated toward the abaxial face of the phyllary; in the center, which is basically occupied by parenchyma, there are several vascular bundles reinforced with sclerenchymal fibers (3: *Dicoma carbonaria* (S. Moore) Humbert, *Decary* 9263 (MO); 4: *Dicoma saligna* Lawalrée, *Gosseiler* 11331 (COI)). —5. The majority of sclerenchymal fibers are either on the adaxial face or on the midrib of the abaxial face, where they protect the vascular bundles (*Dicoma aethiopica* S. Ortiz & Rodr. Oubiña, *Gilbert, Ensermu & Vollesen* 7870 (K)). RD: resin ducts. S: sclerenchyma. Scale bar = 0.1 mm.

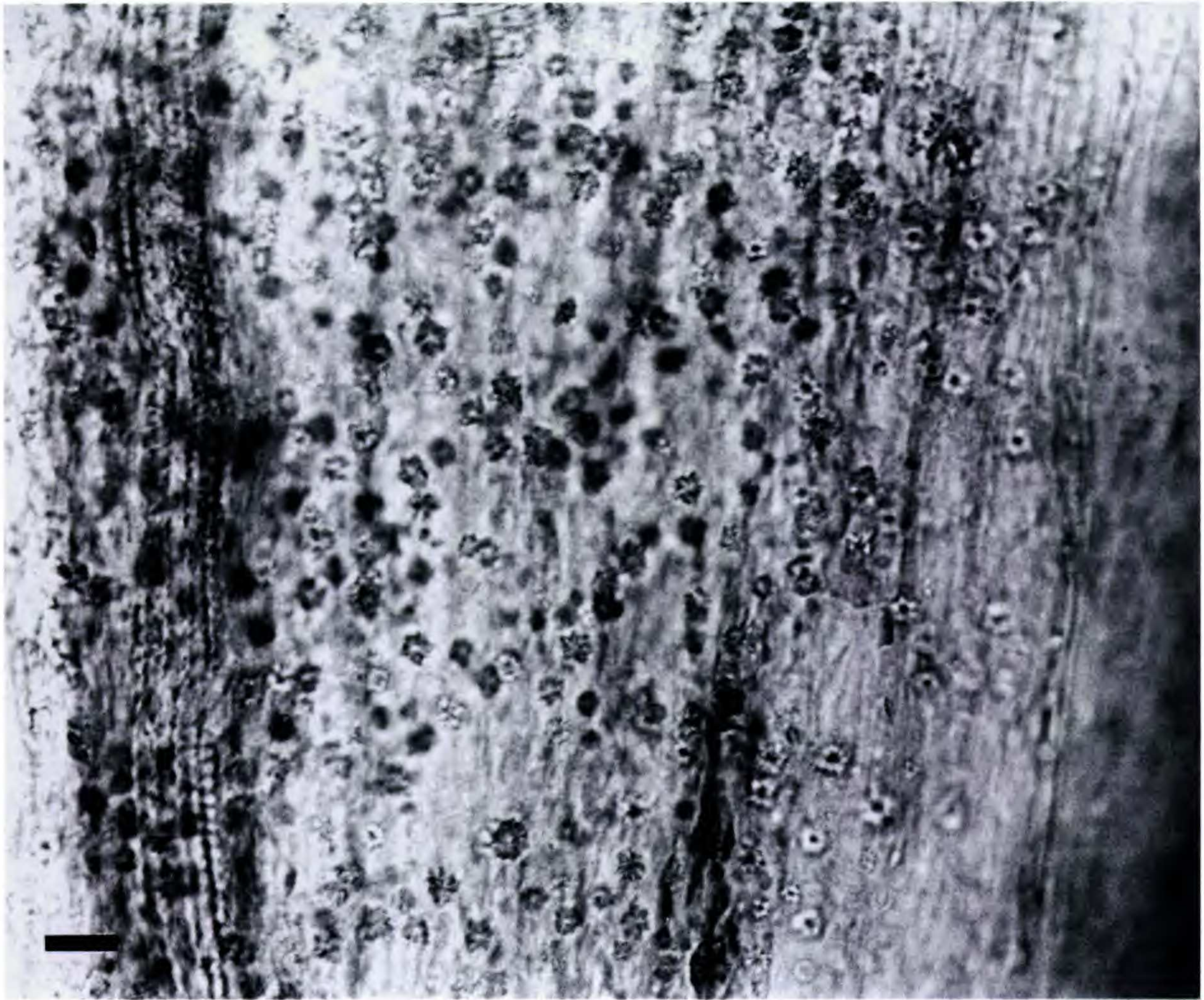


Figure 2. Star-shaped calcium oxalate crystals in the subepidermal cells of the disc corolla of *Dicoma aethiopica* (Gilbert, Ensermu & Vollesen 7870 (K)). Scale bar = 0.01 mm.

(Dormer, 1962), which was always polarized, and cypsela vein union (Karis et al., 1992), which was always at the base. Some of these characters require explanatory comments, as follows:

Character 8. Many of the species studied commonly show more or less bractiform leaves, denominated “subtending leaves” (Pope, 1991, 1992), at the base of the capitula.

Character 13. Many of the species studied have two dark stripes running along the phyllaries.

Character 14. Examination of cross sections of the phyllaries allows four morphological types to be distinguished, most notably on the basis of the arrangement of sclerenchymal fibers. In the first type, the sclerenchymal fibers form a more or less continuous mass occupying the inner part of the phyllary (Fig. 1-1). In the second type, the sclerenchymal fibers, though likewise situated in the central part of the phyllary, form clearly distinct groups separated by a very lax parenchyma, which appears to be aeriferous (Fig. 1-2). In the third type, the sclerenchymal fibers are concentrated toward the abaxial face of the phyllary; in the center, which is basically occupied by parenchyma, there are several vascular bundles reinforced with sclerenchy-

mal fibers (Fig. 1-3, 1-4). In the fourth type, the majority of sclerenchymal fibers are either on the adaxial face or in the midrib of the abaxial face, where they protect the vascular bundles (Fig. 1-5).

Character 21. *Dicoma carbonaria*, and to lesser extent *D. oleaefolia*, have capitula in which all florets are zygomorphic, with one of the corolla lobes separated from the others by a much deeper incision and without an expanded limb; this morphological type seems transitional between the actinomorphic and the ligulate type and is similar to that seen in certain primitive genera of the subfamily Barnadesioideae, such as *Chuquiraga* Juss., *Dasyphyllum* Kunth, and *Schlechtendahlia* Less. (Hoffmann, 1983a; Cabrera, 1977; Bremer, 1994). “True ray” florets have no adaxial lobes and a 3-lobed lamina.

Character 26. This character was initially studied in ray florets (Baagøe, 1977, 1978), but in my opinion is also informative for species that have disc florets only. Indeed, Hansen (1991) studied epidermal cell cuticle ornamentation in disc florets of species of the various genera considered in the present study (despite the fact that the study in question centers on ray florets). This character has

