LEAF MORPHOLOGY OF *CISTANTHE* SPACH (PORTULACACEAE)[1]

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ABSTRACT

Leaves of *Cistanthe* are typically characterized by broad, more or less clasping leaf bases, winged petioles, festooned brochidodromous venation, apically diminished primary veins, sinuous veins, "ribbonlike" veins, and predominantly brachyparacytic and similar stomata. This particular combination of characteristics does not occur in any other taxa in Portulacaceae, although most of the traits occur in individual species of *Rumicastrum*. Leaf morphology is similar in all sections of *Cistanthe* except for the monotypic sect. *Strophiolum*, which lacks sinuous veins and ribbonlike veins. Individual species may, however, possess distinctive foliar traits or combinations of traits. Overall, the leaf morphological evidence corroborates the hypothesis of monophyly of *Cistanthe*, but does not substantially clarify the phylogenetic position of this genus, nor relationships therein. Leaf characters may have utility for additional phylogenetic study.

Although the systematic foliar morphology of the dicotyledons remains poorly surveyed compared to reproductive morphology, its potential for providing phylogenetic information is becoming increasingly appreciated (see, e.g., Gifford & Foster, 1989). Instrumental in the apparent resurgence of foliar morphological study was the refinement of the classification of foliar features, especially for venation pattern (Hickey, 1973) and stomatal features (for review, see Baranova, 1987). When studied in light of the more sophisticated terminology, leaves revealed long-overlooked features that have contributed considerably to the understanding of angiosperm origins and phylogenetic trends (Hickey & Wolfe, 1975). The classification of venation features, in particular, has occasioned analyses of foliar morphology in familial and subfamilial taxonomic studies, for example, by Gillespie (1988) for *Omphalea* (Euphorbiaceae); Keating & Randrianasolo (1988) for Rhizophoraceae; Levin (1986a, b, c) for Phyllanthoideae (Euphorbiaceae); Dickison (1975) for Cunoniaceae; Todzia (1988) for *Hedyosmum* (Chloranthaceae); and others (see Levin, 1986a). Some studies (especially Levin, 1986c) used leaf characters in cladistic analyses, which permitted evaluation of the significance of foliar evolution during the course of phylogeny.

Despite the relative technical simplicity of leaf morphological investigation, systematic studies of Portulacaceae have heretofore made limited use of foliar features. The first detailed and extensive survey of foliar features in the family was by Becker (1895), who studied leaf histology, stomatal morphology, and trichomes in more than 30 species. The systematic significance of trichomes in Portulacaceae was subsequently considered by Chorinsky (1931), Franz (1908), Pax & Hoffmann (1934), and Reiche (1897, 1898). Later, Kelley (1973; see Carolin, 1987, in press; Hershkovitz, 1990a, 1991c) surveyed essentially all species of *Calandrinia* s.l. for trichome morphology. McNeill (1975), in his numerical phenetic analysis of the tribe Montieae, incorporated gross leaf and epidermal features in the database. Hershkovitz (1986) presented a preliminary assessment of leaf venation patterns and their potential taxonomic significance in Portulacaceae. Nyanyano (1986a, b, 1988) described stomata, trichomes, and leaf bundle sheath anatomy in ca. 100 species of Portulacaceae. Carolin (1987), in his phylogenetic analysis of Portulacaceae, included three trichome characters in the database. Otherwise, foliar features have been used primarily in monographs, revisions, and floristic treatments of various Portulacaceae, e.g., by

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Nilsson (1966, 1967, 1970, 1971a, b) for Montieae, Reiche (1898) for Chilean *Calandrinia* s.l., and Rydberg (1932) for several genera.

For various reasons, the use of foliar characters in these studies did not significantly advance the understanding of taxonomic relationships among Portulacaceae. For example, the most distinctive of the observed traits, multicellular trichomes and "kranz" vascular bundles, have a highly restricted incidence in the family and occur in species that were already regarded as closely interrelated (Kelley, 1973; Nyanyano, 1986a, 1988; Reiche, 1897, 1898). Carolin (1987), however, misscored some OTUs for trichome characters, which may have contributed, at least partially, to some spurious results (Hershkovitz, 1990a, in press a, in press b). The stomatal data (Nyanyano, 1986a, b) was interpreted according to Metcalfe & Chalk's (1950) simplistic scheme that recognizes few basic stomatal types. All but Carolin's (1987) study were executed using "pre-cladistic" taxonomic concepts. As a result, the monophyly of existing supraspecific taxon circumscriptions was not seriously questioned, and interpretations of variation did not incorporate the concepts of character polarity and parsimony. Thus, my earlier interpretations of leaf venation pattern evolution in Portulacaceae (Hershkovitz, 1986) reflected not only inadequate sampling, but also unnatural generic and tribal circumscriptions. The monographic and floristic considerations of foliar characters emphasized primarily species delimitations rather than interrelationships.

The present work, which stems from my preliminary survey of leaf venation patterns in Portulacaceae and represents a revision of a chapter of my dissertation (Hershkovitz, 1990a), provides a systematic characterization of gross leaf morphology, leaf venation pattern, and leaf epidermal morphology of *Cistanthe* Spach. *Cistanthe* consolidates ca. 47 species of temperate western North America and South America that had formerly been classified in as many as five genera and four tribes (Hershkovitz, 1990a, b, 1991c). Five sections of *Cistanthe* are recognized here (see Hershkovitz, 1990a, b, 1991c; cf. McNeill, 1974), including *C.* sect. *Cistanthe*, *C.* sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz, *C.* sect. *Philippiamra* (Kuntze) Hershkovitz, *C.* sect. *Calyptridium* (Nutt. in Torrey & A. Gray) Hershkovitz, and *C.* sect. *Strophiolum* (B. Mathew) Hershkovitz. Carolin (1987), in his cladistic analysis of Portulacaceae, determined that the first four of these formed a monophyletic grouping (Fig. 1) evidenced by the nearly universally shared presence of unequal inflorescence bracts. *Cistanthe* sect. *Strophiolum* was later cladistically associated with this group rather than *Lewisia*, based in part on its possession of unequal inflorescence bracts (Fig. 2; Hershkovitz, 1990a, in press c). Elsewhere, I have described the leaf morphology of sect. *Strophiolum* (Hershkovitz, 1990a, in press c) and discussed relationship among the sections of *Cistanthe* and of this genus to other Portulacaceae (Hershkovitz, 1990a, 1991c).

The purpose of such a detailed consideration of leaf morphology in *Cistanthe* is severalfold. First, this study seeks to establish whether the circumscription of the genus, itself representing a radical departure from pre-Carolin (1987) taxonomies of Portulacaceae, receives support from leaf evidence. Second, by defining leaf characters and evaluating character states in *Cistanthe*, this study contributes to the database that can be used for resolving phylogenetic relationships within the genus and of this genus to other Portulacaceae. Third, the data presented in this study contribute to the existing body of information on foliar morphological phenomena and is thus potentially useful for studies of foliar morphological evolution, of the relationship between leaf form and function, and of leaf morphogenesis.

Materials and Methods

1. gross leaf morphology

Gross leaf morphological variation of *Cistanthe* was surveyed primarily from herbarium specimens and described according to the terminology proposed by Dilcher (1974) and Hickey (1971, 1973, 1979). Figures 3–21 illustrate the range of variation in gross leaf morphology in *Cistanthe*; Figures 22–38 illustrate the gross morphology of the leaf apices. These illustrations are arranged according to sectional taxonomy. Table 1 lists vouchers, putative identifications, and full taxonomic citations of all specimens examined for anatomical features. Table 1 also lists additional representative specimens of North American *Cistanthe* examined for gross leaf morphology. I have provided elsewhere a listing of ca. 175 representative collections and putative determinations of South American *Cistanthe* (Hershkovitz, 1991a) and of specimens of *Cistanthe* (*Strophiolum*) *tweedyi* examined for leaf morphology (Hershkovitz, 1990a, in press c).

2. leaf venation pattern

Leaf venation was examined in ca. 250 cleared leaves representing essentially all species of *Cistanthe* and all leaf sizes and shapes in the genus.

TABLE 1. Specimens examined for leaf morphology. Listed below by section are specimens of *Cistanthe* that were examined for leaf morphology, including vouchers of specimens illustrated and/or cited in the present paper. Additional specimens of South American species examined only for gross leaf morphology are listed elsewhere (see Hershkovitz, 1991a), as are specimens of *Cistanthe* sect. *Strophiolum* (see Hershkovitz, in press c). Representative specimens of North American species examined only for gross leaf morphology are denoted below with an asterisk (*). Specimens examined for epidermal morphology but not venation pattern are denoted with a dagger (†). The remaining specimens were sampled for leaf venation studies and some also for epidermal morphology (see Table 2). Identifications are revised from Hershkovitz (1990a) and remain tentative (see Hershkovitz, 1991a).

Cistanthe sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz, Phytologia 68: 269. 1990 ("*Amarantoides*").

Cistanthe ambigua (S. Watson) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. U.S.A. CALIFORNIA: *M. E. Jones s.n.* (UC); *Munz 9982* (UC); *Nelson & Nelson 3287* (US).

Cistanthe calycina (Philippi) Carolin ex Hershkovitz, Phytologia 70: 220. 1991. CHILE. ANTOFAGASTA: *Johnston 3590* (US); *Johnston 5318* (US). ATACAMA: *Werdermann 418* (US).

Cistanthe densiflora (Barnéoud in Gay) Hershkovitz, Phytologia 70: 220. 1991. ARGENTINA. SAN JUAN: *Cabrera 29553* (US); *Castellanos 15520* (US).

Cistanthe salsoloides (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 221. 1991. CHILE. ANTOFAGASTA: *Werdermann 1048* (*leg. Francke*; F, US).

Cistanthe sect. *Calyptridium* (Nutt. in Torrey & A. Gray) Hershkovitz, Phytologia 68: 267. 1990.

Cistanthe monandra (Nutt. in Torrey & A. Gray) Hershkovitz, Phytologia 68: 267. 1990. MEXICO. SONORA: *Wiggins 8193* (US). U.S.A. ARIZONA: *Harris 1477* (US); *Toumey s.n.* (US). CALIFORNIA: *Heller 7641* (US)*.

Cistanthe monosperma (E. Greene) Hershkovitz, Phytologia 68: 267. 1990. U.S.A. CALIFORNIA: *Elmer 3733* (US)†; *Heller 10804* (US).

Cistanthe parryi (A. Gray) Hershkovitz, Phytologia 68: 268. 1990.

Cistanthe parryi var. *arizonica* (J. T. Howell) Kartesz & Gandhi, Phytologia 71: 62. 1991. U.S.A. ARIZONA: *Griffiths 3556* (US).

Cistanthe parryi var. *hessae* (J. H. Thomas) Kartesz & Gandhi, Phytologia 71: 62. 1991. U.S.A. CALIFORNIA: *Thomas & Ernst 6001* (US)*.

Cistanthe parryi var. *nevadensis* (J. T. Howell) Kartesz & Gandhi, Phytologia 71: 62. 1991. U.S.A. NEVADA: *Beatley 5732* (US).

Cistanthe parryi var. *parryi*. U.S.A. CALIFORNIA: *Munz 5726* (UC)*; *Parrish 3081* (UC)*; *Parrish 3725* (US); *Peirson 3124* (UC)*.

Cistanthe pulchella (Eastw.) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Congdon s.n.* (US); *Hamon 80-64* (UC)*; *Hamon 80-194* (UC)*; *Hoover 3442* (US).

Cistanthe pygmaea (Parish ex Rydberg) Hershkovitz, Phytologia 68: 268. U.S.A. CALIFORNIA: *Howell 17427* (CAS)*; *Parish 1803* (holotype, CAS)*; *Twisselmann 16891* (CAS)*.

Cistanthe quadripetala (S. Watson) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Baker 3075* (UC)†; *Hoover 3571* (US); *Parish 3082* (US); *Sharsmith 4345* (US).

Cistanthe rosea (S. Watson) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Alexander & Kellogg 4352* (US); *Duran 2805* (US); *Reveal & Reveal 424* (UC)*. OREGON: *Cusick 2585* (US).

Cistanthe umbellata (Torrey) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Heller 12062* (US); *Jones 2460* (US). OREGON: *Abrams 11351* (US); *Coville & Applegate 422* (US).

Cistanthe sect. *Cistanthe*

Cistanthe arenaria (Cham.) Carolin ex Hershkovitz, Phytologia 70: 211. 1991. CHILE. COQUIMBO: *Wagenknecht 18444* (F, UC). ÑUBLE: *Joseph 3990* (US).

Cistanthe cephalophora (I. M. Johnston) Carolin ex Hershkovitz, Phytologia 70: 212. 1991. CHILE. ANTOFAGASTA: *Werdermann 855* (US).

Cistanthe coquimbensis (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 212. 1991. CHILE. COQUIMBO: *Werdermann 881* (F).

Cistanthe cymosa (Philippi) Hershkovitz, Phytologia 70: 213. 1991. CHILE. ANTOFAGASTA: *Werdermann 853* (US); *Worth & Morrison 15816* (NA).

Cistanthe fenzlii (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 213. 1991. CHILE. BIO-BIO: *Neger s.n.* (M); *Philippi s.n.* (B).

Cistanthe grandiflora (Lindley) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. CHILE. ACONCAGUA: *Morrison et al. 16872* (NA); *West 3959* (F, UC, US). ANTOFAGASTA: *Worth & Morrison 16133* (NA). ATACAMA: *Werdermann 405* (F, UC). BIO-BIO: *Hutchinson 234* (UC, US). COQUIMBO: *Zollner 10284* (NA). U.S.A. CULTIVATED: *Peele 154* (NA).

Cistanthe guadalupensis (Dudley in D. Jordan) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. MEXICO. GUADALUPE IS.: *Lindsay 2635* (UC)*; *Moran 5991* (US)*; *Wiggins & Ernst 174* (UC).

Cistanthe lingulata (Ruíz Lopez & Pavón) Hershkovitz, Phytologia 70: 214. 1991. PERU. ANCASH: *Ferreyra 13532* (US). LA LIBERTAD: *López Miranda 374* (US). LIMA: *Ferreyra 10486* (US).

Cistanthe longiscapa (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 215. 1991. CHILE. ATACAMA: *Johnston 5034* (US); *Werdermann 445* (F).

Cistanthe maritima (Nutt. in Torrey and A. Gray) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. MEXICO. ESTADO DE BAJA CALIFORNIA: *Bacigalupi 3045* (UC); *Webster 21615* (DAV)*; *Wiggins & Ernst 207* (UC).

Cistanthe paniculata (Ruíz Lopez & Pavón) Carolin ex Hershkovitz, Phytologia 70: 216. 1991. PERU. AREQUIPA: *Ferreyra 12022* (US).

Cistanthe picta (Gillies ex Arn. in Cheek) Carolin ex Hershkovitz var. *picta*, Phytologia 70: 217. 1991. CHILE. ACONCAGUA: *Hutchinson 98* (US). ATACAMA: *Johnston 6218* (US). METROPOLITANA: *Kuntze s.n.* (US); *Morrison et al. 16786* (NA)†. O'HIGGINS: *Pennell 12279* (F).

Cistanthe picta var. *frigida* (Barnéoud in Gay) Hersh-

TABLE 1. Continued.

kovitz, Phytologia 70: 218. 1991. CHILE. COQUIMBO: *Morrison et al. 16992* (NA).

Cistanthe weberbaueri (Diels) Carolin ex Hershkovitz, Phytologia 70: 218. 1991. PERU. AREQUIPA: *Ferreyra 12006* (US). LIMA: *Weberbauer 5321* (F).