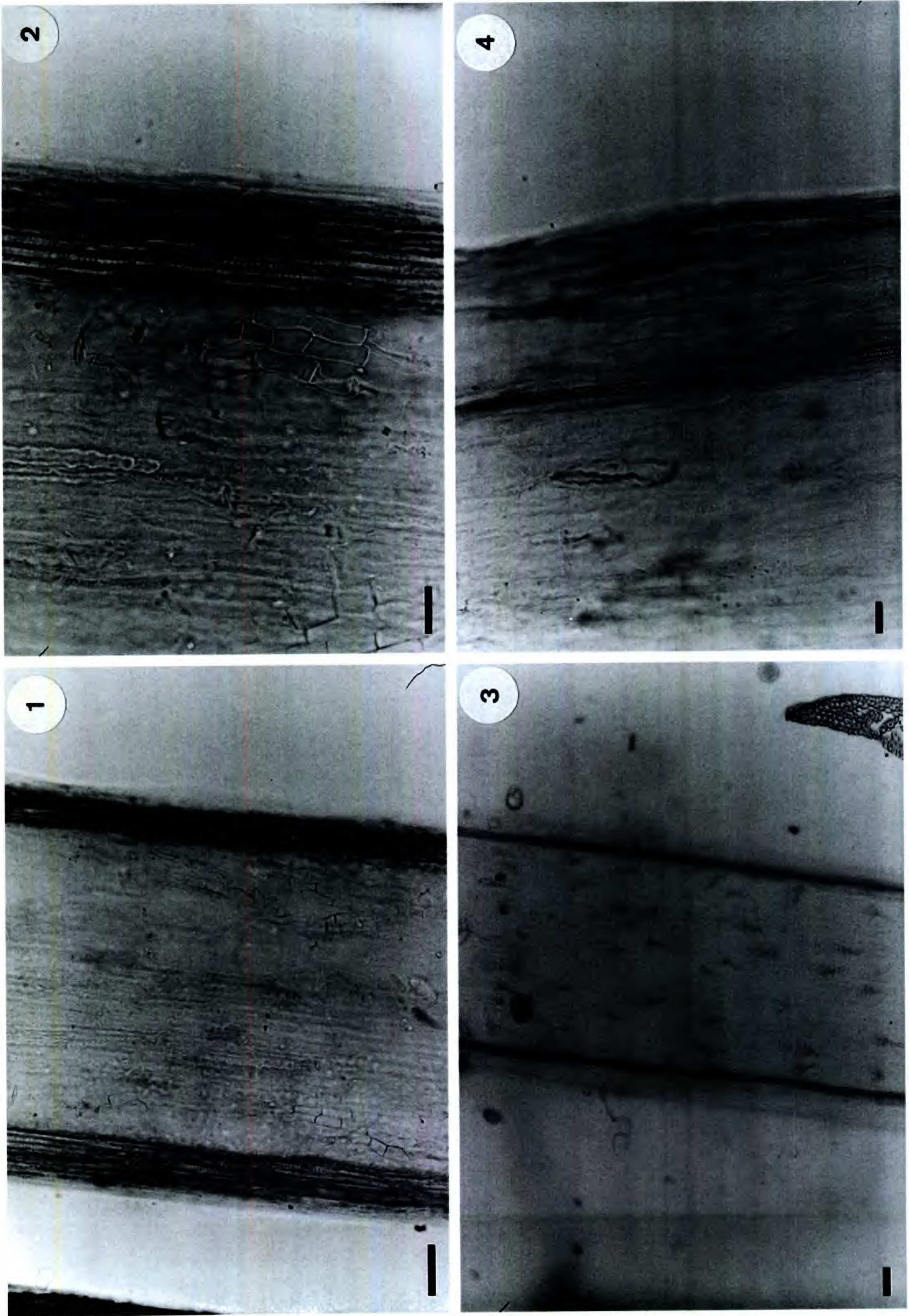


Figure 3. —1, 2. Marginal vascular tissue of the disc corolla lobes of *Dicoma spinosa* (L.) Druce comprising many vessels surrounded by sclerenchymal fibers (*Foucard* 2499 (K)). —3, 4. Submarginal veins of the disc corolla of *Dicoma nachtigalii* O. Hoffm., with fewer vessels and without sclerenchymal fibers (*Pearson* 7642 (K)). Scale bar (1 and 3) = 0.05 mm. Scale bar (2 and 4) = 0.01 mm.

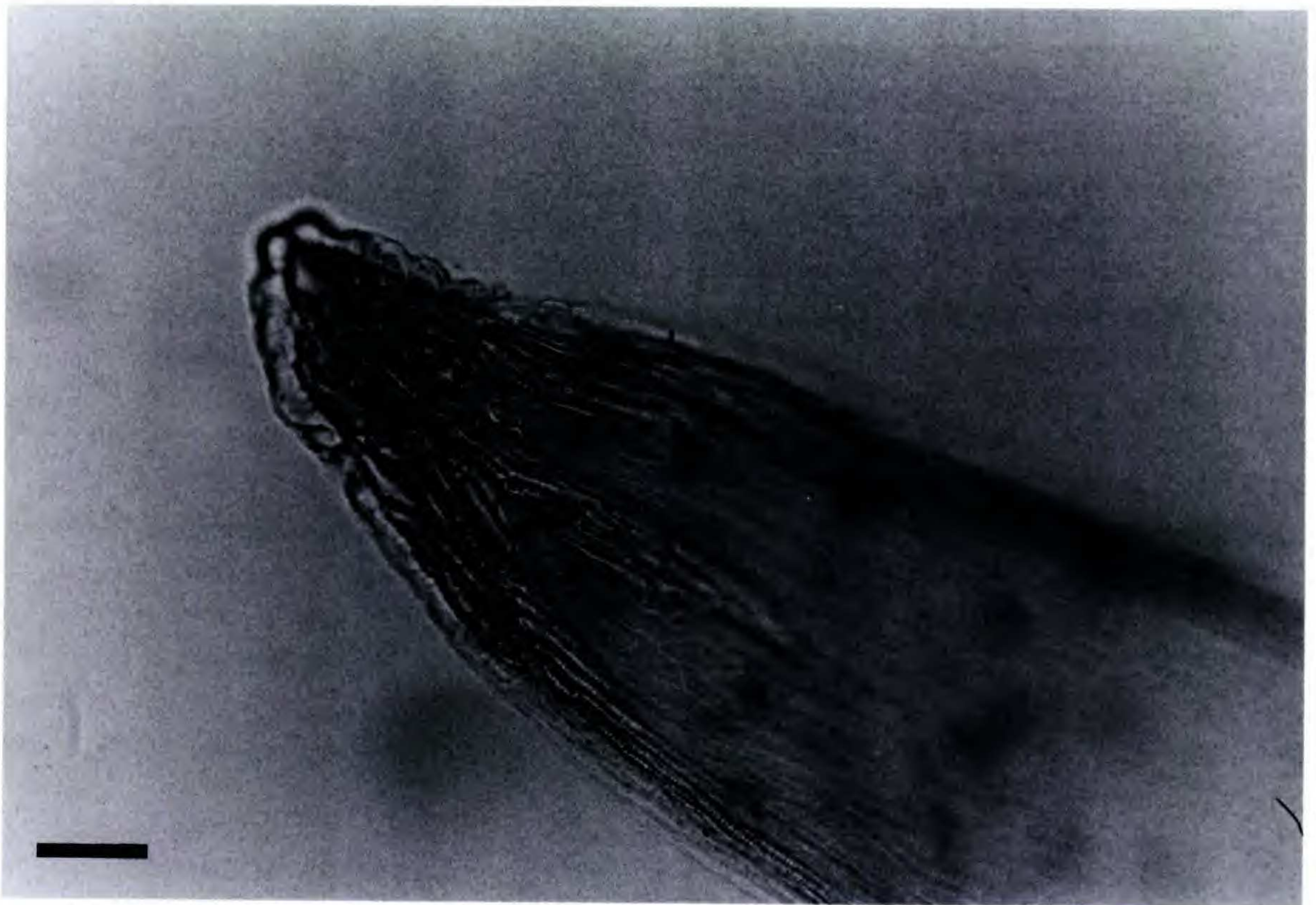


Figure 4. Apex of the disc corolla of *Dicoma aethiopica* (Gilbert, Ensermu & Vollesen 7870 (K)) with thick-bundled veins. Scale bar = 0.05 mm.

likewise proved useful in the present study, in which most of the species considered lack ray florets. “Intestine-like” ornamentation (Karis et al., 1992) is equivalent to Hansen’s “rugose pattern of longitudinal bands” (Hansen, 1991). In the characterization of *Gochnatia* and *Achyrothalamus* I have followed Hansen’s (1991) approach, classifying ornamentation in these two genera as “muti-

sioid” and “senecioid” respectively, though with some reservations, since the distinction between these two typologies was not clearly defined in our material.

Character 28. Some species have long twin glandular hairs with a small apical gland on the corolla (see Karis et al., 1992: 418, fig. 4H). In the rest of the species considered the disc corolla hairs

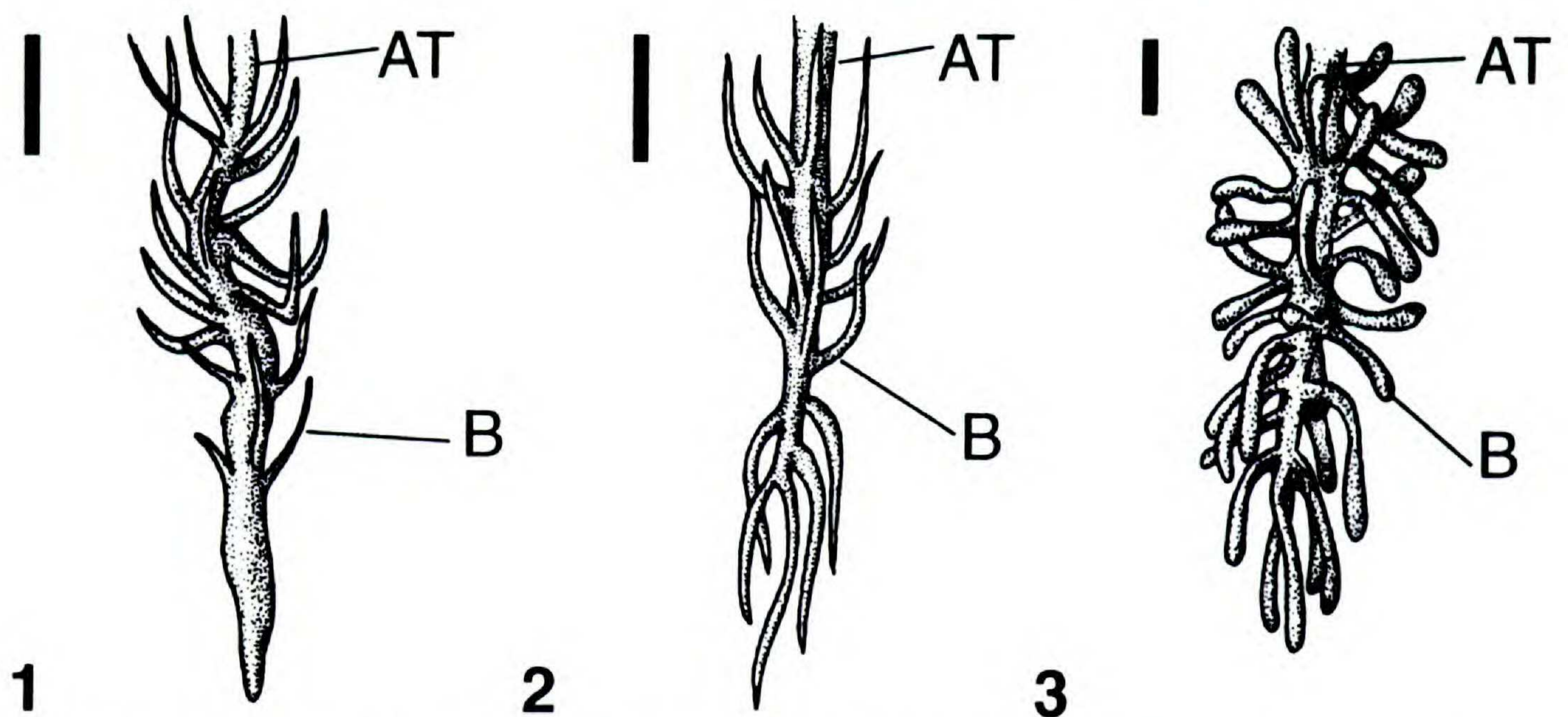


Figure 5. Distal part of the anther tails. —1. Anther apices lack antrorse ramifications and the apex of the anther tail ramifications is acute (*Dicoma saligna*, Gossweiler 11331 (COI)). —2. Anther apices have antrorse ramifications and the apex of the anther tail ramifications is acute (*Dicoma tomentosa* Cass., Nordenstam 2454 (S)). —3. Anther apices have antrorse ramifications and the apex of the anther tail ramifications is obtuse (*Dicoma grandidieri* (Drake) Humbert, Capuron 18643 (K)). AT: anther tail. B: ramifications. Scale bar = 0.05 mm.

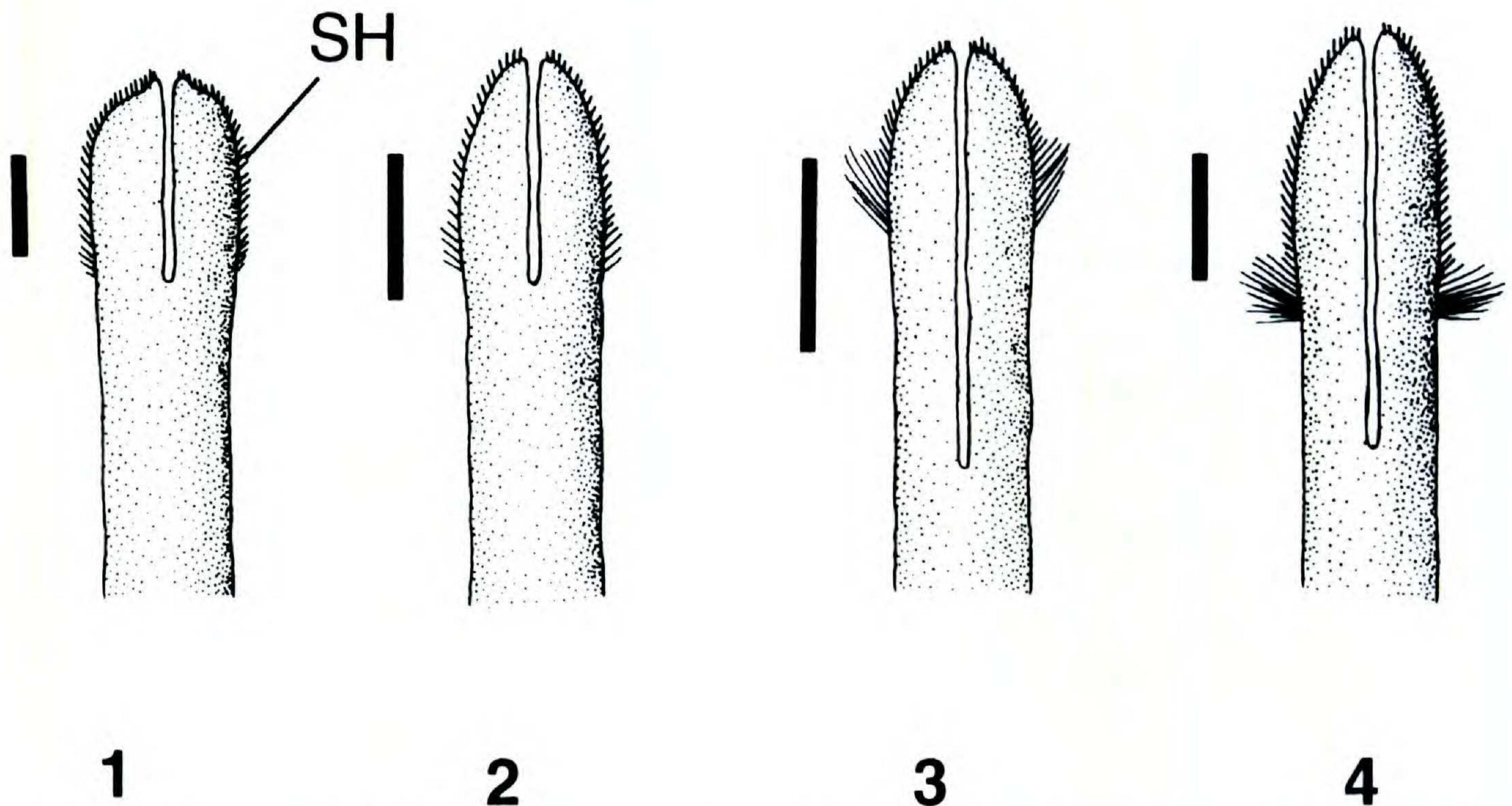


Figure 6. Apical part of the style with sweeping hairs. —1. Short style branches with sweeping hairs of similar length reaching the bifurcation (*Oldenburgia grandis*, Bayliss 4519 (S)). —2. Short style branches with a sub-basal group of sweeping hairs slightly longer than the rest, these almost reaching the bifurcation (*Dicoma sessiliflora* Harv. subsp. *sessiliflora*, Wingfield 4416 (K)). —3. Long style branches with sweeping hairs in a subapical tuft, with a sub-basal group of sweeping hairs conspicuously longer than the rest (*Dicoma bangeolensis* Buscal. & Muschl., Beckett 242 (K)). —4. Long style branches with a long group of sweeping hairs not reaching the bifurcation, these with a sub-basal group of sweeping hairs conspicuously longer than the rest (*Dicoma tomentosa*, Nordenstam 2454 (S)). SH: sweeping hairs. Scale bar = 0.5 mm.

are “short glandular hairs” with a large apical gland (see Karis et al., 1992: 418, fig. 4I). Rarely (either in the first or second type) “twin hairs” are present that are basically similar to the non-myxogenic short ovoid twin hairs of Karis et al. (1992: 418, fig. 4B), which are very short and which lack a conspicuous apical gland.

Character 29. Disc corolla simple hairs are long simple hairs with one or two basal cells (see Karis et al., 1992: 419, fig. 5E).

Character 32. The marginal vascular tissue of the lobes of the corolla of disc florets is thick in some taxa, made up of many vessels and surrounded by sclerenchymal fibers (Fig. 3-1 and 3-2). In the remaining taxa, the marginal veins are narrow, comprised of fewer vessels and without sclerenchymal fibers (Fig. 3-3 and 3-4).

Character 34. Some species show accessory veins of variable length in the corolla lobes, running more or less parallel to the marginal/submarginal veins.

Character 35. In some species, the veins of the disc corolla lobes form a highly characteristic dense bundle (Fig. 4) (see Karis et al., 1992).

Character 36. In most of the species studied, the stamen filaments are inserted at the tube/throat

junction. In *D. carbonaria* and *D. oleaefolia*, by contrast, the stamen filaments are inserted practically at the base of the corolla. The presence of two clearly distinct states is not in agreement with Karis (1993), who reported that this character varies little within each of the tribes of the subfamily Asteroideae (except in the tribe Astereae) and is thus of considerable taxonomic value at the tribal level.

Character 44. *Dicoma carbonaria* and *D. oleaefolia* share an interesting characteristic, the tails of adjacent pairs of anthers being joined, with their ramifications or hairs interwoven. The anthers of the remaining species are clearly separated.

Character 45. In many taxa the apices of the anther tails show characteristic antrorse ramifications, while the ramifications of the rest of the anther tail are always retrorse (Fig. 5-2 and 5-3). In other taxa, however, such apical ramifications are absent (Fig. 5-1).