Cistanthe sp. cf. *C. arenaria*. CHILE. COQUIMBO: *Zollner 10636* (NA: the smaller-leaved specimens of this mixed collection—see Hershkovitz, 1991a). METROPOLITANA: *Joseph 2785* (US—see Hershkovitz, 1991a).

Cistanthe sp. cf. *C. longiscapa*. CHILE. ATACAMA: *Worth & Morrison 16184* (NA; see Hershkovitz, 1991a).

Cistanthe sp. CHILE. COQUIMBO: *Zollner 9807* (NA; see Hershkovitz, 1991a).

Cistanthe sect. *Philippiamra* (Kuntze) Hershkovitz, Phytologia 68: 269. 1990.

Cistanthe celosioides (Philippi) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. CHILE. ANTOFAGASTA: *Biese 613* (UC); *Werdermann 862* (UC, US); *West 3859* (UC); *Worth & Morrison 15820* (UC). ATACAMA: *Werdermann 477* (US).

Leaves of herbarium (rarely ethanol-preserved) specimens were cleared by successive treatments with Fisher Aerosol OT, ca. 10% aqueous sodium hydroxide, and 200% aqueous chloral hydrate, and stained with 1% basic fuchsin in 100% ethanol. The leaves were destained as necessary in ca. 70% ethanol, dehydrated, and mounted in standard media (e.g., Fisher Permount) using appropriately sized glass slides and cover slips. Prior to mounting, selected specimens were counterstained in ca. 0.1% fast green in 1 : 1 absolute ethanol : xylene. Gross venation patterns illustrated in Figures 3–54 were photographed by inserting the cleared leaf specimen into a photographic enlarger, sometimes with a green acetate filter, and projecting the image on photographic paper. Highly magnified venation details were photographed using a compound microscope and brightfield optics sometimes enhanced with variable degrees of Nomarski interference. The optimal preparatory regimen and photographic technique varies with the taxon, and additional information may be obtained upon request.

Venation is described according to the "Hickey system" (Dilcher, 1974; Hickey, 1971, 1973, 1979; Hickey & Wolfe, 1975). I follow Levin (1986a), however, in consistently referring to brochidodromous and higher-order "loops," rather than "arches" and loops (cf. Hickey & Wolfe, 1975). The Hickey system was undoubtedly inspired by, and best adapted to, leaves of taxa having large numbers of "iterations" of architectural features, especially those of woody perennials that bear numerous (hundreds to many thousands of) leaves having more or less uniform morphology, and in which particular venation features are repeated many times in each leaf. Members of *Cistanthe*, however, like most Portulacaceae, are herbaceous perennials and annuals, bearing few (sometimes only 10–20) leaves per season or lifetime, and the major leaf venation features iterate relatively few times. The paucity of leaves per plant can increase the degree of morphological variance in the sample because of heteroblasty. Likewise, the paucity of regularly iterated venation features within a leaf results in greater morphological variance among the iterations. As a result, attempting to discern a leaf architectural "mode" for a species of *Cistanthe* is difficult. Nevertheless, the Hickey system, because of its classification of a large number of venation details, provides a useful framework for the present discussion.

3. EPIDERMAL MORPHOLOGY

Epidermal morphology was examined in more than 37 specimens representing ca. 20 species or species complexes (i.e., including segregate species elsewhere recognized; see Hershkovitz, 1991a) of *Cistanthe*. Emphasis in this study is on the morphology of the stomatal complex on the abaxial intercostal region. Figures 80–94 illustrate the epidermal morphology of selected species. Table 2 provides brief descriptions for all examined specimens, which are vouchered in Table 1. Epidermal peels were obtained from herbarium specimens by treating leaf fragments successively with ca. 10% sodium hydroxide, distilled water, 30% hydrogen peroxide, FAA, and 50% ethanol. This harsh procedure readily separates the abaxial epidermal layer from the mesophyll, although often part or all of the adaxial epidermis is separated as well. Epidermal tissue from the abaxial intercostal region was studied on wet-mounts and subsequently preserved in 50% ethanol. Epidermal peels were photographed using brightfield optics with variable degrees of Nomarski interference. The optimal preparatory regimen and photographic technique varies with the taxon, and additional information may be obtained upon request.

RESULTS

1. GROSS LEAF MORPHOLOGY

Leaves of *Cistanthe* are simple, entire, and somewhat to quite succulent, although the precise degree of succulence could not be determined from herbarium material.

The typical leaf area in different species varies

from less than 10 mm² (*C. picta* var. *frigida*, Fig. 55; and *C. pulchella*), to over 3,000 mm² (*C. grandiflora*; *C. paniculata*, Fig. 3; *C. tweedyi*, see Hershkovitz, 1990a, in press c). According to the leaf area classes defined by Dilcher (1974), the leaf area in *Cistanthe* ranges from microphyllous to mesophyllous.

The leaf shape in species of *Cistanthe* ranges from approximately wide obovate (Figs. 3–6), through narrow oblanceolate (Figs. 12, 14, 19), to essentially linear and/or terete (Figs. 13, 18). The lamina may be essentially straight and symmetrical (Figs. 8, 9, 20) to more often asymmetrical, and slightly curved to S-shaped (Fig. 10). Leaf symmetry usually varies in a species or individual.

The shape of the leaf apex may be acute (Figs. 8, 9, 27), acuminate (Fig. 37), to rounded (Figs. 25, 26, 34), and weakly emarginate (Fig. 17) to weakly mucronate (Fig. 24). Characterization of leaf apex shape is sometimes relative to the point of reference; for example, the leaf shown for *C. weberbaueri* (Figs. 10, 28) is more or less acuminate toward the apex, but rounded at the very tip.

Petiolar development varies in the genus. Typically an individual will have distinctly petiolate and essentially sessile leaves, along with leaves of intermediate morphology. Leaf bases in petiolate leaves constrict more abruptly (Fig. 6) than gradually. Such leaves appear to be differentiated into an elliptical, ovate, orbicular, rhombic, or lanceolate blade portion, and a narrower, winged, petiole portion. In petiolate and sessile leaves, the leaf base broadens at the point of attachment to the stem so that it is nearly or quite clasping. Amplexicaul leaves occur in Peruvian plants that have been referred to *C. paniculata* (Hershkovitz, 1991a).

While the leaves illustrated here more or less typify the species or species complexes shown, the variability is such that putatively closely related species exhibit no obvious consistent distinctions in gross leaf morphology. Likewise, no distinctions among the sections of *Cistanthe* are evident, except to the degree that the more polymorphic sections (i.e., those with more species) vary more than the less polymorphic. Not all species intergrade, however; leaves of *Cistanthe grandiflora*, *C. picta*, *C. ambigua*, and *C. quadripetala*, for example, are readily distinguishable from one another.

2. LEAF VENATION PATTERN

The venation features of *Cistanthe* (except for sect. *Strophiolum*, described and illustrated in Hershkovitz, 1990a, in press c) are selectively illustrated in Figures 3–79. These illustrations are arranged according to subject, from gross venation pattern to finer anatomical details. Within each grouping, illustrations are arranged according to sectional taxonomy.

Because of the apparent variation in gross leaf morphology in species or species complexes, the concomitant variation in venation features, the paucity of iterated venation features in individual leaves, and the difficulties encountered in identifying material (see Hershkovitz, 1991a), useful and reliable descriptions of venation in individual species was largely unobtainable. The descriptions presented here emphasize the venation features characteristic of *Cistanthe* as a whole and the distribution and range of variation of these features. Particular features encountered in only a few taxa are also noted.

Venation type. Venation in *Cistanthe* is usually irregularly festooned brochidodromous (Figs. 3–11, 15–17, 20, 21, 39–46, 50, 51, 53, 54; cf. Hickey & Wolfe, 1975: 547, fig. 5), sometimes only weakly festooned (Figs. 12, 19, 47, 52), less often irregularly brochidodromous with only a hint of festooning (Figs. 13, 14, 48, 49). (See also discussion of secondary veins, below.)

Primary vein. The primary vein is prominent basally (but more so in some taxa than in others; e.g., compare Figs. 13, 17) and much diminished to obsolete apically (Figs. 22–38). The primary vein may be evident as a protruding veinlet at the leaf tip (Figs. 24, 27, 29) or not at all evident at the apex (Figs. 25, 26). Hickey's (1973) parameter for primary vein size—relative width midway between the blade base and apex—cannot be satisfactorily evaluated in *Cistanthe*, because the blade is not readily definable (see above). The primary vein course varies, but usually shows a slight zigzag or angular shift in course away from the departing secondary veins (Figs. 6, 15, 55). (See also comments on general vein course, below.)

Secondary veins. Prominent secondary veins are generally few—three to four pairs per leaf—and their number is apparently not strongly correlated with leaf size (e.g., compare Figs. 6, 55). The basalmost secondary veins are often less prominent and more decurrent or more acutely angled than the apical secondaries. The secondary veins generally change course abruptly and form loops with suprajacent secondary veins. These secondary loops are often situated one-half to two-thirds the distance from the primary vein to the leaf margin in broader leaves (Figs. 3–6) and proportionally closer to the leaf margin in narrower leaves (Fig. 10). Sometimes secondary loops fail to form or form only weakly in leaves otherwise possessing

such loops (Figs. 15–17). Tertiary loops are barely evident in the narrowest leaves (Figs. 48, 49) but are present, sometimes along with 4° and 5° loops, in broader leaves (Figs. 39–46, 50–54).

Intersecondary veins. Simple intersecondary veins are sometimes present in the intercostal regions, especially in broader leaves (Figs. 4–7, 10, 11, 20, 21).

Tertiary veins. Tertiary veins are irregularly developed, variable in size, and, because of intergradation in prominence between lower and higher vein orders, sometimes difficult to identify throughout the leaf. Those arising from the apical side of the secondary veins are generally more prominent than those arising from the basal side. The branch angle varies but is generally more acute on the apical side of the secondary veins than the basal. The tertiary vein pattern is ramified to reticulate but sometimes varies in different parts of the same leaf. Rarely, the tertiary veins are nearly percurrent (Fig. 16).

Higher-order veins (excluding freely ending veinlets). In the smallest and/or narrowest leaves, the highest vein order is essentially equivalent to the tertiary veins (Figs. 47–49, 55). In the largest leaves, a fourth order of veins is present. Fourth-order veins are not always readily distinguishable as such throughout the lamina because ramifications of the tertiary veins can be highly variable in prominence. Fourth-order veins, tentatively identified as such in Figures 39–43, 45, 46, 50, 51, 53, 54, are usually ramified or rarely more orthogonally reticulate, as in *C. longiscapa* (Fig. 40). Fifth-order veins are rarely distinguishable as such, e.g., in *C. paniculata* (Fig. 39), *C. longiscapa* (Fig. 40), and *C. monosperma* (Fig. 51).

Marginal venation. The marginal venation ranges from incomplete (Figs. 42, 44) to somewhat looped (Fig. 39) but is usually intermediate between these forms.

Freely ending veinlets. The freely ending veinlets are highly variable in length and degree of branching (Figs. 56–67) and may be prominently dilated with respect to the penultimate veins (Figs. 64–66) or hardly dilated at all (Fig. 60). The veinlets are sometimes distally coalesced with adjacent veinlets and/or veinlet branches (Figs. 56, 61–63). The terminal tracheary elements of the dilated veinlets are usually numerous, short, and densely clustered. Similarly short tracheary elements ("tracheoids") also occur rarely along the highest-order veins (Fig. 56). The terminal elements of the less dilated veinlets are more elongate and less densely clustered (Figs. 60, 67).

Areoles. Areoles are difficult to define in *Cistanthe* because the vein orders are not well differentiated, but they are probably best characterized as imperfect to incomplete, and least well developed in the smaller or narrower leaves (Figs. 48, 49, 55). Hickey's illustration of "incomplete" areolation (1979: 37, fig. 117) shows local differences in venation density. Such differences are generally not present in larger leaves of *Cistanthe*, in which the venation is more or less uniformly dense, although the shape and size of ultimate enclosures in a leaf are highly variable (Figs. 56–61). The number of veinlets per ultimate enclosure is typically 0–2 but may be more in the elongate enclosures that adjoin major veins.

Other venation features

a. Vein course. The veins are sinuous in most or all vein orders in most species, although individuals of some species may have less sinuous or straight veins, especially in *C. umbellata* (Fig. 16), *C. monosperma* (Figs. 17, 51), *C. tweedyi* (Hershkovitz, 1990a, in press c), and in some leaves and/or higher vein orders of *C. picta* (Fig. 58). Sinuous venation is possibly an artifact of specimen shrinkage during drying or preparation, but it nevertheless represents a diagnostic trait because similarly prepared leaves of other succulent-leaved members of Portulacaceae do not have sinuous veins (e.g., *Lewisia* spp.; Hershkovitz, in press c).

b. Three-dimensional venation. A few species of *Cistanthe* have veins that interconnect in more than one plane, i.e., have three-dimensional venation. Three-dimensional venation occurs in leaves that are especially succulent but not necessarily more succulent than leaves with two-dimensional (planar) venation. In the *C. grandiflora* complex (see Hershkovitz, 1991a), the finer veins in the central and basal portion of the leaf blade form a complex three-dimensional network (Fig. 68). In *C. paniculata*, the fine veins in the central and basal portion of the leaf blade may form a planar reticulum adaxial to the plane of the major veins (Fig. 69). In the cylindrical leaves of *C. ambigua*, the primary vein occurs toward the adaxial surface, and the departing veins follow the contour of the leaf toward the abaxial surface (Figs. 18, 35, 70). Toward the leaf apex, the marginal venation interconnects abaxially, forming a basketlike reticulum.

c. Vein density. Gibson (1982) estimated the density of venation by dividing the number of vascular bundles present in a leaf cross section by the length of the section, and by measuring the distance between bundles. He observed that vein density is much lower in succulent leaves of desert perennials

than in nonsucculents. Vein density in members of *Cistanthe*, which are succulent, was here estimated by counting the number of veins crossing arbitrarily delimited transects of the photographs in Figures 39–54 and dividing by the length of the transect, yielding data equivalent to that obtained by Gibson's method. *Cistanthe grandiflora* (Fig. 44) was not measured because of its extensive three-dimensional venation. The density values averaged slightly less than 5 veins/mm and were mostly lower than the 7 veins/mm minimum reported by Gibson for nonsucculent desert perennials. The highest value observed in *Cistanthe* was ca. 9.5 veins/mm in the small, linear leaves of *C. fenzlii* (Fig. 49). The lowest values, ca. 2.5 veins/mm, were found in *C. paniculata* (Fig. 39) and *C. quadripetala* (Fig. 50).

d. Tracheary element wall pitting. Mostly helical but also annular, scalariform, and reticulate wall thickenings occur (see also below). Scalariform to reticulate thickenings predominate in vessel elements in the primary (and sometimes higher-order) veins of some species (e.g., *C. lingulata*, Fig. 71, and *C. ambigua*, Fig. 72), whereas helical thickenings predominate in the prominent veins of others.

e. Vein anatomy. The finer veins in most species of *Cistanthe* are flat, or "ribbonlike" (Figs. 73–79). These veins are often sinuous and usually one cell-layer thick and up to eleven (perhaps more) tracheary elements wide (Fig. 76). The elements on one side have annular wall thickenings, and those toward the other have progressively less steep helical and, in some cases, scalariform (Fig. 75) to nearly reticulate (Fig. 74) thickenings. Some of the more prominent veins may also be ribbonlike but are more than one cell-layer thick and approach the "normal" condition in vascular plants, in which the tracheary elements are arranged in clusters rather than ribbons and have more or less the same type of secondary wall thickening throughout the vein. Ribbonlike veins appear to be common and characteristic of essentially all the fine veins in some taxa (e.g., *C. quadripetala*, Fig. 60) or relatively rare or absent among the fine veins of others (e.g., *C. picta*, Fig. 58, and *C. umbellata*, Fig. 61). They are absent in sect. *Strophiolum* (Hershkovitz, 1990a, in press c). Ribbonlike leaf veins apparently have not been described in any other vascular plants.