Character 55. In several taxa the stylar sweeping hairs reach (or almost reach, or extend beyond) the point of bifurcation of the style branches. In most of the other species considered, the stylar sweeping hairs form a short subapical tuft that Hansen (1991) and Bremer (1994) considered characteristic of the species of the “*Dicoma* group.” In

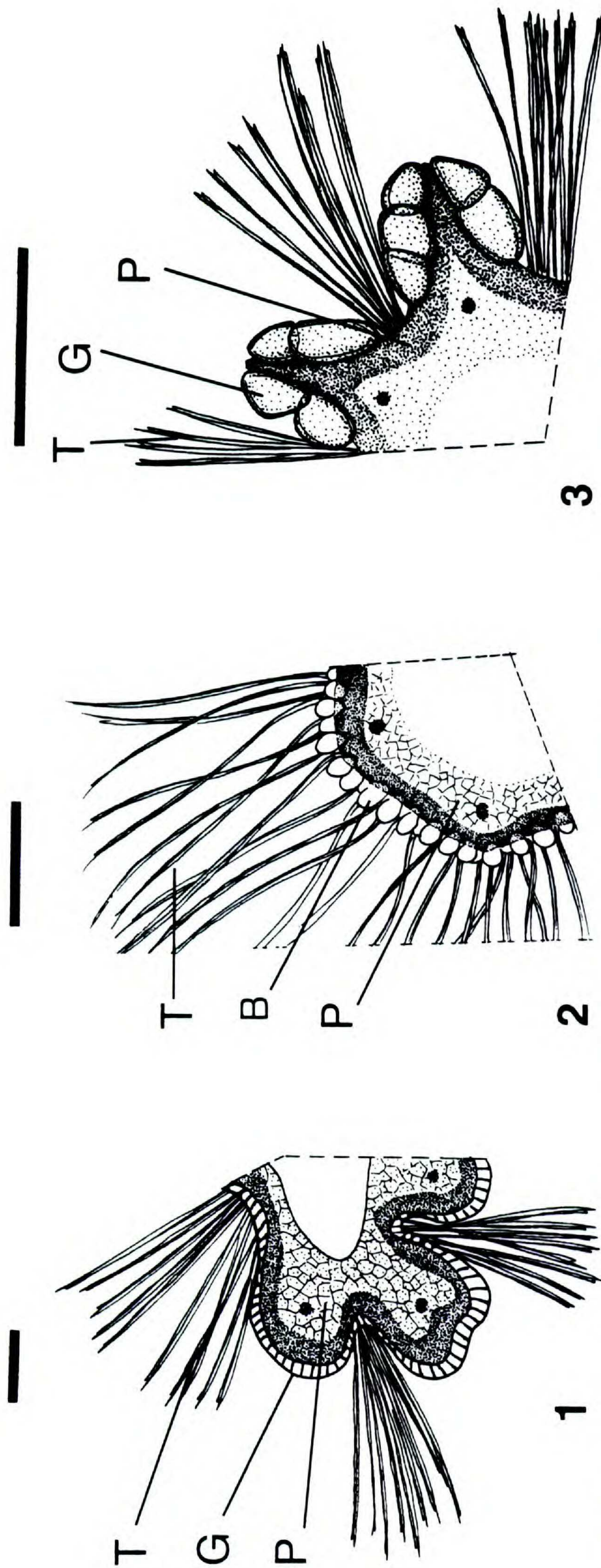


Figure 7. Cross section of the cypselas of *Dicoma* —1. Cypselar ribbed, with superficial glands in a continuous layer, and twin hairs located between the ribs with base not bulbous-glandular (*D. carbonaria*, Chauvet 359 (K)). —2. Cypselar not ribbed, without superficial glands and with twin hairs located all around the cypselar and with bulbous-glandular base (*D. saligna*, Gossweiler 11331 (COI)). —3. Cypselar ribbed, with superficial glands on the ribs, and twin hairs located between the ribs and with base not bulbous-glandular disposed between the ribs (*D. tomentosa*, Nordenstam 2454 (S)). B: base of the twin hairs bulbous-glandular. G: superficial glands. P: pericarp. T: twin hairs (see text). Scale bar = 0.25 mm.



Figure 8. Twin hairs with bulbous-glandular base on the cypsela of *Dicoma saligna* (Gossweiler 11331 (COI)). Scale bar = 0.1 mm.

Dicoma tomentosa and *D. welwitschii*, a third pattern is observed: the sweeping hairs extend from close to the apex toward the bifurcation, but do not reach it.

Character 59. Cypselas of neuter marginal florets are rudimentary and may or may not have a rostrum.

Character 62. Many of the studied taxa have unicellular cypselum-surface glands containing a resinous material. These may be located between the ribs on the rib walls (Fig. 7-3), between the ribs in the intercostal grooves, or forming a continuous layer around the cypselum (Fig. 7-1), as in the *D. carbonaria* group. *Dicoma fruticosa* shows a morphology intermediate between types 1 and 2, and was coded as inapplicable for this character.

Character 63. Simple twin hairs have the two cells joined, and bifurcate twin hairs have the two cells separated (Karis et al., 1992: 418, fig. 4A).

Character 65. In some species the cypselum twin hairs have a conspicuously bulbous glandular base that contains a resinous material (Fig. 7-2 and 8). In other species the base of the cypselum twin hairs may be somewhat bulbous but is never glandular.

Character 66. In *Pasaccardoa grantii* and *P. jeffreyi*, the twin hairs of the lower part of the cypselum are thicker than the rest; in the remaining species all hairs of the cypselum are similar.

Character 67. Biseriate glands are composed of two rows of cells and a collapsed apical head,

and occur in the cypselas of many of the taxa analyzed. In many cases these are not easy to see and often are situated between the superficial glands (see character 62).

Character 68. Subepidermal calcium oxalate crystals are observed in the immature testa of all species. They are subsequently hidden from view by the epidermis of the mature testa. In some species needle-shaped crystals and square to short-rectangular crystals, without uniform orientation, are present in roughly equal proportion (Fig. 9-1). In others, by contrast, almost all the crystals are narrowly rectangular and oriented in the same direction (Fig. 9-2).

Character 69. The first character state corresponds to the testa type defined by Grau (1980) for *Gochnatia* (testa with lateral and basal walls of the epidermal cells strengthened). Similar but not identical morphologies are observed in *Pasaccardoa grantii*, *P. jeffreyi*, and some species of *Dicoma*: in these cases the testa morphology is similar to the *Gochnatia* type, but the cells of the epidermis are of irregular shape, not linear. The second character state is the *Erythrocephalum* type as defined by Grau (1980); in addition to *Erythrocephalum*, the species of *Achyrothalamus* and *Pleiotaxis* fall into this category (basal walls of the epidermal cells of the testa with reinforcements, which give to the cells a lacunose appearance in frontal view). The third character state is the *Dicoma* type as defined

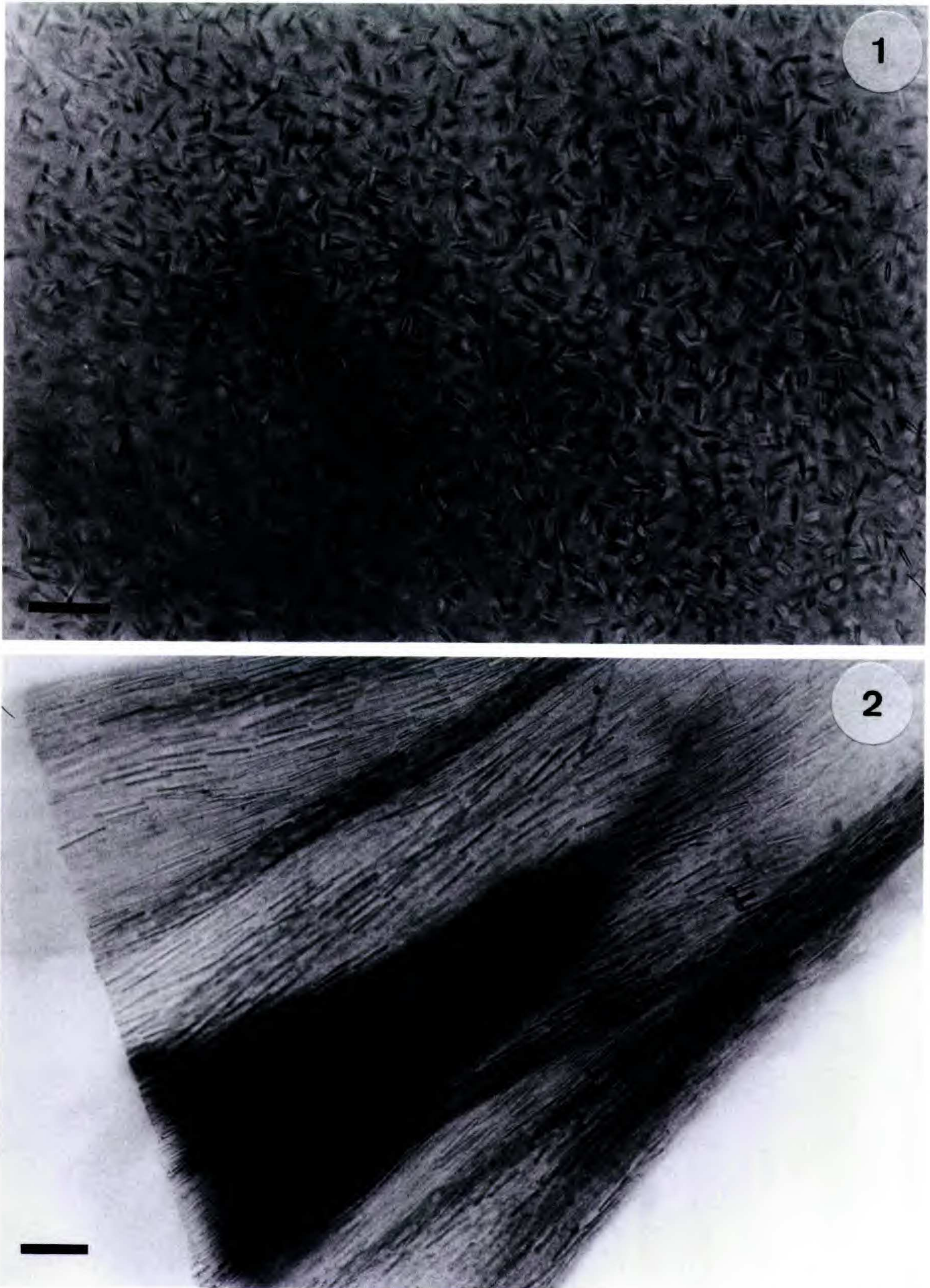


Figure 9. Calcium oxalate crystals in the immature testa (testa subepidermis). —1. Nonoriented needle-shaped crystals and square to short-rectangular crystals in the testa of *Dicoma zeyheri* (Mogg 16306 (K)). —2. Long-rectangular crystals oriented in the same direction in *Dicoma montana* (L. E. Codd 8689 (K)) (see text). Scale bar = 0.05 mm.

by the same author (basal walls of the epidermal cells of the testa strengthened with ribs). The fourth character state, observed in *D. welwitschii* and *P. baumii*, is very similar to that observed in the other species of *Pasaccardoa*, except that the epidermal cells of the testa are traversed by thick bands. We have not been able to characterize testa morphology in the *Oldenburgia* material studied; similarly, Kar-

is et al. (1992) were unable to determine whether or not the testa of the species of this genus is “collapsed.” The testas of the two species of the *D. carbonaria* group show a morphology similar to Grau’s (1980) *Perezia* type (testa with epidermal cells not strengthened), though study of additional material is necessary to confirm this.

Character 70. In some species the lateral and

Table 4. Data matrix. The characters are numbered in accordance with the text and Table 3. Character state unknown is indicated with a question mark, and inapplicable with a dash. Polymorphic taxa are coded with the following symbols: A = (0&1), B = (0&2), C = (1&2), D = (2&3).

	1	11111	11112	22222	22223	33333	33334	44444	44445	55555	55556	66666	66667	77777	77	
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67
<i>Gochnatia</i>	0000	000A	0000	0000	0000	000A	0000	0000	0000	0000	0000	0000	0000	0000	0000	00
<i>Oldenburgia</i>	0000	00A0	00010	0000	10000	0A000	0000A	00000	0A00	0000A	00000	00B00	010?	00000	00	00
<i>Erythrocephalum zambesianum</i>	10100	00100	00000	00001	1001A	20000	01010	00200	10100	11100	11132	00000	00101	01011	1-110	00
<i>Erythrocephalum scabrifolium</i>	10100	001A0	00000	00001	00010	20000	?010	00100	10100	11100	11132	01000	00101	01011	1-110	00
<i>Erythrocephalum microcephalum</i>	10100	00010	00000	00001	00010	20000	01001	00200	01000	11100	11132	01000	0010?	01011	1-110	00
<i>Achyrothalamus marginatus</i>	10100	000A0	00000	10011	0001A	30000	11010	00200	01000	11100	11132	01000	00101	01011	3----	--
<i>Pleiotaxis pulcherrima</i>	10000	00000	00000	10000	00010	20000	11011	00200	01000	11100	11132	00000	00000	01011	00000	00
<i>Pleiotaxis rugosa</i>	10000	00000	00000	10010	00000	20000	11011	00100	01000	11100	1A132	00000	002--	01011	00000	00
<i>Pleiotaxis subpaniculata</i>	10000	000A0	00000	10000	000?	20000	11010	00100	01000	10030	00000	00000	00000	01011	00000	00
<i>Pasaccardoa jeffreyi</i>	10100	00100	01021	00000	31011	21001	01000	01100	10001	00132	11011	13010	10100	10100	1-000	00
<i>Pasaccardoa grantii</i>	10000	00110	01021	00000	3101A	21001	01000	01100	10001	00132	11011	13010	10100	10100	1-000	00
<i>Pasaccardoa baumii</i>	10000	00000	01021	00000	310?	21000	?10A0	01100	10001	00132	11111	12010	01130	1-000	00	00
<i>Dicoma dinteri</i>	00000	00111	01131	00000	00001	20001	01000	01100	10001	00132	11101	12010	00121	00000	00	00
<i>Dicoma bangeolensis</i>	00000	00011	01131	00000	00001	20001	01000	01100	00000	00132	11101	12010	00121	20000	00	00
<i>Dicoma schimperi</i>	10000	00110	11131	00000	00001	20001	01000	01100	10001	00131	11101	12010	00121	00010	00	00
<i>Dicoma elegans</i>	1A0A0	101A0	011D1	00000	01001	20001	01000	01100	10001	00132	11101	12010	01121	00000	02	00
<i>Dicoma nachtigalii</i>	00010	0A110	01131	00000	0000A	20001	01001	01100	10001	00132	11101	12010	00121	00000	00	00
<i>Dicoma fruticosa</i>	00000	00110	01131	00010	31001	20001	?1001	01C00	10000	0013?	11101	1?010	00121	00000	00	00
<i>Dicoma montana</i>	00000	00110	01131	00000	00001	20001	01000	01100	10001	00132	11101	12010	00121	00000	00	00
<i>Dicoma aethiopica</i>	10000	00110	01131	00000	00001	20001	01000	01100	?0000	00132	11101	12010	00121	00000	00	00
<i>Dicoma niccolifera</i>	11000	001A0	01131	00000	0100A	20001	11001	00C00	00000	00132	11101	12010	00121	00000	01	00
<i>Dicoma capensis</i>	11000	00110	01131	000A0	01001	20001	01001	00100	00000	00132	11101	12010	00121	00000	01	00
<i>Dicoma gillettii</i>	00000	001A0	01A30	00000	00000	20001	01001	01100	10101	00131	11101	12010	00121	00?	00	00
<i>Dicoma welwitschii</i>	10000	00100	01021	00A00	000?	21001	01001	01100	10001	00122	11101	12010	01130	1-000	00	00
<i>Dicoma tomentosa</i>	10000	01110	11131	00A00	0000A	20001	01000	01100	10001	00122	11101	12010	00121	20000	00	00
<i>Dicoma anomala</i>	10000	00110	01131	00000	00001	20001	0100?	01100	?0000	00112	11101	12010	00121	00000	00	00
<i>Dicoma picta</i>	00000	00010	01131	00010	31001	20001	0100?	01100	10000	00112	11101	12010	00121	00000	00	00
<i>Dicoma cana</i>	000A0	10010	10021	01010	0000A	10101	00100	01110	10000	00011	11100	00001	00000	00000	00	00
<i>Dicoma spinosa</i>	00001	00A10	10021	0AA10	0000A	?0111	001A0	01110	10001	00011	11100	1000A	01000	1-000	00	00
<i>Dicoma grandidieri</i>	00001	001A1	00021	01110	00000	10101	00100	01100	00001	00012	11100	10001	00000	00000	00	00
<i>Dicoma sessiliflora</i>	100A0	00A00	10021	01110	00000	10100	00100	01100	10001	00012	11100	00001	01000	01000	00	00
<i>Dicoma zeyheri</i>	100A0	00000	10021	01110	00000	1010A	00100	01100	?0001	00011	11100	00001	01000	01000	00	00
<i>Dicoma saligna</i>	10000	001A0	00021	01110	00000	10101	00100	01100	10001	00011	11100	00001	01000	01000	00	00
<i>Dicoma relhanooides</i>	00001	00110	00021	0AA10	0000A	10101	00110	01100	10001	00012	11100	10001	01000	1-000	00	00
<i>Dicoma carbonaria</i>	00010	00111	00020	00000	20100	20010	21000	1A101	00010	00011	01101	11010	01??1	00001	10	00
<i>Dicoma oleaeefolia</i>	00010	00111	00020	00000	20100	20010	21000	10101	00010	00011	01101	110A0	010?	00001	10	00