3. VARIABILITY IN VENATION FEATURES

A thorough analysis of the infraspecific variation in venation features of putative species of *Cistanthe* was not undertaken in the present investigation because of poorly defined species limits and the large amount of herbarium material needed for such a study. The limited sampling, however, suggested constancy of venation features in some taxa. This is demonstrated by a comparison of large and small leaves of *C. picta* (Figs. 6, 55), *C. grandiflora* (Figs. 8, 9), and the *C. umbellata* species complex (Figs. 16, 17; see Hinton, 1975). The illustrations show that the larger and smaller leaves of each pair resemble each other more than either does similar-sized leaves of other species (although no other leaves as small as that shown in Fig. 55 are illustrated).

The leaves of *C. grandiflora* appear distinguishable by the co-occurrence of the following traits: (1) a small protrusion of the weakened primary vein at the apex (Fig. 27); (2) relatively fine secondary veins and vein loops, the latter forming proximal to the primary vein; (3) a relatively narrow (< 30°) secondary vein angle; (4) prominently dilated terminal veinlets, often juxtaposed with extremely fine penultimate veins; and (5) three-dimensionally reticulating veins in the central and basal portion of the leaf.

Leaves of members of the *C. umbellata* complex are distinguishable on the basis of: (1) primary veins that are particularly prominent toward the leaf base and nearly to quite obsolete at the apex; (2) prominent secondary veins, some of which are prominently looped while others are ramified and not looped; (3) numerous festooning loops; (4) relatively well developed third and fourth vein orders; and (5) a paucity of sinuous veins and ribbonlike veins.

The venation of the leaf of *C. picta* shown in Figure 55 does not closely resemble that of the larger counterpart (Fig. 6). Nevertheless, the former appears to resemble the latter more than it does any other leaf shown in Figures 3–21 because of: (1) the massiveness of the primary vein toward the base and its obsolescence at the apex; (2) the zig-zagging character of the primary vein; (3) the relatively broad angle of the secondary veins; and (4) the paucity of sinuous and ribbonlike veins. Note that venation in *C. picta* is similar to that in the *C. umbellata* complex but has less regularly festooned loops and apparently broader secondary vein angles. Preliminary measurements also indicate a greater vein density in *C. picta* (6–7 veins/mm) than in comparable leaves in the *C. umbellata* complex (3.5–5.5 veins/mm).

In all of the cases described above, the smaller leaves differ from the larger leaves primarily in having lower "rank" (Hickey, 1971); i.e., the higher vein orders and, concomitantly, higher orders

of festooning loops are less or not distinguishable in the smaller leaves.

4. EPIDERMAL MORPHOLOGY

a. Stomatal morphology. Nyanyano (1986a, b) referred to stomata in *Cistanthe* sects. *Calyptridium* and *Philippiamra* as paracytic. Nyanyano (1986a) illustrated paracytic stomata in *C.* (*Cistanthe*) *grandiflora*; otherwise his results for *Cistanthe* sects. *Cistanthe* and *Amarantoideae* cannot be determined because he did not report results for individual species, and he included these sections of *Cistanthe* in *Calandrinia* s.l., in which both paracytic and tetracytic stomata were reported. Contrary to what Nyanyano (1986a, b) claimed, his characterizations of stomatal types correspond to the simplistic classification proposed by Metcalfe & Chalk (1950), rather than the more precise classification proposed by Wilkinson (1979), in which different types of paracytic (e.g., brachyparacytic) stomata are distinguished. Becker (1895) also reported the presence of two lateral subsidiary cells (= paracytic s.l.) in sect. *Calyptridium*.

The principal morphological features of stomata in *Cistanthe* are illustrated for several species in Figures 80–94 and diagrammed in Figure 95. Table 2 summarizes stomatal morphology for several specimens vouchered in Table 1. The stomata are described below following Wilkinson's (1979) terminology except as noted.

The most common stomatal type found in *Cistanthe* is brachyparacytic (Fig. 95B), in which the guard cells are flanked by a pair of subsidiary cells but not enclosed by them. The morphology of the lateral subsidiary cells varies: the shape ranges from reniform (i.e., contoured to the shape of the guard cell; Fig. 95I, J) to more rectangular (Fig. 95L, M) to polygonal (Fig. 95O, P). The width of the subsidiary cells ranges from relatively narrow (Fig. 95I, L, O) to broad (Fig. 95J, M, P). The broader cells are intermediate between distinct subsidiary cells and ordinary epidermal cells. A similar range of variation exists when two subsidiary cells are adjacent to a guard cell (Fig. 95K, N, Q), although the outer subsidiary cell is generally broader than the inner. The opposing subsidiary cells in a brachyparacytic stomatal complex may differ in morphology with respect to the variants noted in Figure 95. To some degree, the variation described above might reflect the optical plane of section. More likely, however, a three-dimensional shape analysis will reveal an even greater degree of variation in subsidiary cell morphology.

Infraspecific variation in stomatal type, not reported by Nyanyano (1986a, b), was found in all specimens, although some specimens were more variable than others. Aside from brachyparacytic, the variants in stomatal type include (cf. Wilkinson, 1979): hemiparacytic (Fig. 95A; only one of the guard cells with a distinct subsidiary cell); amphibrachyparacytic (Fig. 95D; two pairs of flanking subsidiary cells); hemi-amphibrachyparacytic (type proposed herein; Fig. 95C; a total of three lateral subsidiary cells); tetracytic (Fig. 95E; two pairs of subsidiary cells, one pair parallel and one pair perpendicular to the long axis of the guard cells); hexacytic (Fig. 95F; similar to the preceding but with two pairs of lateral subsidiary cells); staurocytic or anomotetracytic (Fig. 95G; three to five subsidiary cells surrounding the guard cells); and anomocytic (Fig. 95H; no distinct subsidiary cells present).

In addition, variants more or less intermediate between pairs of the above listed types and having no formal names occur. In one relatively common variant, one lateral subsidiary cell (or two adjacent cells) is divided transversely (Fig. 95R, S). In rare instances, both flanking cells are divided. Although Wilkinson (1979: 100) noted that this type should not be confused with laterocytic stomata, no sharp structural distinction can be made. Such stomata in *Cistanthe* are here arbitrarily designated brachyparacytic with one or both lateral cells split. *Cistanthe* stomata are thus distinguished from those typifying certain *Lewisia* species, in which the guard cells are flanked by four to eight subsidiary cells (Hershkovitz, 1990a, in press c). In another variation, an elongate subsidiary cell perpendicular to the guard cells occurs at one pole but not the other (Fig. 95T). When such cells occur at both poles, tetracytic and hexacytic stomata may be formed.

A character of the stomatal complex that correlates with morphological type is the number of epidermal cells, whether defined as subsidiary cells or not, that directly border the guard-cell pair ("contact cells," cf. Esau, 1977: 94). This character is useful independently of stomatal type because the distinction between subsidiary cells and ordinary epidermal cells is often arbitrary. Because most examined species of *Cistanthe* have predominantly brachyparacytic stomata (or structurally similar types shown in Fig. 95A–F), the number of contact cells is usually four: two lateral subsidiary cells plus one subsidiary or ordinary epidermal cell at each pole. Occasionally, two ordinary epidermal cells border the guard-cell pair at one or, exceptionally, both poles, so that the number of contact cells is five or, less often, six. It seems potentially possible for more than six contact cells to occur in *Cistanthe* (e.g., if both flanking cells

TABLE 2. Epidermal morphology in some species of *Cistanthe*. Listed below are stomatal types and other epidermal features found on the abaxial intercostal area of selected species and specimens of *Cistanthe*. The species are listed according to section, and the vouchers are cited in Table 1. Epidermal morphology of sect. *Strophiolum* is described elsewhere (Hershkovitz, in press c). The stomatal types, described in the text, are listed, with the suffix "-cytic" omitted. The frequency of the stomatal types in the specimens are denoted as follows: ++, common to predominant type; +, present and recurring throughout the specimen; (+), observed but rare and not recurring throughout the specimen. The evaluations are subjective and intended only to show the general pattern of variation in the genus.

Section Species (voucher)	Anomo-	Hemi-brachy-para-	Brachy-para-	Hemi-amphi-brachy-para-	Amphi-brachy-para-	Tetra-
sect. *Amarantoideae*						
C. ambigua (*Nelson & Nelson 3287*)		+	++	++		
C. calycina (*Werdermann 448*)			++			
C. densiflora (*Cabrera 29553*)			++	++		
C. densiflora (*Castellanos 15520*)			+	++	++	
C. salsoloides (*Werdermann 1048*)			+	++	++	
sect. *Calyptridium*						
C. monandra (*Harris 1477*)		+	+	+		
C. monosperma (*Elmer 3733*)			++	++	++	
C. monosperma (*Heller 10804*)		+	+	+	++	+
C. parryi var. *parryi* (*Beatley 5732*)		(+)	++	++	(+)	
C. parryi var. *parryi* (*Parrish 3725*)			++	++		
C. pulchella (*Congdon s.n.*)	+	++	++			
C. quadripetala (*Hoover 3571*)			+			
C. quadripetala (*Sharsmith 4345*)	++	++	+			
C. rosea (*Duran 2805*)	++	++				
C. umbellata (*Abrams 11351*)			++	++	++	+
C. umbellata (*Heller 12062*)			++	++	++	
C. umbellata (*Jones 2460*)		(+)	++	++	(+)	
sect. *Cistanthe*						
C. cymosa (*Werdermann 853*)		++	++			
C. cymosa (*Worth & Morrison 15816*)	+	++	++	++		
C. fenzlii (*Neger s.n.*)	(+)	+	+	+	+	+
C. grandiflora (*Hutchinson 234*)			+	++	++	
C. grandiflora (*Morrison et al. 16872*)			+	++	++	
C. grandiflora (*Peele 154*)	(+?)	(+)	++	++		
C. grandiflora (*Zollner 10284*)			++	++	++	
C. lingulata (*Ferreyra 10486*)		(+)	++	++	++	
C. longiscapa (*Johnston 5034*)	+	++	++			
C. paniculata (*Ferreyra 12022*)			++	++	++	
C. picta var. *picta* (*Kuntze s.n.*)	+	+	+	+	+	+
C. picta var. *picta* (*Morrison et al. 16786*)	+	+	+	+	+	+
Cistanthe sp. cf. *longiscapa* (*Worth & Morrison 16184*)		++	++			
Cistanthe sp. (*Zollner 9807*)			++	+	(+)	+
sect. *Philippiamra*						
C. celosioides (*Werdermann 477*)			++	++	++	
C. celosioides (*Werdermann 862*)			++	++	++	

TABLE 2. Continued.

Hexa-	Stauro-	Split lateral subsidiary cell	3 contact cells	Epidermal cell outline	Comments
		+		orthogonal	
	+			sinuous	
				sinuous	poor specimen
				orthogonal	
				orthogonal	single polar subsidiary cell sometimes present; papillar cells along leaf margin
		+		orthogonal	small sample
		+		orthogonal	single polar subsidiary cell sometimes present; stomata sunken
+	+	+		orthogonal	stomata highly variable; some papillar cells; stomata sunken
		(+)		orthogonal	papillar cells present; stomata sunken
	+	+		orthogonal to arcuate	few papillar cells present; stomata sunken
				orthogonal to sinuous	few papillar cells present; stomata somewhat sunken
	+				small sample; stomata sunken
			(+)	orthogonal	stomata sunken
				orthogonal	papillar cells present; stomata sunken
+	+	+		orthogonal	stomata highly variable; stomata sunken
(+)	(+)	+		sinuous to orthogonal near midrib	single polar subsidiary cell sometimes present; papillar cells present; stomata sunken
				orthogonal	papillar cells present; stomata sunken
				orthogonal	papillar cells present; some stomata sunken
				orthogonal	
+	+	+		orthogonal to sinuous	stomata highly variable; papillar cells present along leaf margin
				orthogonal	
+	(+)	(+)		orthogonal to arcuate	some polar subsidiary cells present
		(+)		orthogonal to sinuous	
(+)				orthogonal	stomata somewhat sunken
		+	(+)	sinuous	other odd stomatal variants present
		(+)	(+)	sinuous	other stomatal variants present
				orthogonal	stomata somewhat sunken; small sample
	+	+	(+)	sinuous	stomata highly variable
	+	+	(+)	sinuous	stomata highly variable
	(+)			orthogonal	large papillar cells present
	+	+	(+)	somewhat sinuous	other stomatal variants present; small papillar cells along leaf margin
				orthogonal	
				orthogonal	

TABLE 3. Stomatal index, stomatal density, and mean stomatal length in selected members of *Cistanthe*. Vouchers are cited in Table 1. For all measurements, (N) = the number of stomata sampled. All measurements are based on photographs.

Section	Species (voucher)	Stomatal index (N)	Stomata/ mm² (N)	Stoma length (μm) [x ± SD (N)]
sect. *Amarantoideae*	*C. ambigua* (*Nelson & Nelson 3287*)	13.6 (22)	100 (37)	21.9 ± 2.2 (20)
	C. salsoloides (*Werdermann 1048*)	11.1 (22)	69 (24)	24.8 ± 2.4 (20)
sect. *Calyptridium*	*C. parryi* var. *parryi* (*Beatley 5732*)	13.7 (44)	144 (101)	27.3 ± 4.2 (20)
	C. quadripetala (*Sharsmith 4345*)	26.7 (34)	157 (55)	26.4 ± 2.5 (20)
	C. umbellata (*Abrams 11351*)	9.5 (23)	240 (48)	23.8 ± 2.0 (20)
sect. *Cistanthe*	*C. cymosa* (*Werdermann 853*)	13.5 (36)	60 (53)	17.8 ± 2.3 (17)
	C. cymosa (*Worth & Morrison 15816*)	15.6 (45)	233 (63)	15.8 ± 1.1 (20)
	C. fenzlii (*Neger s.n.*)	10.7 (52)	203 (78)	25.1 ± 1.9 (20)
	C. grandiflora (*Werdermann 405*)	11.1 (22)	30 (24)	35.1 ± 3.5 (20)
	C. grandiflora (*Worth & Morrison 16133*)	8.8 (29)	23 (36)	35.6 ± 3.3 (20)
	C. picta var. *picta* (*Kuntze s.n.*)	12.3 (33)	250 (45)	19.0 ± 1.0 (20)
	C. lingulata (*Ferreyra 10486*)	13.3 (42)	203 (78)	30.1 ± 1.8 (20)
	C. sp. cf. *longiscapa* (*Worth & Morrison 16184*)	13.3 (20)	115 (33)	15.6 ± 1.9 (20)
C. sect. *Philippiamra*	*C. celosioides* (*Werdermann 477*)	15.2 (12)	139 (12)	22.7 ± 1.69 (11)
	C. celosioides (*Werdermann 862*)	12.4 (11)	111 (15)	17.9 ± 1.48 (9)

are divided and more than one ordinary epidermal cell borders the guard-cell pair at one or both poles), but no more than six cells bordering the guard-cell pair were observed, and this number is rare.

While all examined material of *Cistanthe* possessed some variation in stomatal morphology, the pattern and degree of variation differ among the taxa (see Table 2). The least variation occurred in members of the *C. grandiflora* complex (Fig. 80), in which amphi- and hemi-amphibrachyparacytic stomata predominate, while other types are rare. Relatively little variation also characterizes *C. lingulata* (Fig. 85), *C. salsoloides* (Fig. 90), and *C. celosioides* (Fig. 94). Greater variation occurs in *C. picta* (Figs. 82, 83), *C. fenzlii* (Fig. 84), and *C. umbellata* (Fig. 92). High proportions of hemibrachyparacytic stomata (e.g., *C. cymosa*, Fig. 88) or anomocytic stomata (e.g., *C. quadripetala*, Fig. 91) are uncommon in the genus. "Double" stomata, in which two guard-cell pairs adjoin, were observed in *C. cymosa* and *C. quadripetala* (Figs. 88, 91).