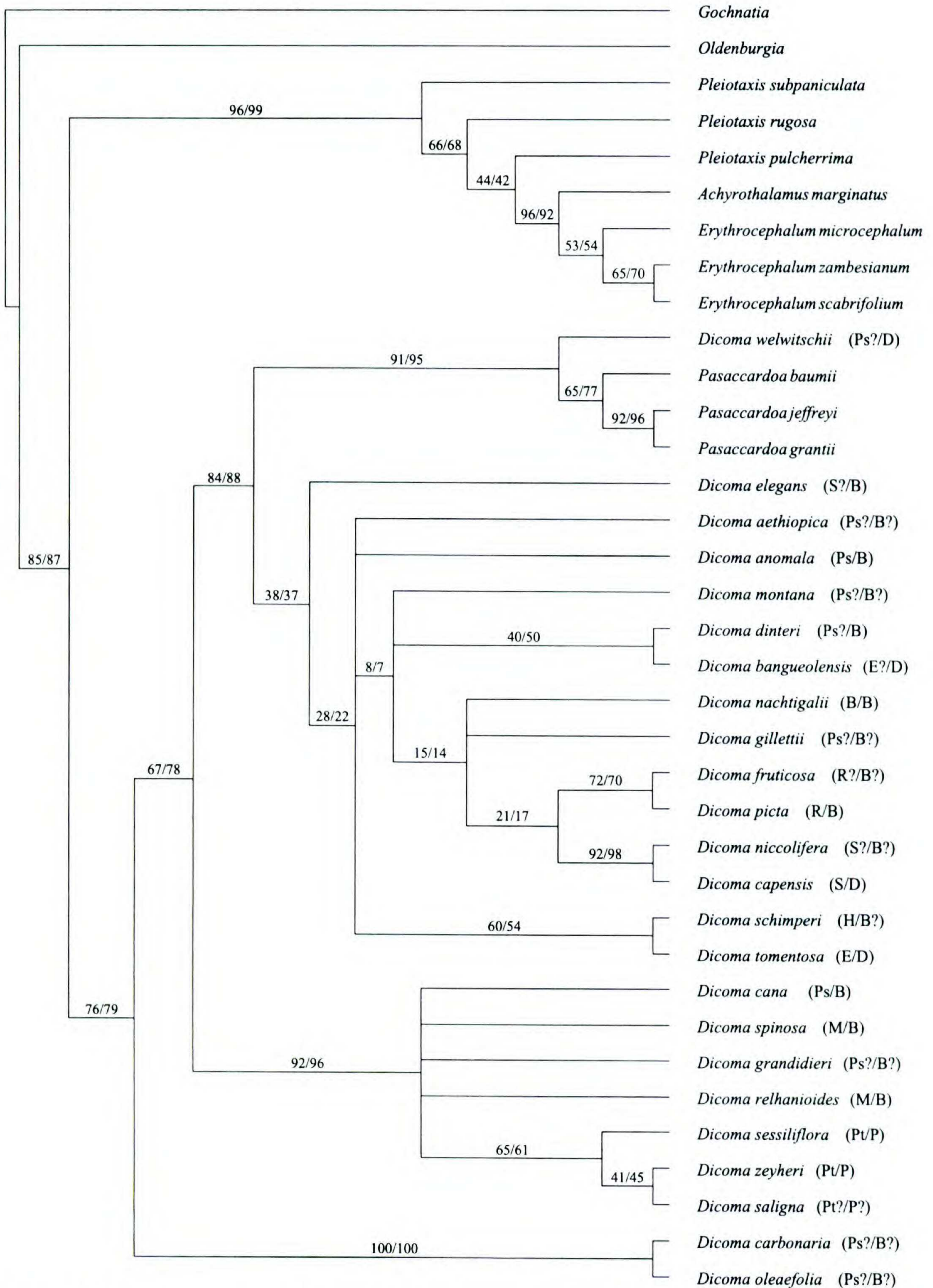


Figure 10. Strict consensus tree of *Dicoma* and related genera, based on the six equally most parsimonious cladograms obtained from analysis of the data in Table 4. The numbers at each node are % jackknife support (before the slash) and % bootstrap support (after the slash). Letters in parentheses after *Dicoma* species indicate the section to which each species belongs. Sections proposed by Hoffman (1893a) (before the slash): S, *Steirocoma*; R, *Rhigiothamnus*; E, *Eudicoma*; M, *Macleodium*; H, *Hochstetteria*; Ps, *Psilocoma*; B, *Brachyachaenium*; Pt, *Pterocoma*. Sections proposed

basal walls of the epidermal cells of the testa are strengthened with a highly characteristic morphology, U-shaped in cross section and similar to that of Grau's (1980) *Gochnatia* subgroup. In the remaining species only the basal walls are thickened with ribs.

Character 71. Pappus is only absent in *Achyrothalamus*. In the remaining species it is formed by rather fine bristles, as in *Pleiotaxis* and in many species of *Dicoma*, by bristles and scales as in *D. banguelensis* and *D. tomentosa*, or by scales only as in *Erythrocephalum*, *Pasaccardoa*, *Dicoma welwitschii*, *D. spinosa*, and *D. relhanioides*.

Character 73. *Erythrocephalum* has a pappus of narrow caducous scales, while in all other species considered the pappus is persistent.

Character 77. In most of the species analyzed the pappi of the different flowers that make up the capitulum are all of similar length. In *Dicoma niccolifera* and *D. capensis*, the pappi of the marginal florets are much longer than those of the disc florets. In *D. elegans*, the internal pappus bristles of the marginal florets are as long as the pappus of the disc florets, while the external pappus bristles of the marginal florets are much longer than the pappus of the disc florets.

Polarization of characters was determined by the outgroup comparison method (Stevens, 1980; Watrous & Wheeler, 1981; Maddison et al., 1984), using *Gochnatia* Kunth and *Oldenburgia* Less. as outgroups. Both genera are of the tribe Mutisieae, and in Karis et al.'s (1992) analysis they are basal to the taxa included in the ingroup. *Gochnatia* is a heterogeneous genus with nearly 68 species (Bremer, 1994), mostly from the Americas, though also Asia. For outgroup comparison, I selected 5 species of *Gochnatia*, representatives of three of the five sections of the genus (*G. amplexifolia* (Gardner) Cabrera, *G. attenuata* (Britton) Jervis & Alain, *G. cordata* Less., *G. microcephala* (Griseb.) Jervis & Alain, and *G. picardae* (Urb.) Jiménez) with similar habit to those of the *Dicoma* group. *Oldenburgia* is a genus of four species endemic to the Cape area in South Africa, from which three species (*O. grandis* (Thunb.) Baill., *O. papionum* DC., and *O. paradoxo* Less.) were selected.

Characters with only two states of which one was autapomorphic were not included in the analysis.

Wagner parsimony analysis of the data matrix (Table 4) was performed on a PC with the aid of

the program PAUP* 4.0 (Swofford, 1998). Cladograms were generated using a heuristic search with the TBR (tree bisection-reconnection) branch-swapping algorithm with random additions (100 replicates). Support values for each clade were obtained by jackknife analysis (100 replicates) (Farris et al., 1996) and bootstrap analysis (Felsenstein, 1985). Successive weighting (Farris, 1969) was performed for generating cladograms where the relative weight of homoplasious characters was reduced. All multistate characters were treated as nonadditive. Some characters were coded as polymorphic for some terminals. In the data matrix, unknown character states were indicated with "?", and inapplicable character states were indicated with a dash.

RESULTS

The cladistic analysis yielded six equally most parsimonious cladograms, each 186 steps long, with a consistency index (CI) of 0.513, and a retention index (RI) of 0.82, including in both cases the only uninformative character of the matrix. The six cladograms showed only minor differences. One of the six cladograms is shown in Figure 11.

Analysis with successive weighting gave two cladograms (Fig. 12), with identical major-clade topology to the six equally most parsimonious cladograms (and the corresponding strict consensus tree) obtained without successive weighting. However, the two successive-weighting cladograms differed from the no-weighting strict consensus tree in the internal topology of the major clades.

In the strict consensus tree (Fig. 10), the first division split (a) the first clade, comprising the genera *Pleiotaxis*, *Achyrothalamus*, and *Erythrocephalum*, from (b) the genera *Dicoma* and *Pasaccardoa*. The second division split (a) the Madagascan endemics *D. carbonaria* and *D. oleaefolia* (hereinafter referred to as the *D. carbonaria* group) from (b) the remaining species of *Dicoma* and *Pasaccardoa*. The third division split (a) the seven species of the *Dicoma* sections *Pterocoma* DC., *Macleodium* Less., and *Psilocoma* Harvey, hereinafter referred to as the *D. sessiflora* group, from (b) the remaining species of *Dicoma* plus the three species of *Pasaccardoa*. The fourth division gave the last two major clades, one comprising *Dicoma welwitschii* and the *Pasaccardoa*

←

by Wilson (1923) (after the slash): D, *Dimorphae*; B, *Barbellatae*; P, *Plumosae*. Question marks indicate that the species in question has not been assigned to any section before this paper (see Table 1).

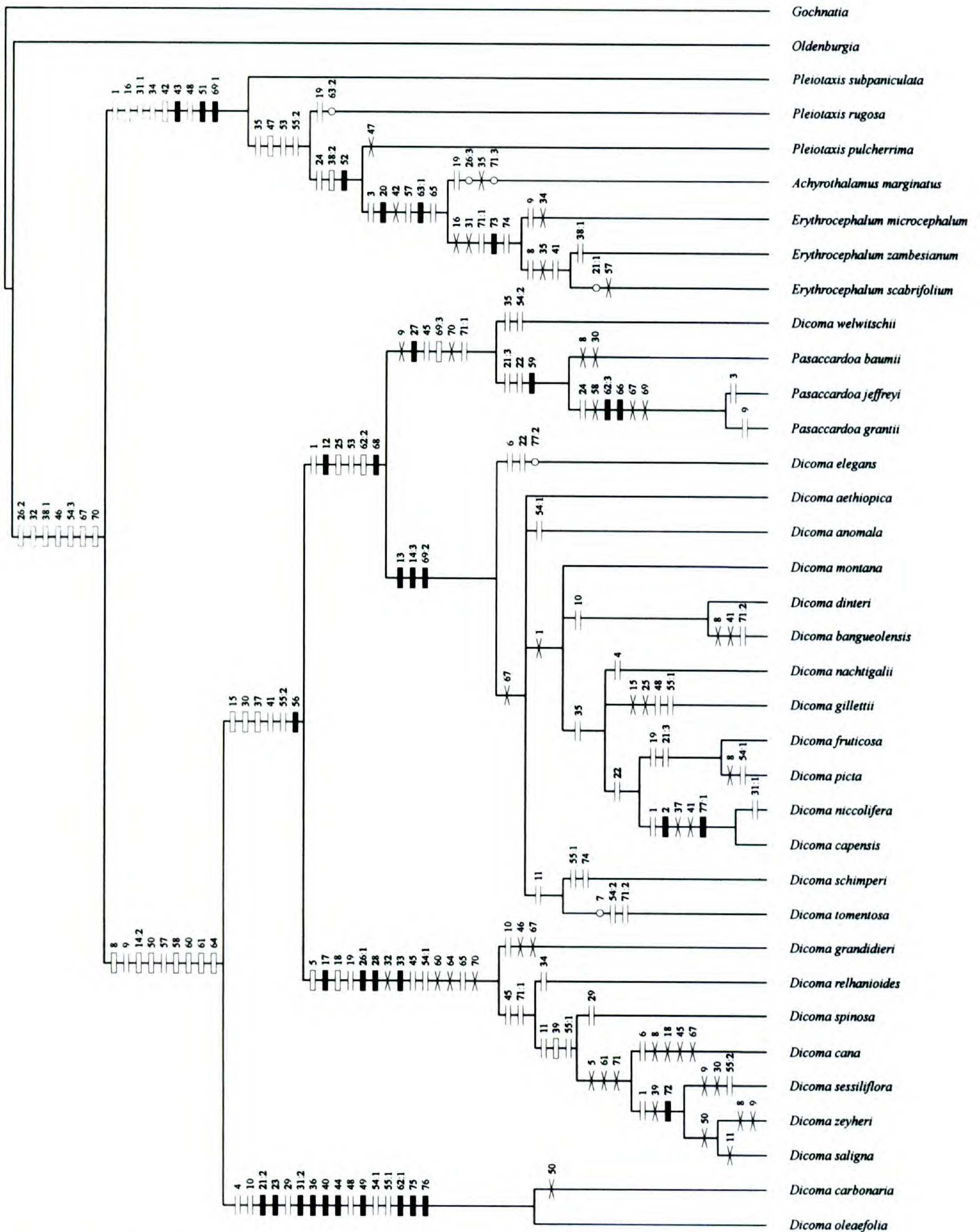


Figure 11. One of the six equally most parsimonious cladograms of *Dicoma* and related genera illustrating the character distribution. Character numbering follows that shown in Tables 3 and 4. ■ synapomorphy ($c = 1$). □ synapomorphy ($c < 1$). ○ autapomorphy. = parallelism. X reversal.

species, the other comprising the species I refer to as the *D. tomentosa* group.

In general, the five major clades revealed by the analysis are adequately supported by jackknife and

bootstrap values (see Fig. 10), and the results of the analysis can therefore be considered sufficiently reliable to provide a basis for elucidation of phylogenetic relationships among the genera and spe-

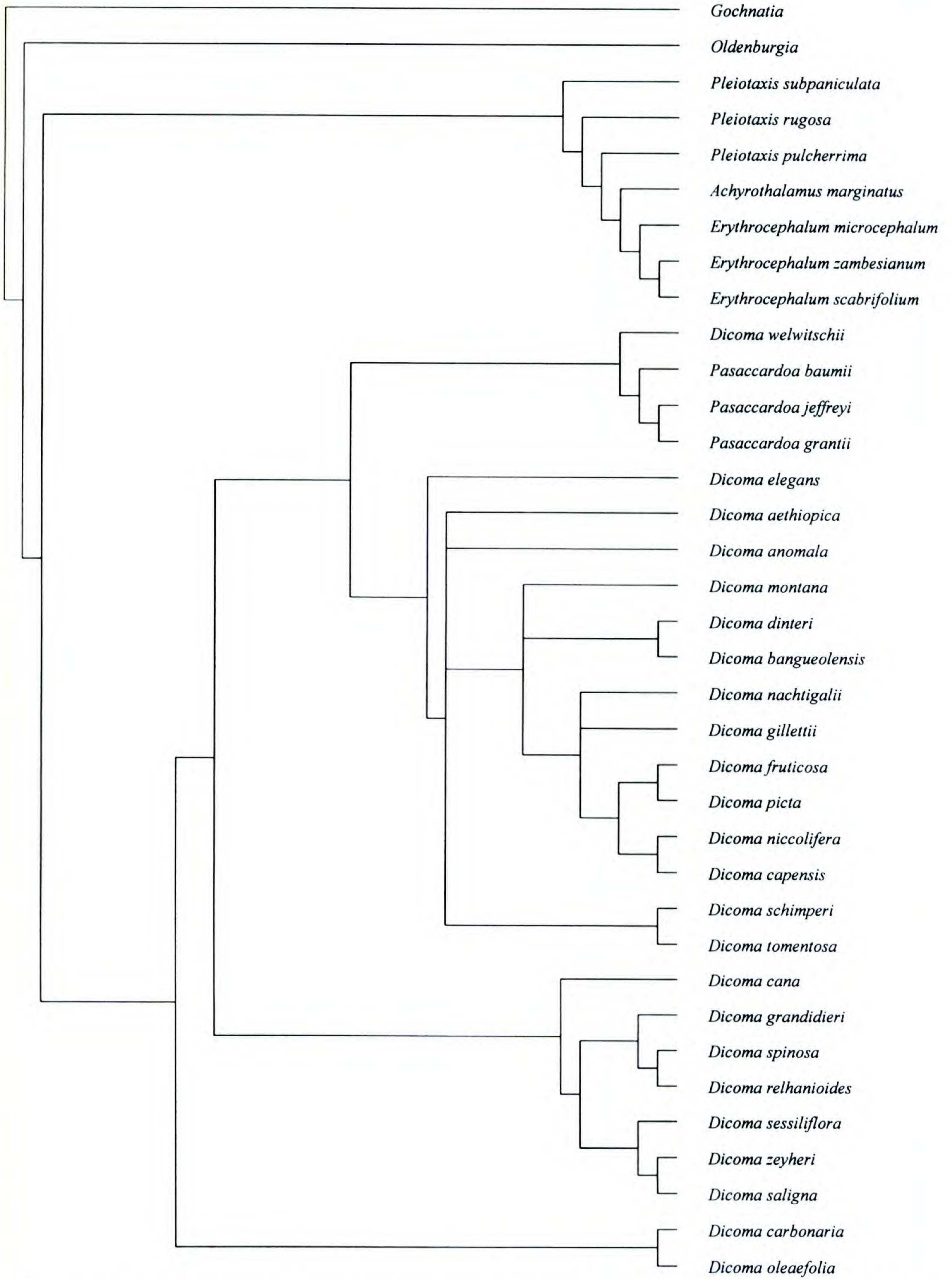


Figure 12. One of the two equally most parsimonious cladograms of *Dicoma* and related genera obtained in the successive weighting analysis.

cies considered. Only the clade corresponding to the *D. tomentosa* group had low jackknife and bootstrap support.

DISCUSSION

The results of the analysis reported here contradict those of Karis et al. (1992), in that *Erythrocephalum* and *Pleiotaxis* appear to be more phylogenetically advanced than *Dicoma*.

The analysis indicates that the genera *Pleiotaxis*, *Achyrothalamus*, and *Erythrocephalum* constitute a monophyletic group (see Fig. 10), the members of which share a number of apomorphic characters, some of which are exclusive (such as anther tails with subrounded to subacute apex, or style branches separated). Within this group, *Erythrocephalum* and *Pleiotaxis* appear to be paraphyletic. Nevertheless, confirmation of this would require a cladistic analysis of these three genera alone, with consideration of all or most of the species included within them; the present study focused on the species of *Dicoma* and on the characters relevant to the taxonomy of this genus. Such an analysis should try to identify other characters that although of little diagnostic value in the present study might be of value in an analysis of these three genera alone. Despite these reservations, it is of interest that *Achyrothalamus* and *Erythrocephalum* showed only minor differences (characters 16, 19, 26, 31, and 71); of these characters, the absence of a pappus (character 71) is the most widely used to distinguish between *Achyrothalamus* and *Erythrocephalum* (which has a caducous pappus). In this connection, our observations show that bifid twin hairs are present on the cypsela of *Achyrothalamus*, and that these hairs are apparently identical to those previously considered to be diagnostic of *Erythrocephalum* and *Hyaloseris* (Karis et al., 1992). The presence of these hairs in *Achyrothalamus* does not seem to have been taken into account when deciding to consider this taxon as a separate genus, presumably because they have not previously been detected: there is no mention of them in the original description of the genus (Hoffmann, 1893b), and Bremer (1994) described the cypselas of *Achyrothalamus* as glabrous.