Sunken stomata occur in several taxa (Table 2) and are often variably present in an epidermal specimen. Sunken stomata are most prominent and frequent in sect. *Calyptridium*, e.g., *C. rosea* (Fig. 93) and *C. umbellata* (Fig. 92). Sunken stomata are illustrated in *C. grandiflora* (Fig. 80), *C. longiscapa* (Fig. 81), and *C. cymosa* (Fig. 88).

Biometric stomatal parameters (stomatal index, stomatal density, and stomatal size) were only sporadically surveyed in *Cistanthe* (Table 3). The preliminary data suggest only limited taxonomic utility of these parameters. The stomatal index values are similar to those noted for other angiosperms (cf. Wilkinson, 1979). The lower stomatal densities observed are typical of those found in other succulent-leaved species (cf. Gibson, 1982). Likewise, the stomatal lengths are in the "normal" range found in other plants (cf. Wilkinson, 1979). The stomatal index in *C. quadripetala* is greater than in other species of *Cistanthe*, but the stomatal density and length in *C. quadripetala* are not remarkable. The high stomatal index in this case apparently reflects the high incidence of anomocytic stomata in *C. quadripetala*; i.e., the total number of subsidiary cells will correlate with the ratio of guard cells to subsidiary and ordinary epidermal cells. The correlation between low stomatal density and high stomatal length in the *C. grandiflora* complex has been reported for other xerophytic herbs (Wilkinson, 1979).

Other biometric parameters, including the variation in stomatal index or density on the abaxial versus adaxial surface of the leaf and angle of orientation of the guard cell axis relative to the leaf axis, were not measured. Leaves of *Cistanthe*, like all Portulacaceae, are amphistomatic (cf. Nyanyano, 1986a, b), and the stomatal index and/or density might be expected to be lower on the adaxial surface, although superficial observations of a few adaxial epidermal layers did not indicate

that the difference was marked. In the intercostal region, the guard cell axis appears to be oriented randomly (see Figs. 80–94). No average or modal angle of divergence of the guard-cell axis was calculated here. Toward the leaf midrib, however, the guard-cell axis appeared to be more commonly oriented in the direction of the leaf axis.

b. Stomatal ontogeny. Ontogeny of the stomatal complex was not studied, nor was the precise sequence of cell division generally inferable from the mature stomatal morphology, because it is known that particular structural types of stomata are derivable from different ontogenetic pathways (Farooqui, 1981a, b; Rasmussen, 1981). Superficially, however, ontogeny of the stomatal complex appears to vary in *Cistanthe*. For example, in *C. salsoloides* (Fig. 90), the structure of the stomatal complex suggests mesogenous development, whereas the subsidiary cells of *C. ambigua* (Fig. 89) appear to be mesoperigenous or perigenous. (Payne (1979) doubted whether stomata can be truly perigenous (i.e., the guard cells developing directly from an otherwise undifferentiated protodermal cell), but this hypothesis does not seem to require that any or all structurally distinct subsidiary cells be derived mesogenously.) There appears to be no reason why stomatal ontogeny could not vary in a species. Indeed, variation in mature stomatal morphology in individual leaves of *Cistanthe* suggests that this may be the case.

c. Other epidermal cell features. The surface outline of ordinary epidermal cells in the leaf intercostal region in *Cistanthe* ranges from orthogonal and nearly isodiametric in surface view (Figs. 80, 86, 90, 92–94) to irregular in shape with sinuous radial walls (Figs. 81, 84, 85). The entire range of variation occurs in individuals of some taxa, e.g., in *C. picta* (Figs. 82, 83). As might be expected, ordinary epidermal cells toward or overlying the midrib tend to be more elongate and quadrangular, presumably reflecting the pattern established by the young, rapidly elongating leaf primordium.

Ordinary epidermal cells of some *Cistanthe* species are more or less dimorphic, with large cells interposed among the smaller cells associated (or intergrading) with subsidiary cells (Figs. 89, 90). In extreme cases, the large cells form epidermal alveolae or papillae, such as in a specimen referable to *Cistanthe longiscapa* (*Worth & Morrison 16184*, see Table 1, Figs. 86, 87) and in species of sect. *Calyptridium* (Table 2), including *C. rosea* (Fig. 93). The epidermis of *C. cymosa* (Fig. 88) also appears somewhat papillate. Alveoli and/or papillae have been reported previously in "*Calandrinia lamprosperma* I. M. Johnston" (aff. *Cistanthe grandiflora*; Hershkovitz, 1991a; Johnston, 1929; but see also Kelley, 1973), in sect. *Calyptridium* (Hinton, 1975), and in *C. cephalophora* (I. M. Johnston) Carolin ex Hershkovitz (Kelley, 1973). The presence of papillate/alveolate cells in species of sect. *Calyptridium* varies among individuals (Hinton, 1975; pers. obs.).

Discussion

1. Leaf morphology and the circumscription of *Cistanthe*

Table 4 outlines a syndrome of nine leaf traits that typify *Cistanthe* and summarizes the distribution of these features in this genus and elsewhere in Portulacaceae. Leaf morphological data and illustrations for species of *Lewisia* and *Calandrinia* are presented elsewhere (Hershkovitz, 1990a, in press b, in press c), and the data for the remaining Portulacaceae will be presented in future publications. The taxonomic circumscriptions used in Table 4 are based on those proposed by Carolin (1987, in press), except for *Cistanthe*, which follows the present paper, and for *Calandrinia*, which follows Hershkovitz (1990a, in press a).

As indicated in Table 4, most of the leaf traits typifying *Cistanthe* are not universally present in the genus, and all occur elsewhere in the family. Hence, none can be designated a priori as a synapomorphy diagnostic of the genus, nor can any of their evolutionary polarities in the genus be determined a priori. Table 4 also indicates, however, that no other genus of Portulacaceae possesses the entire *Cistanthe* leaf-trait syndrome. Moreover, many of the traits of *Cistanthe* are rare in the other genera in which they occur. Therefore, the leaf morphology of *Cistanthe* appears to corroborate other morphological evidence for the naturalness of the genus as circumscribed here (Hershkovitz, 1990a, 1991c). That no distinctions between sect. *Calyptridium* and the remainder of *Cistanthe* are discernable from Table 4 should not be overlooked. Leaf morphology provides no evidence in support of Carolin's (1987, in press) retention of sect. *Calyptridium* as a distinct genus.

2. Leaf morphology and the relationship of *Cistanthe* to other Portulacaceae

Leaves of *Cistanthe* share features with various taxa throughout Portulacaceae (compare Table 4 and Fig. 2). The greatest degree of similarity appears to exist between *Cistanthe* and species of the Australian genus *Rumicastrum*. The absence

TABLE 4. Leaf traits of *Cistanthe*. Listed below are several leaf traits that occur commonly to universally among species of *Cistanthe*, their distribution in the genus, and their distribution elsewhere among Portulacaceae (Hershkovitz, 1991c, in press a, in press b, in press c, unpublished).

Trait	Distribution in *Cistanthe*	Distribution elsewhere among Portulacaceae
Winged petiole differentiated from blade	Rarely absent in broader-leaved species	Common in Montieae and *Calandrinia* sects. *Calandrinia* and *Monocosmia*; rare in *Lewisia* spp.; in one *Rumicastrum* sp.
Leaf base broad, nearly or quite clasping	All species	Montieae, *Calandrinia*, *Lewisia*, *Lenzia*; otherwise apparently absent
Festooned brochidodromous venation pattern	All species except those in which the leaves are extremely small and/or narrow	Weakly evident in broader-leaved *Talinum* spp., *Ceraria* spp., and *Portulaca* spp.; rarely and weakly evident in *Lewisia* spp.; *Talinella*
Primary vein weak to obsolete at leaf apex	Weak to obsolete in all species	Weak but usually evident in *Rumicastrum* and *Talinopsis*; weak to obsolete in *Portulacaria*, *Talinaria*, *Ceraria* spp., *Portulaca* spp., and *Calandrinia* sect. *Calandrinia* spp.
4° veins distinct	Distinct in several larger-leaved species throughout the genus, absent in smaller- and narrower-leaved species	Evident in broader leaves of *Ceraria* spp.; rarely distinct in *Portulaca*, as in *P. lutea*; weakly evident in broad leaves of *Claytonia megarhiza*, broader-leaved *Lewisia* spp., *Calandrinia* sects. *Acaules* and *Calandrinia* spp., and *Talinum* sect. *Talinum* spp.
Sinuous veins	In nearly all examined species except *C. tweedyi*, but hardly evident in the *C. umbellata* complex and individuals of the *C. picta* complex	Evident in some *Ceraria* spp., *Talinum* spp., and *Rumicastrum* spp.
Ribbonlike veins	Distribution same as sinuous veins	Present in (all?) species of *Talinum* sect. *Phemeranthus* but not common nor well-developed in *Talinum* sect. *Talinum*; in many, but not all *Rumicastrum* spp.; and in *Talinopsis* and *Grahamia*
Predominance of brachyparacytic stomata (incl. hemi-, amphi-, and "hemi"-amphivariants, see Fig. 95)	Characteristic of nearly all species	Characteristic of many Montieae spp.; *Calandrinia* sects. *Dianthoideae*, *Hirsutae*, and a few *Acaules* spp.; *Lenzia*; stems of *Talinum* sect. *Talinum* spp. but probably not leaves; rare in *Lewisia* spp. and *Rumicastrum* spp. (see also Nyanyano, 1986b)
Contact cells mostly 4, otherwise mostly 5, rarely 3 or 6, probably never 2 or more than 6	In all species	In all examined Montieae, *Calandrinia* and *Lenzia* spp.; in at least two *Rumicastrum* and one *Lewisia* spp.; otherwise probably rare in these genera; in *Talinum* sect. *Talinum* stems, but probably not leaves

of both festooned brochidodromous venation and strongly differentiated higher vein orders in *Rumicastrum* species is not surprising because their leaves are usually small and/or relatively narrow. Most species of *Rumicastrum* have a type of three-dimensional venation not evident in *Cistanthe* (Hershkovitz, unpublished), but the planar venation patterns in other species are hardly distinct from

those in the very narrow-leaved species of *Cistanthe*. The phylogenetic significance of this similarity remains to be determined.

The large number of shared leaf traits for *Cistanthe* and *Rumicastrum* indicated in Table 4 may be misleading because some traits typical of the former occur only rarely in the latter and not in combination with other traits. For example, the petiolar morphology characteristic of many species of *Cistanthe* occurs only in *Rumicastrum pumila* (F. Muell.) ined. (≡ *Calandrinia pumila* F. Muell.). This species is also similar to typical *Cistanthe* in its stomatal morphology, but it lacks ribbonlike veins and has a primary vein that is prominently dilated at the leaf apex. Moreover, this species has pantoporate-operculate pollen, which is regarded in terms of aperture number and morphology as derived in *Rumicastrum* (Kelley, 1973; Carolin, 1987; Hershkovitz, 1990a, in press a). Otherwise, I have found *Cistanthe*-like stomatal morphology only in *Rumicastrum remota* (I. M. Black) ined. (≡ *Calandrinia remota* I. M. Black), a species with 12–15-pantocolpate pollen, which is the putatively primitive condition in *Rumicastrum* (Kelley, 1973; Hershkovitz, 1990a, in press a; but see also Carolin, 1987). *Rumicastrum remota* has a three-dimensional venation pattern typical of many species of *Rumicastrum* and unlike three-dimensional venation in any species of *Cistanthe*. Other species of *Rumicastrum* possess various stomatal types having three, rather than four or five, contact cells; e.g., anisocytic (Hershkovitz, unpublished).

Leaves of *Cistanthe* are mostly less similar to those of other genera of Portulacaceae than to those of *Rumicastrum*. With respect to their leaf morphological similarity to *Cistanthe*, most Portulacaceae fall into one of two categories: (1) those taxa having in common with *Cistanthe* characters of gross and epidermal morphology, e.g., Montieae, *Calandrinia*, and *Lewisia*; and (2) those taxa having in common with *Cistanthe* venation features, e.g., *Talinum*, *Ceraria*, and others listed in Table 4. These two groups are otherwise potentially distinct cladistically (see Fig. 2), as well as biogeographically: the first group, along with *Cistanthe*, comprises the genera of Portulacaceae that occur predominantly westward from the American cordillera, and the second group comprises most of the taxa that occur predominantly eastward from the American cordillera and in southern Africa (Hershkovitz, 1990a–c, in prep.). Thus, while the leaf data presented here do not resolve the phylogenetic position of *Cistanthe*, they seem to suggest a pivotal position of this genus in Portulacaceae, potentially linking the eastern American/African, western American, and Australian members of the family.

3. LEAF MORPHOLOGY AND RELATIONSHIPS WITHIN *CISTANTHE*

Leaf morphology appears to have limited utility for diagnosing or assessing relationships among the sections of *Cistanthe*. Sections of *Cistanthe* are not distinguishable on the basis of leaf features, although, as noted, the monotypic sect. *Strophiolum* lacks sinuous veins and ribbonlike veins. Distinctions in venation pattern and epidermal morphology are not evident among Reiche's (1897, 1898) subdivisions of *Cistanthe* sect. *Cistanthe* (i.e., *Calandrinia* sects. *Cistanthe*, *Rosulatae*, *Arenariae*, and *Andinae*), except to the degree that Reiche's circumscriptions of *Calandrinia* sects. *Cistanthe* and *Andinae* consist of the *Cistanthe grandiflora* and *Cistanthe picta* species complexes, respectively (Hershkovitz, 1991a). Kelley's (1973) assignments of the extra-Chilean species of *Cistanthe* to Reiche's (1897, 1898) sections of *Calandrinia* cannot be independently corroborated by venation and epidermal evidence. The monophyly of *Cistanthe* sect. *Calyptridium* might be evidenced by the pervasiveness of sunken stomata and leaf surface papillae (see Table 3), but both traits occur elsewhere in the genus. Likewise, the absence of sinuous and ribbonlike veins in *Cistanthe* sect. *Strophiolum* is not unique to this taxon. Nevertheless, the sectional status of sect. *Strophiolum* is recognized partially on the basis of these traits (Hershkovitz, 1990a, in press c).

The utility of leaf morphology in elucidating species-level phylogeny in *Cistanthe* is limited to the degree that the variable characters show constancy in otherwise diagnosable taxa and are polarizable. The utility is, therefore, inherently restricted given the poorly defined species limits in *Cistanthe* and uncertainty regarding outgroups of the genus (Hershkovitz, 1990a, 1991a). Reiche (1897) emphasized gross leaf morphology in his keys to the Chilean species of *Cistanthe*, but the apparent high degree of plasticity and continuous range of variation in gross leaf morphology as observed here contribute to the inadequacy of Reiche's keys for identifying the Chilean material. The results presented above, however, provide at least some evidence that species or species complexes (e.g., *Cistanthe grandiflora*, *C. picta*, *C. umbellata*) can be distinguished by their combined leaf traits. It is possible, therefore, that multivariate morphometric analyses of leaf morphological pa-

TABLE 5. Leaf traits having a restricted occurrence in *Cistanthe*. Listed below are leaf traits rare in *Cistanthe*, their distribution in the genus (see text), and their distribution elsewhere among Portulacaceae (Hershkovitz, in press 1991c, in press a, in press b, in press c, unpublished).

Trait	Distribution in *Cistanthe*	Distribution elsewhere among Portulacaceae
Leaves over 3,000 mm²	*C. grandiflora* complex, *C. paniculata* complex, and *C. tweedyi*	*Talinum* sect. *Talinum*, *Lewisia congdonii*, *L. cotyledon*, and *Claytonia* spp.
Fifth-order veins distinct	*C. umbellata* complex; weakly evident in *C. longiscapa* and *C. paniculata*	Absent
Three-dimensional venation	*C. grandiflora* complex, *C. paniculata* complex, and *C. ambigua*	*Talinum* sect. *Phemeranthus*, nearly all *Portulaca* sect. *Portulaca*, *Talinopsis*, *Grahamia*, *Schreiteria*, *Lewisia rediviva*; some, but not all *Anacampseros* spp. and *Rumicastrum* spp.
Large proportion of anomocytic stomata	*C. quadripetala*	*Lewisia triphylla*, *L. kelloggii*, and *Montia* spp. (see also Nyanyano, 1986a, b)
Papillae/alveoli on leaf surface	Variably present in sect. *Calyptridium* and specimens of sect. *Cistanthe* (see text)	*Anacampseros* spp., one species of *Calandrinia* sect. *Acaules*, one species of *Rumicastrum*
Amplexicaul leaves	Specimens of *C. paniculata* complex (see text)	*Claytonia* spp., but probably not homologous (see text)

rameters may help refine ideas on species limits in *Cistanthe*.

A few leaf traits in certain species of *Cistanthe* are possibly or likely derived in the genus (Table 5): (1) leaves larger than 3,000 mm²; (2) fifth-order leaf venation; (3) three-dimensional leaf venation; (4) a large proportion of anomocytic stomata; (5) papillate or alveolate cells throughout the leaf surface; and (6) amplexicaul leaves. There is no compelling structural or phylogenetic evidence that these traits are symplesiomorphic with similar traits in other Portulacaceae. The leaf-size character is most troublesome, because leaf size varies in all taxa and, presumably, is influenced by environmental factors. The size of the largest leaves in *Cistanthe*, however, exceeds that found in all but a few scattered taxa in the family. The relatively strong differentiation of higher vein orders found in a few species of *Cistanthe* is almost certainly derived because this trait is absent elsewhere in the family. Three-dimensional venation is a complex characteristic because more than one manifestation is present in *Cistanthe* and in other Portulacaceae. In at least some cases, other members of Portulacaceae with three-dimensional venation seem to be most closely related to species with planar venation. For example, in *Portulaca*, three-dimensional venation is restricted to *P.* sect. *Portulaca* (Hershkovitz, unpublished). This section is thought to be derived in the genus (Geesink, 1969, 1987). Therefore, three-dimensional venation has probably evolved several times in the family. In *Cistanthe*, anomocytic stomata are common only in a species of sect. *Calyptridium*. This section is probably relatively derived in the genus (Hershkovitz, 1990a, 1991c). The leaf surface papillae/alveoli that occur in *Cistanthe* appear to be very large cells that protrude beyond the smaller epidermal cells; those in *Anacampseros* and *Calandrinia* sect. *Acaules* are more hairlike, and those in the latter are also ribbed (Hershkovitz, 1990a, in press b). Unribbed papillae have been reported in *Rumicastrum quadrivalvis* (F. Muell.) ined. (≡ *Calandrinia quadrivalvis* F. Muell.; cf. Kelley, 1973) but the specimen was not vouchered and other specimens of *R. quadrivalvis* lack papillae (Hershkovitz, 1990a, in press b). The amplexicaul leaves that occur in *C. paniculata* are not homologous with superficially similar "perfoliate" leaves in species of *Claytonia*, which are formed by the congenital fusion of two leaves at a node.

Because the characters listed in Table 5 are mostly restricted to recognized species or species complexes, they provide little insight into the phylogeny of *Cistanthe*. For example, epidermal papillae/alveoli may represent a synapomorphy of sect. *Calyptridium*, but these species are presumably closely related in any case (Hershkovitz, 1990a,

1991c; Hinton, 1975). An especially close relationship between papillate-leaved species in sect. *Calyptridium* and sect. *Cistanthe* is not supported by additional characters. Large leaves and similar three-dimensional venation may be indicative of relationship between the *C. grandiflora* and *C. paniculata* complexes. These species complexes occupy adjacent desert habitats in northern Chile and southern Peru, respectively. Both possess long-haired seeds, which are otherwise of restricted occurrence in *Cistanthe* (Kelley, 1973), although glabrous seeds also occur in both complexes (Hershkovitz, 1990a, 1991a; Johnston, 1929). Otherwise, leaves of *C. paniculata* (Figs. 3, 22, 39), which have very wide, obovate laminae and relatively well developed vein orders, more closely resemble leaves of the northern Chilean *C. longiscapa* complex (Figs. 4, 23, 40; cf. Figs. 8, 9, 27, 44), in which long-haired seeds also occur (Hershkovitz, 1990a, 1991a). Kelley (1973) assigned *Cistanthe paniculata* to *Calandrinia* sect. *Cistanthe* Reiche, which includes the *Cistanthe grandiflora* complex (Reiche, 1898), whereas Reiche (1898) assigned *Cistanthe longiscapa* to the highly variable *Calandrinia* sect. *Rosulatae* Reiche.

4. LEAF FORM, FUNCTION, AND EVOLUTION IN *CISTANTHE*

While the aim of this survey of leaf morphological diversity in *Cistanthe* was to help resolve phylogenetic and taxonomic questions, the data pose questions on the relationship of leaf form to function and evolution. Such questions cannot be answered from a survey of herbarium specimens alone, but preliminary data such as that generated here might provide a focus for future ecophysiological and evolutionary investigations. Only a few aspects of leaf form that have been studied with respect to function will be considered in the data presented here for *Cistanthe*, including gross leaf morphology, leaf venation pattern, sinuous and ribbonlike veins, and subsidiary cell morphology.

Givnish (1979, 1982, 1984) has developed several models that relate aspects of leaf form (e.g., leaf shape, arrangement, venation pattern) to the optimization of photosynthetic ability and the minimization of the metabolic cost of leaf support and supply. Givnish (1979) suggested rosette-forming herbs might be expected to have obovate leaves that, collectively, form a circular photosynthetic area that mimics an optimally efficient light-capturing structure. *Cistanthe* species have predominantly basal and/or suprabasal leaves and usually have relatively few cauline leaves except in species that form secondary rosettes along prostrate branches. The leaves are, in accordance with Givnish's model, typically obovate to oblanceolate (see above). In the *Cistanthe picta* complex, which has more diffusely arranged cauline leaves (Hershkovitz, 1991a; Reiche, 1898), the basal leaves are sessile and oblanceolate to obovate while the cauline leaves tend to be more petiolate with orbicular to ovate blades. The morphology of the cauline leaves might be explained with reference to Givnish's (1979) stem-leaf packing model, which purports that stem-leaf bases are evolutionarily honed to eliminate the portion that would be shaded by other leaves. Departures from the predicted form of *Cistanthe* leaves (e.g., linear leaves or petiolate leaves with a small, distal, rhombic blade portion, as in the *Cistanthe arenaria* complex; Hershkovitz, 1991a; Reiche, 1898) might best be explained as adaptations to xeric conditions, in which the leaf area is reduced to resist overheating and reduce water loss.

Givnish (1979) also noted that obovate leaves of rosette-forming plants, which are supported by the ground, or especially thick cauline leaves, which are supported independently of the vascular tissue, may tend to evolve parallel venation in order to maximize the efficiency of water and nutrient supply. He supposed that the pinnate venation pattern typical of dicotyledons provides an optimal support system (but a suboptimal supply system) for the cantileverlike form of cauline leaves. Superficially, it would appear that leaves of *Cistanthe* are supported primarily by their thickness and broad, clasping leaf bases, or, in the case of rosette leaves, by other leaves and/or the ground. The primary vein in *Cistanthe* does not seem to be well-suited for support because of its irregular, zig-zag, or sinuous course and its relatively small size in the broader portion of the leaf blade. Yet venation in *Cistanthe* is basically pinnate, although the secondary veins may arise at a particularly narrow angle (e.g., in *C. guadalupensis*, Fig. 5, a species with all basal leaves; Hershkovitz, in press c; Rydberg, 1932). Thus, the pinnate venation patterns of *Cistanthe* appear to represent an exception to Givnish's (1979) model.

The functional significance of the peculiar ribbonlike veins of *Cistanthe* is difficult to evaluate without more detailed anatomical and developmental data. In the vascular bundles of primary stem tissue, the centrifugally developing sequence from protoxylem elements with annular thickenings to metaxylem elements with scalariform thickenings is thought to facilitate vascular supply during the course of stem elongation and maturation. A

similar function might be suspected for ribbonlike veins if the succulent leaves continue to grow for a prolonged period after becoming functional. Whether the sinuousness of the veins serves any function cannot be evaluated without prior determination that this is not a preparatory artifact. The sinuousness might reflect the ability of the leaf to expand and contract under oscillating water regimes.

The functional significance of subsidiary cell shapes and arrangements does not appear to have been extensively studied. Reviews of stomatal function and cell biology (e.g., Sack, 1987; Salisbury & Ross, 1985) tend to emphasize the structure and physiology of the guard cells, while reviews of stomatal supracellular morphology (e.g., Wilkinson, 1979) emphasize gross form and development. Payne's (1979) brief review of stomatal morphology is unusual in considering both.

Reviews of stomatal function emphasize that guard cells are protoplasmically isolated from other leaf cells (Sack, 1987), and that the "surrounding cells" (≡ contact cells) serve as a source of potassium ions that are transported into guard cells and affect stomatal opening (Salisbury & Ross, 1985). The morphology and spatial distribution of the contact cells undoubtedly influence this physiological process (Payne, 1979; Salisbury & Ross, 1985: 62, figs. 3–9), but whether extreme differences in stomatal complex morphology (e.g., in hexacytic vs. anomocytic stomata) have any net effect on this process is not clear. Payne (1979) observed a correlation between mesogenous stomatal development (presumably resulting in guard cells surrounded by distinct subsidiary cells) and the ability of the plant to withstand water stress, e.g., in succulent leaves. Leaves of *Cistanthe* are unquestionably succulent and presumably dry-adapted, yet mesogenous stomatal development does not appear to be the rule, or perhaps even especially common, in the genus (see above). In any case, *Cistanthe* (and/or other Portulacaceae in which marked differences in stomatal morphology occur in closely related taxa; Hershkovitz, in press b, in press c), might provide a natural system for investigating subsidiary cell/guard cell physiological interactions.

The development of the stomatal complex has been studied extensively among angiosperms, but as with physiology, the functional significance of the various ontogenetic pathways is apparently poorly understood. Payne (1979) proposed a sort of "tailoring" function for subsidiary cells; i.e., their development compensates for the difference in cell enlargement between ordinary epidermal and guard cells. This hypothesis seems plausible in instances where the perimeter of a stomatal complex (i.e., the guard and apparent subsidiary cells) conforms to the dimensions of the adjacent ordinary epidermal cells, e.g., in Figures 80 and 81. The hypothesis does not, however, explain the anomocytic condition (Fig. 91), in which the guard cells are directly adjacent to the much larger epidermal cells, or instances where the perimeter of the stomatal complex appears to have greater dimensions than those of the adjacent epidermal cells (e.g., Fig. 84).

The goal of understanding the functional or adaptational value of leaf morphological features renders an understanding of the taxonomy and phylogeny of the plants in question all the more important. The fact that the leaf traits of *Cistanthe* conform to simple functional models in some ways but not others indicates that additional factors, be they genetic or epigenetic, sometimes influence leaf morphology in the genus. The genetic factors, collectively, reflect evolutionary history. Correlations are evident between the leaf traits of *Cistanthe* and environmental or developmental factors, but one should not overlook the fact that the collection of leaf traits shared by most or all members of the genus seem to correlate best with the co-occurrence of functionally unrelated traits, e.g., unequal inflorescence bracts. In other words, the leaf morphology of *Cistanthe* correlates best with other evidence that members of the genus share a common ancestor. Collectively, leaf traits permit members of *Cistanthe* to be distinguished from other members of Portulacaceae, including those that occupy at least the same general geographic region, and probably more so from other angiosperms, including those that might superficially resemble members of *Cistanthe* and/or occupy the same habitat. Resolution of phylogenetic relationships within *Cistanthe* (and Portulacaceae in general) will help clarify which traits were inherited from a more remote ancestor and which evolved more recently as members of the genus came to occupy their present habitats.

Literature Cited

Baranova, M. A. 1987. Historical development of the present classification of morphological types of stomates. Bot. Rev. (Lancaster) 53: 53–79.

Becker, C. 1895. Beitrag zur vergleichenden Anatomie der Portulacaceen. Doctoral Dissertation. Universität Erlangen, Erlangen.

Carolin, R. C. 1987. A review of the family Portulacaceae. Austral. J. Bot. 35: 383–412.

———. Portulacaceae. *In* K. Kubitzki (editor), Families and Genera of Vascular Plants, Volume 2. Springer Verlag, Heidelberg. (in press).

CHORINSKY, F. 1931. Vergleichend-anatomische Untersuchung der Haar-gebilde bei Portulacaceen und Cactaceen. Osterr. Bot. Z. 80: 308–327.

DICKISON, W. C. 1975 [1976]. Leaf anatomy of Cunoniaceae. J. Linn. Soc., Bot. 71: 275–294.

DILCHER, D. L. 1974. Approaches to the identification of angiosperm leaf remains. Bot. Rev. (Lancaster) 40: 1–157.

ESAU, K. 1977. Anatomy of the Seed Plants, 2nd edition. John Wiley & Sons, New York.

FAROOQUI, P. 1981a. Ontogeny of the tricytic stoma—variations and modifications. Proc. Indian Acad. Sci. (Plant Sci.) 90: 85–89.

———. 1981b. Ontogeny of the anomocytic stoma—variations and modifications. Proc. Indian Acad. Sci. (Plant Sci.) 90: 245–252.

FRANZ, E. 1908. Beiträge zur Kenntnis Portulaceen und Basellaceen. Bot. Jahrb. Syst. (Beibl. 97) 42: 1–46.

GEESINK, R. 1969. An account of the genus *Portulaca* in Indo-Australia and the Pacific (Portulacaceae). Blumea 17: 275–307.

———. 1987. Theory of classification of organisms. Pp. 91–126 *in* E. F. de Vogel (editor), Manual of Herbarium Taxonomy: Theory and Practice. UNESCO/MAB, Jakarta.

GIBSON, A. C. 1982. The anatomy of succulence. Pp. 1–17 *in* I. P. Ting & M. Gibbs (editors), Crassulacean Acid Metabolism. Waverly Press, Baltimore.

GIFFORD, E. M., JR. & A. S. FOSTER. 1989. Morphology and Evolution of Vascular Plants, 3rd edition. W. H. Freeman & Co., New York.

GILLESPIE, L. J. 1988. A Revision and Phylogenetic Analysis of *Omphalea* (Euphorbiaceae). Ph.D. Dissertation. University of California, Davis, California.

GIVNISH, T. J. 1979. On the adaptive significance of leaf form. Pp. 375–407 *in* O. T. Solbrig et al. (editors), Topics in Plant Population Biology. Columbia Univ. Press, New York.

———. 1982. On the adaptive significance of leaf height in forest herbs. Amer. Naturalist 120: 353–381.

———. 1984. Leaf and canopy adaptations in tropical forests. Pp. 51–84 *in* E. Medina et al. (editors), Physiological Ecology of Plants of the Wet Tropics. Dr. Junk, The Hague.

HERSHKOVITZ, M. A. 1986. Notes on leaf architecture and phylogeny in the Portulacaceae. Amer. J. Bot. 73: 766. [Abstract.]

———. 1990a. Phylogenetic and Morphological Studies in Portulacaceae. Ph.D. Dissertation. University of California, Davis, California.