The clade comprising *Dicoma carbonaria* and *D. oleaefolia* (the "*D. carbonaria* group") (see Fig. 11) is well defined and clearly separated from the remaining species of *Dicoma*. Important apomorphic character states shared by these species include (a) capitulum of all florets zygomorphic [since the subfamily Barnadesioideae is one of the most primitive groups within the Asteraceae (Bremer, 1994), the

character state considered apomorphic, as observed in *D. carbonaria* and *D. oleaefolia*, should in a wider context probably be viewed as a reversion to a more primitive type; like Cabrera (1959), Bremer (1987), and Karis et al. (1992), I consider the most primitive state to be that in which all florets are actinomorphic] (character state 21.2), (b) disc corollas much longer than involucre (23.1), (c) disc corolla veins separated as far as the corolla base (31.2), (d) stamens inserted close to the base of the corolla [the marginal nerves of the corolla remain separated to the base of corolla, as in certain species of the genus *Stenopadus*, of the Guayana Highlands (Carlquist, 1957; Bremer, 1994), one of the most primitive genera or possibly the most primitive genus (Hansen, 1991; Karis et al., 1992; Bremer, 1993a, b, 1994) of the Mutisieae] (36.1), (e) anther projected beyond the corolla, (f) anther tails of contiguous anthers joined (44.1), (g) style with four veins (49.1), (h) superficial cypsela glands disposed in a continuous layer all around the cypsela (62.1), (i) pappus much longer than involucre (75.1), and (j) pappus bristles patent after fruiting (76.1). All of these synapomorphic characters, some relating to relevant aspects of floral morphology, together with a series of plesiomorphic characters not observed in the remaining species of *Dicoma* (such as the presence of resin ducts, the absence of star-shaped calcium oxalate crystals in subepidermal cells of the corolla, and the presence of narrow style branch nerves), support the consideration of the *D. carbonaria* group as a clearly distinct clade, and raise the possibility that these two arborescent Madagascan endemics should be considered as a separate genus. This would entail resurrecting the genus *Cloiselia* S. Moore, described by this author (Moore, 1906) for *C. carbonaria* (*D. carbonaria*). I am unaware of other species of *Dicoma* with floral characteristics like those observed in the *D. carbonaria* group; certain of these characters, as mentioned above, are clearly primitive (corolla ligulate but without expanded limb, stamens inserted close to the base of the corolla, abundant long simple hairs on the corolla surface). These characters suggest a relationship with the genera of the Barnadesioideae (notably *Dasyphyllum*, *Chuquiraga*, and *Schlechtendahlia*) and the likewise primitive South American Mutisieae genus *Stenopadus* (see Cabrera, 1977; Bremer, 1994). This raises the possibility that the relationship between the African Mutisieae and the more primitive South American representatives of this tribe is perhaps closer than is currently admitted. This would be consistent with the hypothesis of Bremer (1993a, b, 1994), whereby the Asian species of Mutisieae were derived from

the South American species as a result of westward spread across the Pacific. It is also possible that the primitive characteristics of the *D. carbonaria* group reflect the isolation and protection from competition that has affected the evolution of many other plant and animal lineages on Madagascar. Of the *Dicoma* species not considered in the present study, the only taxon showing some degree of external morphological similarity to the species of the *D. carbonaria* group is *D. incana* (Bak.) O. Hoffm., likewise arborescent and likewise endemic to Madagascar; note, however, that floral morphology characters in this species follow the normal pattern for the genus.

The next clade (see Fig. 11) comprises two clades, one of them including the seven species that I refer to as the *D. sessiliflora* group. That this clade is genuinely representative of a phylogenetic entity is supported by a series of relevant non-homoplastic (CI = 1) synapomorphic characters, including innermost phyllaries more or less entirely scarious (17.1), and corolla with long twin glandular hairs (28.1). Other synapomorphic characters are homoplastic (CI < 1), due either to parallel evolution (e.g., phyllary anatomy, marginal veins of the disc corolla lobes in marginal or almost marginal position, base of the twin hairs of the cypsela very conspicuously bulbous-glandular) or to reversions to the plesiomorphic state (e.g., innermost phyllaries shorter than the contiguous outer series, no antrorse branches at the apex of the anther tails). Plesiomorphic characters shared by the members of this group include marginal veins of the disc corolla lobes broad (32.0), cypsela ribs absent or very slender (60.0), and twin hairs all around the cypsela (64.0). Confirmation that the *D. sessiliflora* group constitutes a distinct entity within *Dicoma*, or possibly a separate genus, will require a more detailed analysis considering all the species in the group. It is worth noting that some of the species of this group are more adapted to woodland conditions than those of the *D. tomentosa* group (which, together with *D. welwitschii* and *Pasaccardoa*, constitutes its sister group); the species of the *D. tomentosa* group, though sometimes occurring in woodland habitats, are generally better adapted to dry, open sites, and even sub-desert or desert habitats (see Lisowski, 1991; Pope, 1992).

The members of this latter clade (see Fig. 11) share a number of apomorphic characters including (a) a conspicuous phyllary midrib (12.1), (b) disc corolla lobes recurved at apex [the corolla lobes have a recurved apex, with the apices of the anthers and the pistil exerted; this may reflect the adaptation of most species of this group to desert or sub-

desert environments in which pollinators are very scarce, so that there is selection in favor of at least partial anemophily (see Whitehead, 1969; Lane, 1996)] (25.1), (c) cypsela ribs conspicuously strong (60.1), (d) cypsela with twin hairs between the ribs (as also observed in the *D. carbonaria* group, and presumably reflecting parallel evolution) (64.1), and (e) immature testa (subepidermal layer of the testa) with long-rectangular crystals oriented in the same direction (68.1). This group splits into two clades: one in which *D. welwitschii* appears as a sister group of the three species of *Pasaccardoa*, and another comprising the *D. tomentosa* group. The latter might be referred to as *Dicoma* s. str., since it contains *D. tomentosa*, the type species of the genus.

In view of the topology of the cladogram (Figs. 10–12), one possible approach would be to transfer the species of the genus *Pasaccardoa* to *Dicoma*. Alternatively, *Pasaccardoa* could be maintained, in view of its various synapomorphic characters, one non-homoplastic (cypsela of the marginal florets with rostrum) and others shared with other species but not with the members of the *D. tomentosa* group (disc corolla tube abruptly dilating into limb, margin of the disc corolla lobes conspicuously sclerified, no antrorse branches at the apex of the anther tails, pappus of scales). *Pasaccardoa* also has a number of relevant plesiomorphies including presence of a cylindrical disc floret cypsela, and *Gochnatia*-type testa. This view is supported by the fact that *D. welwitschii*, which the analysis indicated to be a sister group to *Pasaccardoa*, shows a number of character states different from those of the *D. tomentosa* group, some apomorphic (phyllary sclerenchymal fibers concentrated on the abaxial face, margin of the lobes of the disc corollas conspicuously sclerified, absence of antrorse branches at the apex of the anther tails, testa of *D. welwitschii* type, pappus of scales) and some plesiomorphic (capitulum wider than 20 mm, absence of dark stripes along the phyllaries, and lateral and basal walls of testal epidermal cells strengthened). Some of these characters are shared with the species of *Pasaccardoa*. However, the inclusion of *D. welwitschii* within *Pasaccardoa* does not seem to be justifiable, in view of the marked differences with respect to the species of this genus, notably *P. grantii* and *P. jeffreyi*. These two species, in addition to *P. procumbens* (not included in the present analysis), appear to form a highly homogeneous group, with exclusive synapomorphic characters (such as twin hairs of the cypsela base conspicuously enlarged, and cypsela surface glands positioned between the ribs in the intercostal grooves) and other apomorph-

ic characters that are not exclusive but that are not present in *D. welwitschii* (capitulum made up of "true-ray" marginal florets and actinomorphic disc florets, marginal florets neuter, and cypsela of the marginal florets with rostrum). By contrast, *D. welwitschii* shows a series of apomorphic characters including apex of the disc corolla lobe without thick-bundled veins, disc floret cypsela obconic, and testa of *D. welwitschii* type. The cladogram may thus indicate that *D. welwitschii* (from the central plateaus of Angola, and also present in Zaire) is a distinct genus. Nevertheless, this possibility would have to be confirmed by an analysis including all, or nearly all, species of *Dicoma*.

Of the previously proposed sections of the genus *Dicoma*, *Dimorphae* and *Barbellatae* of Wilson (1923) are clearly paraphyletic (see Table 1, Figs. 10, 11). Considering the sections accepted by Hoffmann (1893a), the results of the present analysis are more or less consistent with *Brachyachaenium* Baker (*D. nachtigalii*), *Macladium* (Cass.) DC. (*D. spinosa* and *D. relhanioides*), and *Pterocoma* DC. (sect. *Plumosae* Wilson) (*D. sessiliflora*, *D. zeyheri*, and *D. saligna*).

Other sections, such as *Steirocoma* DC. (*D. capensis* and *D. niccolifera*, but not *D. elegans*) and *Rhigiothamnus* (Less.) DC. (*D. picta* and *D. fruticosa*), may be monophyletic; however, and apart from the monotypic sections *Hochstetteria* (DC.) O. Hoffm. (*D. schimperi*) and *Eudicoma* DC. (*D. tomentosa*), the species of my *D. tomentosa* group do not appear to form coherent monophyletic groups assignable to any of the sections previously described.

Broadly speaking, the results of the present analysis (Figs. 10–12) suggest that taxa with primitive characters, like those of the *D. carbonaria* group, may be precursors of the genus *Dicoma* that have survived as relict populations in Madagascar. It seems reasonable to hypothesize that these precursors gave rise to a lineage of xeromorphic taxa with small, spiny, coriaceous leaves (such as *D. spinosa*, *D. relhanioides*, *D. grandidieri*, and *D. cana*). The remaining species of the *D. sessiliflora* group, with scarcely coriaceous, scarcely spiny, and more or less broad leaves (*D. sessiliflora*, *D. saligna*, and *D. zeyheri*) probably originated from that lineage in adaptation to moister, shadier conditions. The origin of this group, and of the genus as a whole, would thus appear to have been in Madagascar and southern Africa, as found by Eldenäs and Andenberg (1996) for the genus *Anisopappus* (which has a similar distribution and ecology to *Dicoma*). On this hypothesis, the remaining species of the genus

arose, probably later, generally in open dry, including sub-desert and desert, environments.

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