———. 1990b. Nomenclatural changes in Portulacaceae. Phytologia 68: 267–270.

———. 1991a. Taxonomic notes on *Cistanthe*, *Calandrinia*, and *Talinum* (Portulacaceae). Phytologia 70: 209–225.

———. 1991b. More Centrospermae I: the portulacaceous alliance. Amer. J. Bot. 78(6, pt. 2): 191. [Abstract.]

———. 1991c. Phylogenetic assessment and revised circumscription of *Cistanthe* Spach (Portulacaceae). Ann. Missouri Bot. Gard. 78: 1009–1021.

———. In press a. A revised circumscription and sectional taxonomy of *Calandrinia* Kunth (Portulacaceae). Ann. Missouri Bot. Gard.

———. In press b. Leaf morphology of *Calandrinia* Kunth (Portulacaceae). Ann. Missouri Bot. Gard.

———. In press c. Leaf morphology and taxonomic analysis of *Cistanthe tweedyi* (nee *Lewisia tweedyi*; Portulacaceae). Syst. Bot.

HICKEY, L. J. 1971. Evolutionary significance of leaf architectural features in the woody dicots. Amer. J. Bot. 58: 469. [Abstract.]

———. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17–33.

———. 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 *in* C. R. Metcalfe & L. Chalk (editors), Anatomy of the Dicotyledons, 2nd edition, Volume 1. Clarendon Press, Oxford.

——— & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

HINTON, W. F. 1975. Systematics of the *Calyptridium umbellatum* complex (Portulacaceae). Brittonia 27: 197–208.

JOHNSTON, I. M. 1929. Papers on the flora of northern Chile. Contr. Gray Herb. n.s. 85: 1–164.

KEATING, R. C. & V. RANDRIANASOLO. 1988. The contribution of leaf architecture and wood anatomy to the classification of the Rhizophoraceae and Anisophyllaceae. Ann. Missouri Bot. Gard. 75: 1343–1368.

KELLEY, W. A. 1973. Pollen Morphology and Relationships in the Genus *Calandrinia* H.B.K. (Portulacaceae). M.S. Thesis. California State University, Northridge, California.

LEVIN, G. A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

———. 1986b. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic analysis. Ann. Missouri Bot. Gard. 73: 86–98.

———. 1986c. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic analysis. Syst. Bot. 11: 515–530.

MCNEILL, J. 1974. Synopsis of a revised classification of Portulacaceae. Taxon 23: 725–728.

———. 1975. A generic revision of Portulacaceae tribe Montieae using techniques of numerical taxonomy. Canad. J. Bot. 53: 789–809.

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

NILSSON, Ö. 1966. Studies in *Montia* L. and *Claytonia* L. and allied genera. I. Two new genera, *Mona* and *Paxia*. Bot. Not. 119: 265–285.

———. 1967. Studies in *Montia* L. and *Claytonia* L. and allied genera. III. Pollen morphology. Grana Palynol. 7: 279–363.

———. 1970. Studies in *Montia* L. and *Claytonia* L. and allied genera. IV. The genus *Crunocallis* Rydb. Bot. Not. 123: 119–148.

———. 1971a. Studies in *Montia* L. and *Claytonia* L. and allied genera. V. The genus *Montiastrum* (Gray) Rydb. Bot. Not. 124: 87–121.

———. 1971b. Studies in *Montia* L. and *Claytonia* L. and allied genera. VI. The genera *Limnalsine* Rydb. and *Maxia* Ö. Nilss. Bot. Not. 124: 187–207.

NYANYANO, B. L. 1986a. Tribal and Generic Relationship and Classification of the Portulacaceae (Centrospermae). Ph.D. Dissertation. University of Reading, England.

———. 1986b. Taxonomic significance of the stomatal complex in the Portulacaceae. Feddes Repert. Beih. 97: 763–766.

———. 1988. Leaf anatomical studies in the Portulacaceae (Centrospermae) with regards to photosynthetic pathway. Folia Geobot. Phytotax. 23: 99–101, pls. 1, 2.

Pax, F. & K. Hoffmann. 1934. Portulacaceae. Pp. 234–262 *in* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 2. Auflage, Band 16c. Engelmann, Berlin.

Payne, W. W. 1979. Stomatal patterns in embryophytes: their evolution, ontogeny, and interpretation. Taxon 28: 117–132.

Rasmussen, H. 1981. Terminology and classification of stomata and stomatal development—a critical survey. J. Linn. Soc., Bot. 83: 199–212.

Reiche, K. 1897. Zur Systematik der Chilenischen Arten der Gattung *Calandrinia*. Ber. Deutsch. Bot. Ges. 15: 493–503.

———. 1898. Flora de Chile, Volume 2. Univ. Chile, Santiago.

Rydberg, P. A. 1932. Portulacaceae. Pp. 279–336 *in* R. Britton et al. (editors), North American Flora, Volume 21. New York Bot. Gard., Bronx, New York.

Sack, F. D. 1987. The development and structure of stomata. Pp. 59–89 *in* E. Zieger et al. (editors), Stomatal Function. Stanford Univ. Press, Stanford, California.

Salisbury, F. B. & C. W. Ross. 1985. Plant Physiology, 3rd edition. Wadsworth Publ., Belmont, California.

Todzia, C. A. 1988. Chloranthaceae: *Hedyosmum*. Fl. Neotropica Monogr. 48. New York Bot. Gard., Bronx, New York.

Wilkinson, H. P. 1979. The plant surface (mainly leaf). Pp. 97–165 *in* C. R. Metcalfe & L. Chalk (editors), Anatomy of the Dicotyledons, 2nd edition, Volume 1. Clarendon Press, Oxford.

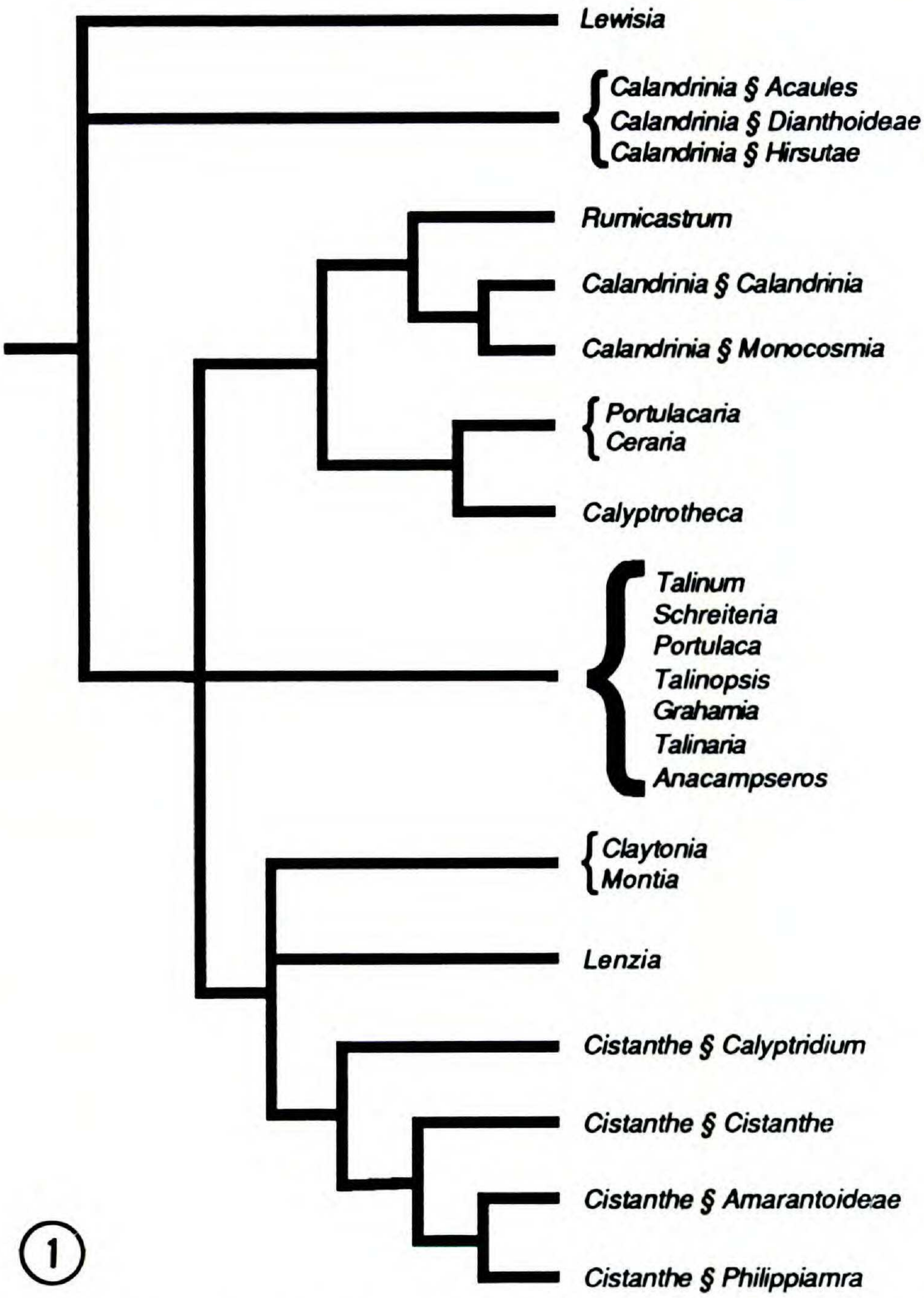


FIGURE 1. Simplified reproduction of Carolin's (1987: 402, fig. 7) most parsimonious cladogram of Portulacaceae, emphasizing the relationships among major clades and among members of *Cistanthe*. The taxonomy follows Carolin (1987, in press), except for *Cistanthe* and *Calandrinia*, which follows Hershkovitz (1990a, 1991c, in press a). The synapomorphies supporting the branching structure shown are problematic (see Hershkovitz, 1990a, 1991c).

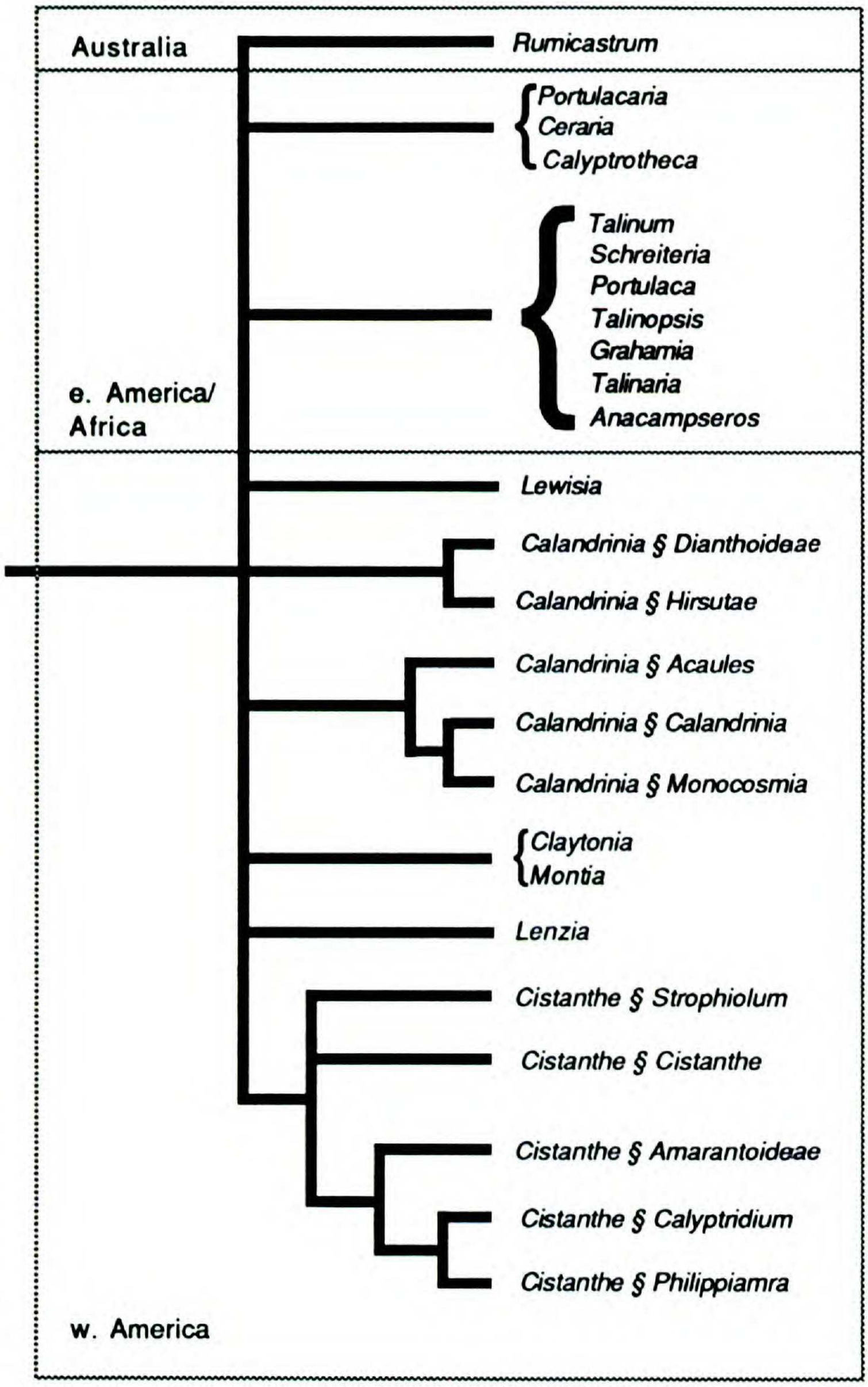
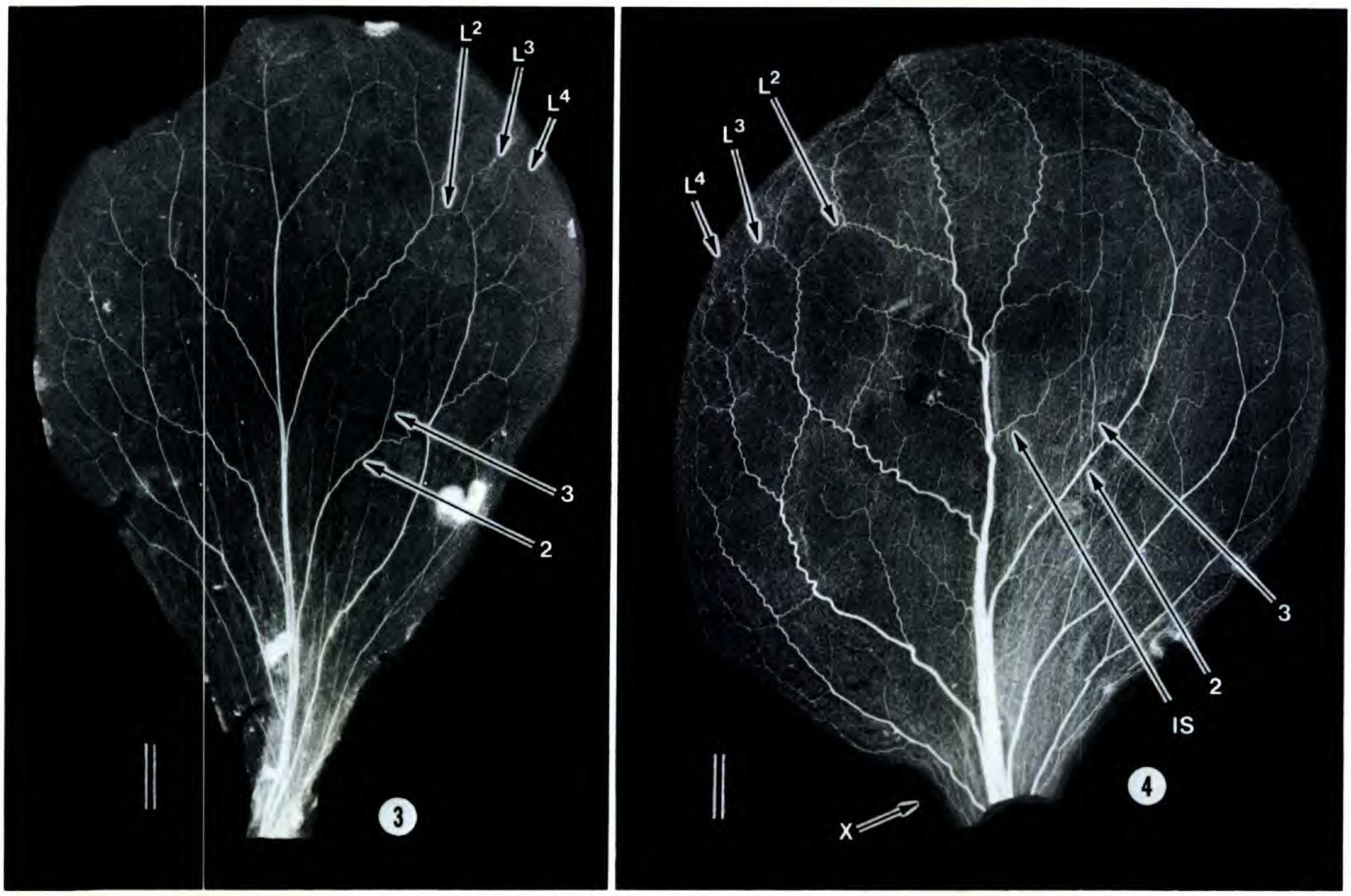


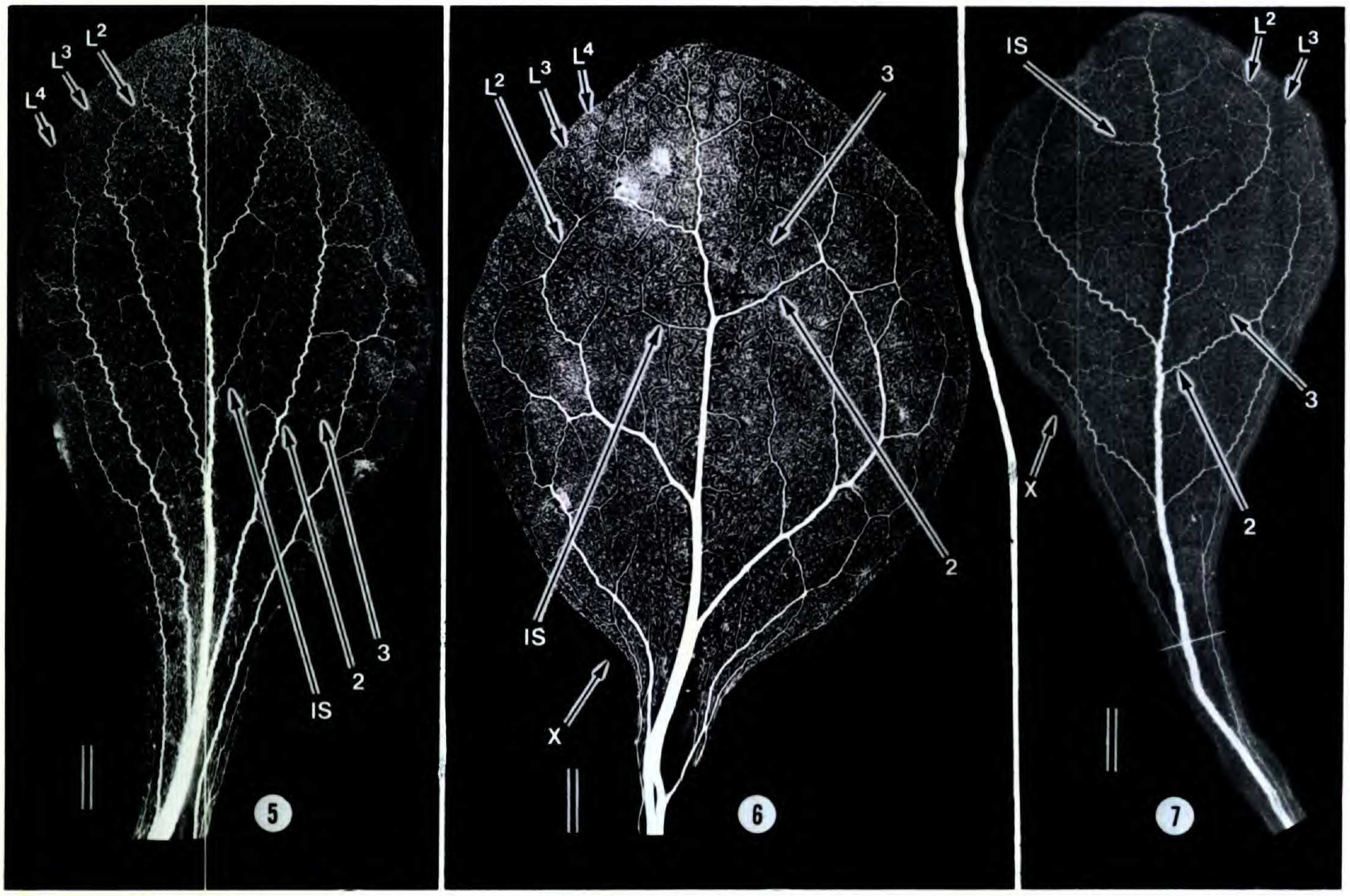
FIGURE 2. Revised cladogram of Portulacaceae emphasizing relationships among the sections of *Cistanthe* (see Hershkovitz, 1990a, 1991c) and showing relationships of *Calandrinia* sects. *Calandrinia* and *Monocosmia* I have proposed elsewhere (see Hershkovitz, 1990a, in press a). The taxonomy follows Carolin (1987, in press), except for *Cistanthe* and *Calandrinia*, which follows Hershkovitz (1990a, 1991c, in press a). The boxes enclosing portions of the diagram circumscribe the regions of endemism or greatest endemism of the included taxa (Carolin, 1987; Hershkovitz, 1990a, 1991c, in press a, in prep.).

→

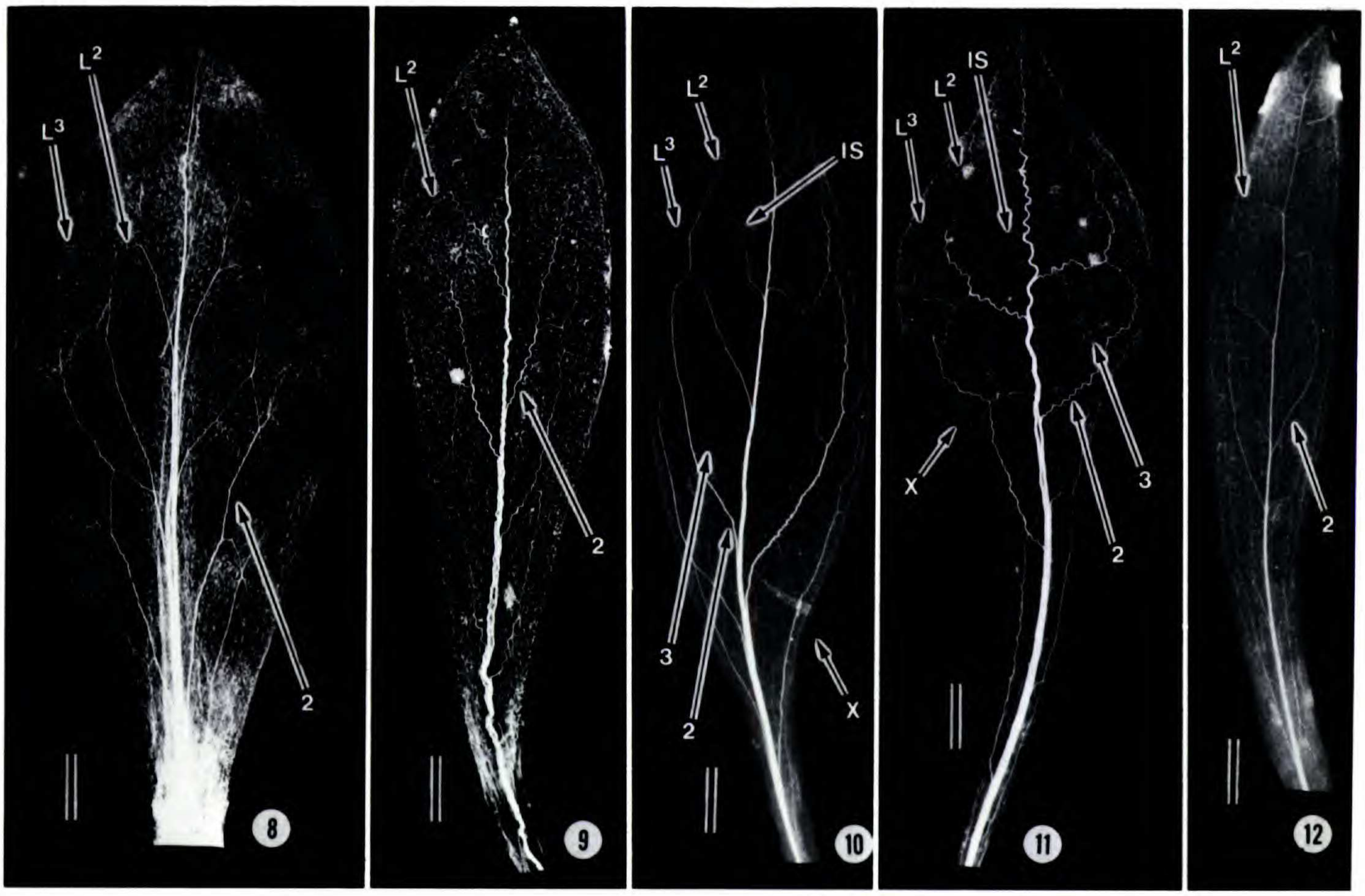
FIGURES 3–55. Gross venation features in *Cistanthe*. All vouchers are listed in Table 1. The specimens in Figs. 22–54 are the same as those in Figs. 3–21 and are not reidentified except where necessary. 1, primary vein, 2, secondary vein, etc.; L^2, secondary loop, L^3, tertiary loop, etc.; IS, intersecondary vein; X, the approximate position of the constriction between the blade and winged petiole.



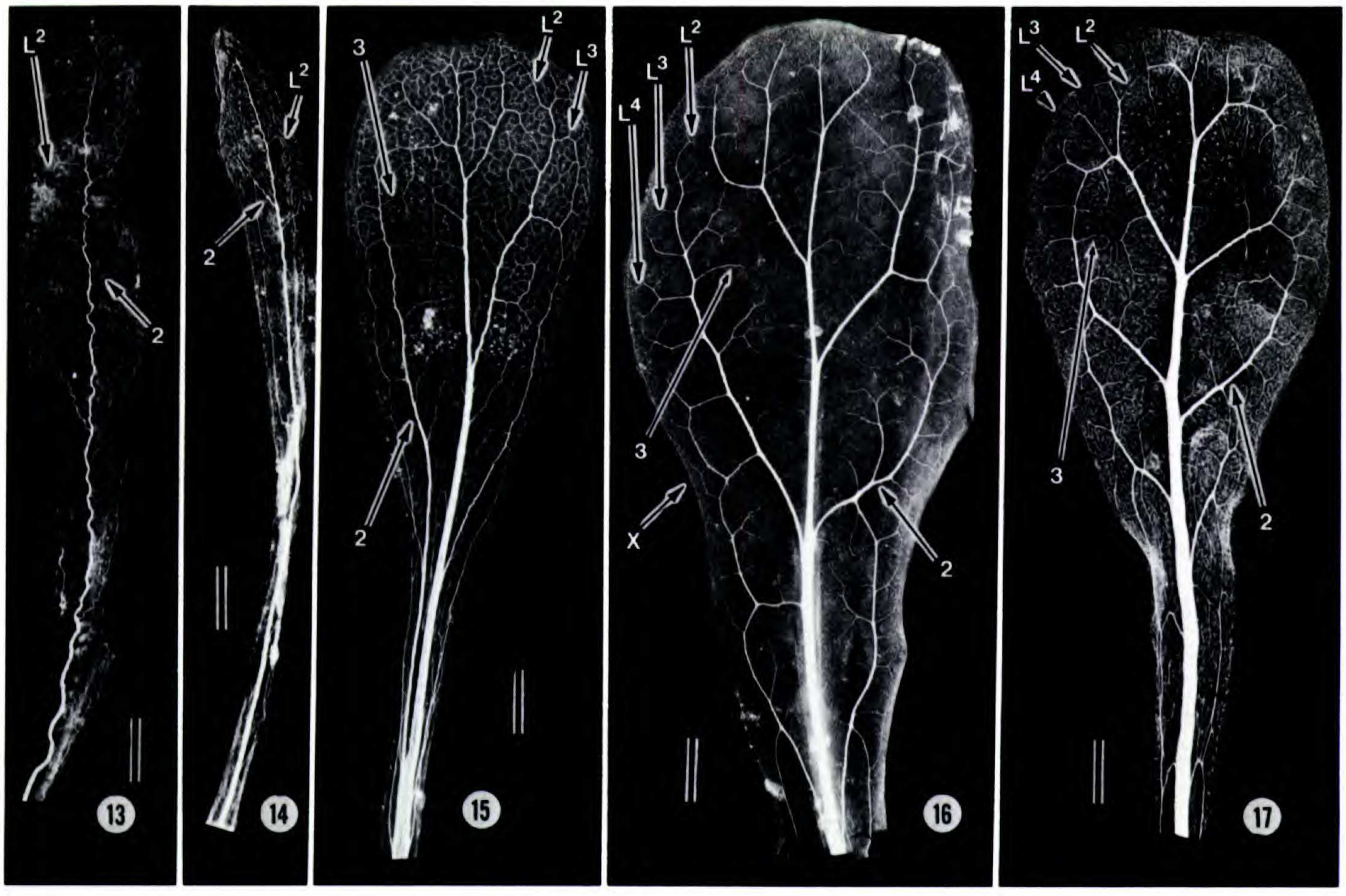
FIGURES 3, 4. Cleared whole leaves of *Cistanthe* sect. *Cistanthe*.—3. *C. paniculata* (*Ferreyra 12022*).—4. *C. longiscapa* (*Johnston 5034*). The petiole, ca. half as long as the blade, is not shown. Scale bars are (mm) ca. 6.2 and 3.0, respectively.



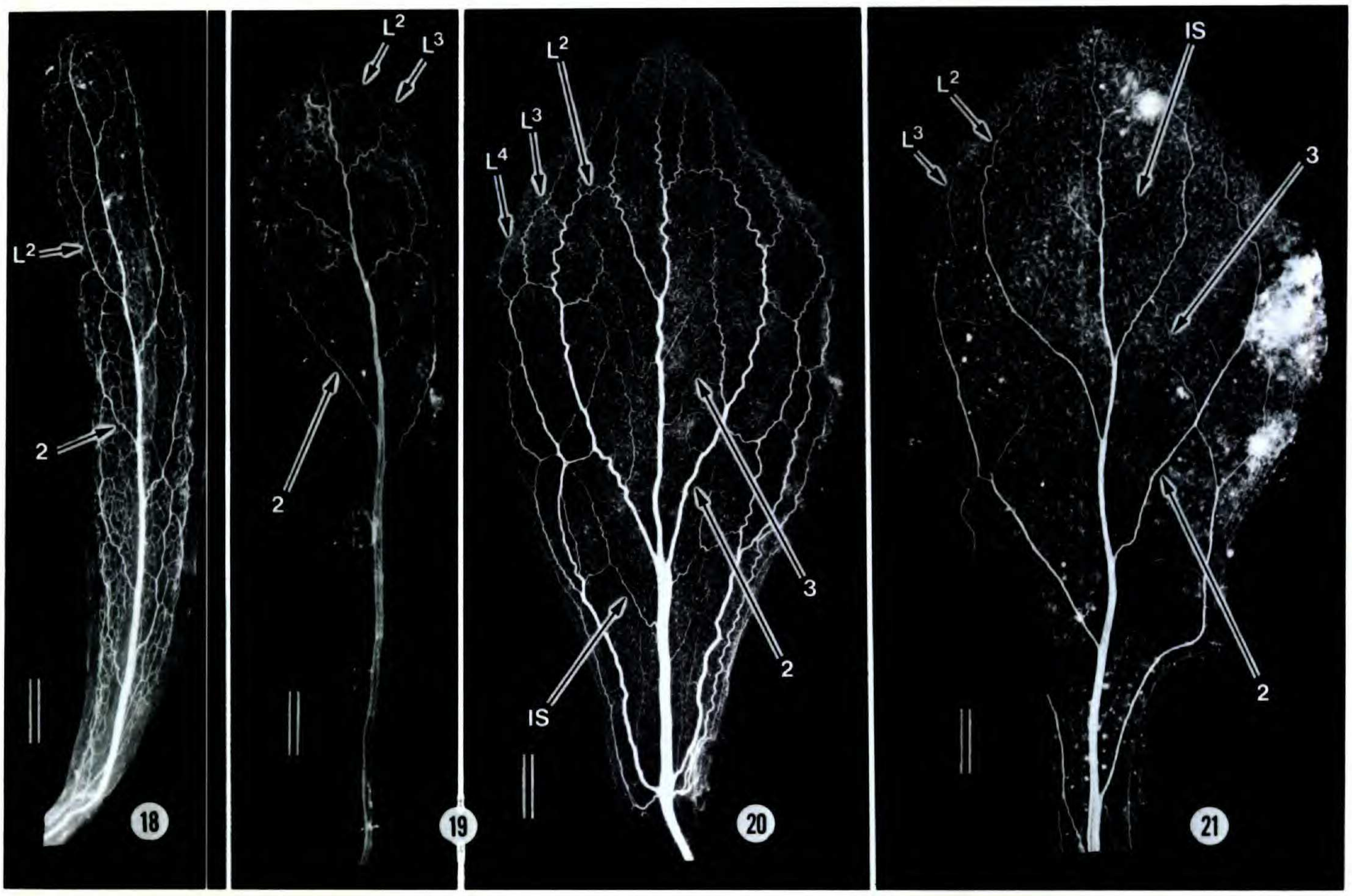
FIGURES 5–7. Cleared whole leaves of *Cistanthe* sect. *Cistanthe*.—5. *C. guadalupensis* (*Wiggins & Ernst 174*).—6. *C. picta* var. *picta* (*Kuntze s.n.*).—7. *C. coquimbensis* (*Werdermann 881*). Scale bars are (mm) ca. 4.6, 2.0, and 2.5, respectively.



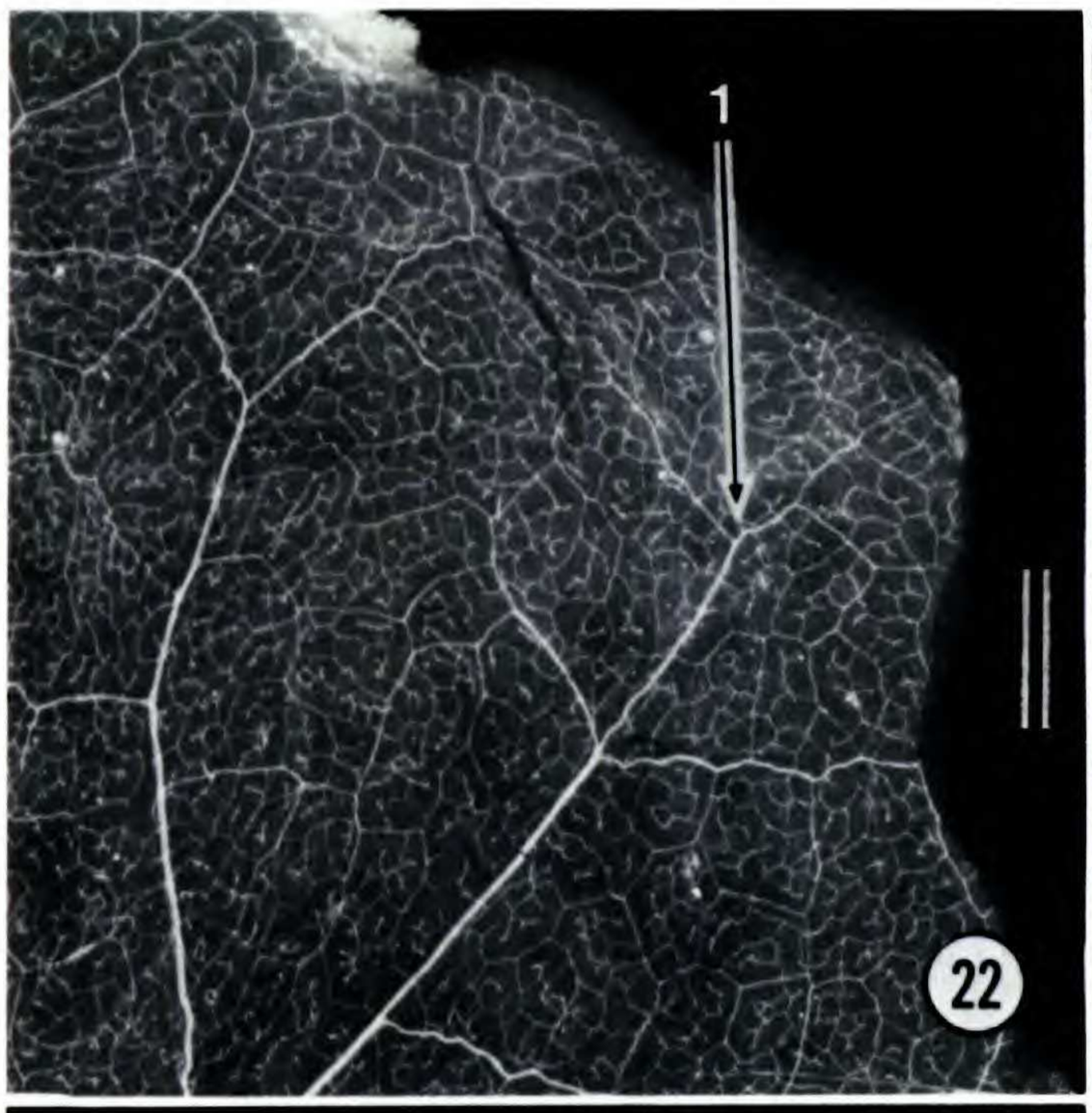
FIGURES 8–12. Cleared whole leaves of *Cistanthe* sect. *Cistanthe*.—8. *C. grandiflora* (*Werdermann 405*).—9. *C. grandiflora* (*Morrison et al. 16872*).—10. *C. weberbaueri* (*Weberbauer 5321*).—11. *C.* sp. cf. *arenaria* (*Zollner 10636*).—12. *C. lingulata* (*Lopez 374*). Scale bars are (mm) ca. 4.5, 2.8, 3.3, 3.0, and 2.1, respectively.

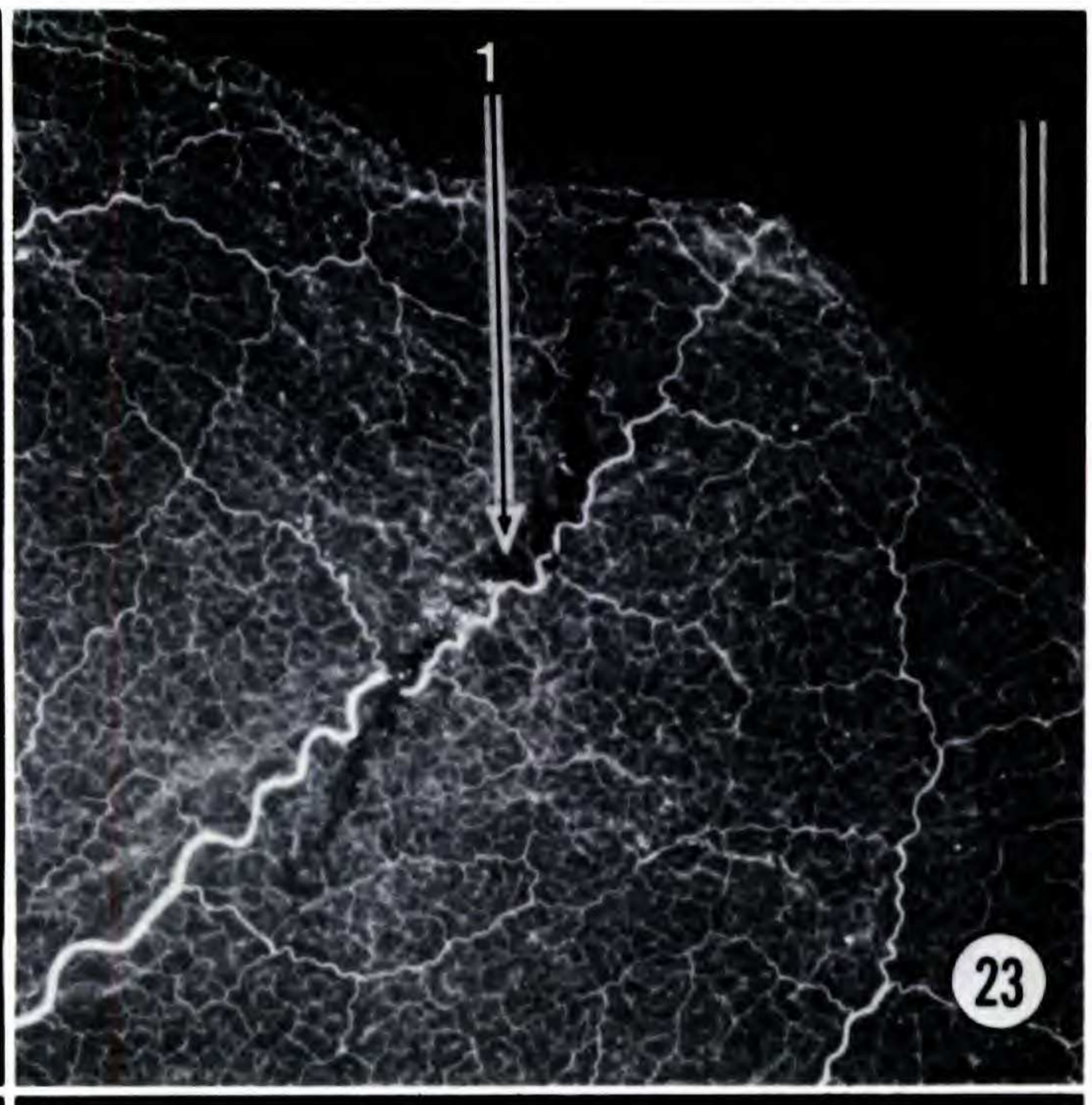


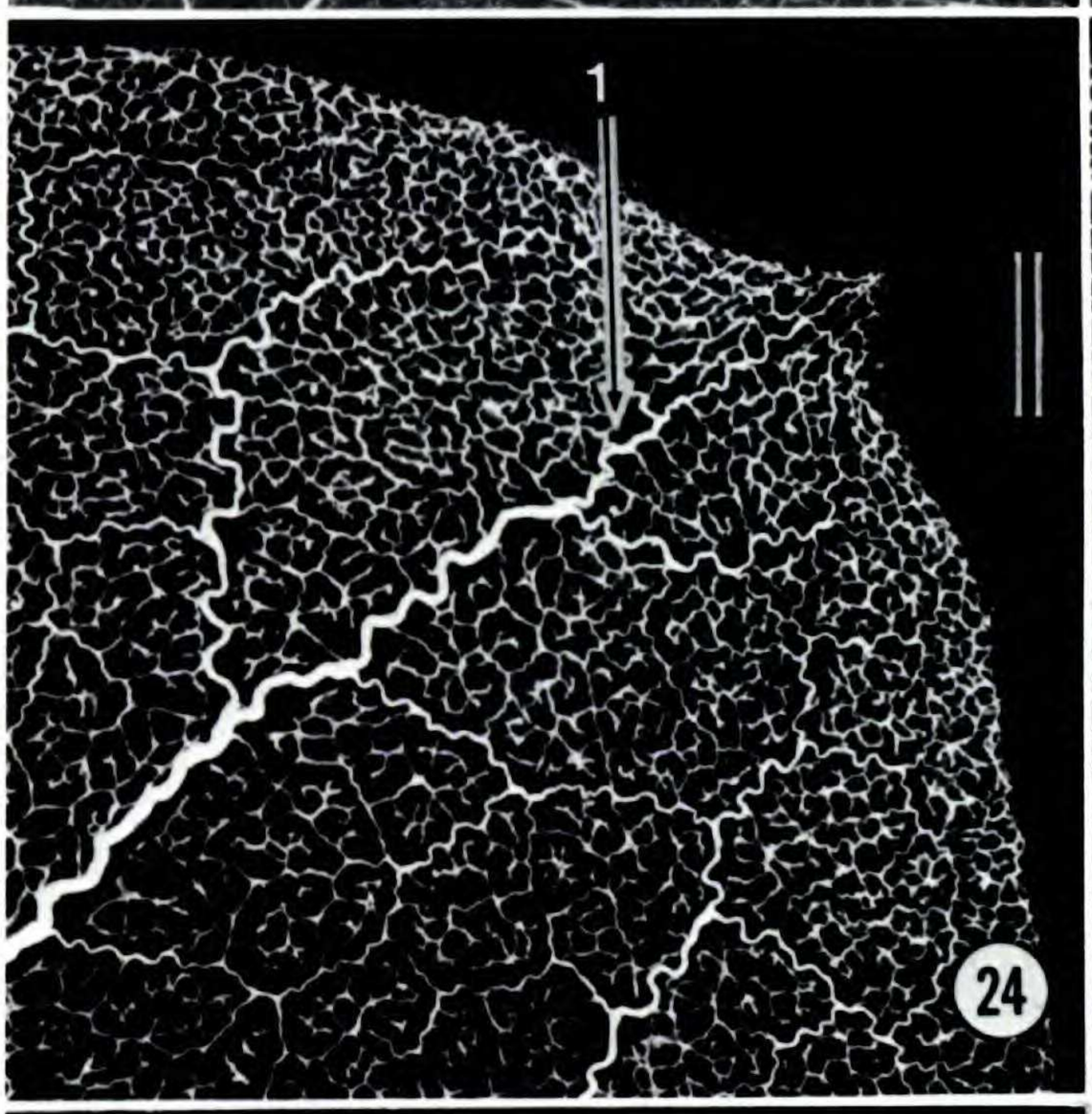
FIGURES 13–17. Cleared whole leaves of *Cistanthe* sects. *Cistanthe* (13, 14) and *Calyptridium* (15–17).—13. *C.* sp. (*Zollner 9807*).—14. *C. fenzlii* (*Philippi s.n.*).—15. *C. quadripetala* (*Hoover 3571*).—16. *C. monosperma* (*Heller 10804*). The petiole, ca. as long as the blade, is not shown.—17. *C. umbellata* (*Jones 2460*). Scale bars are (mm) ca. 2.8, 1.6, 3.4, 3.8, and 2.2, respectively.

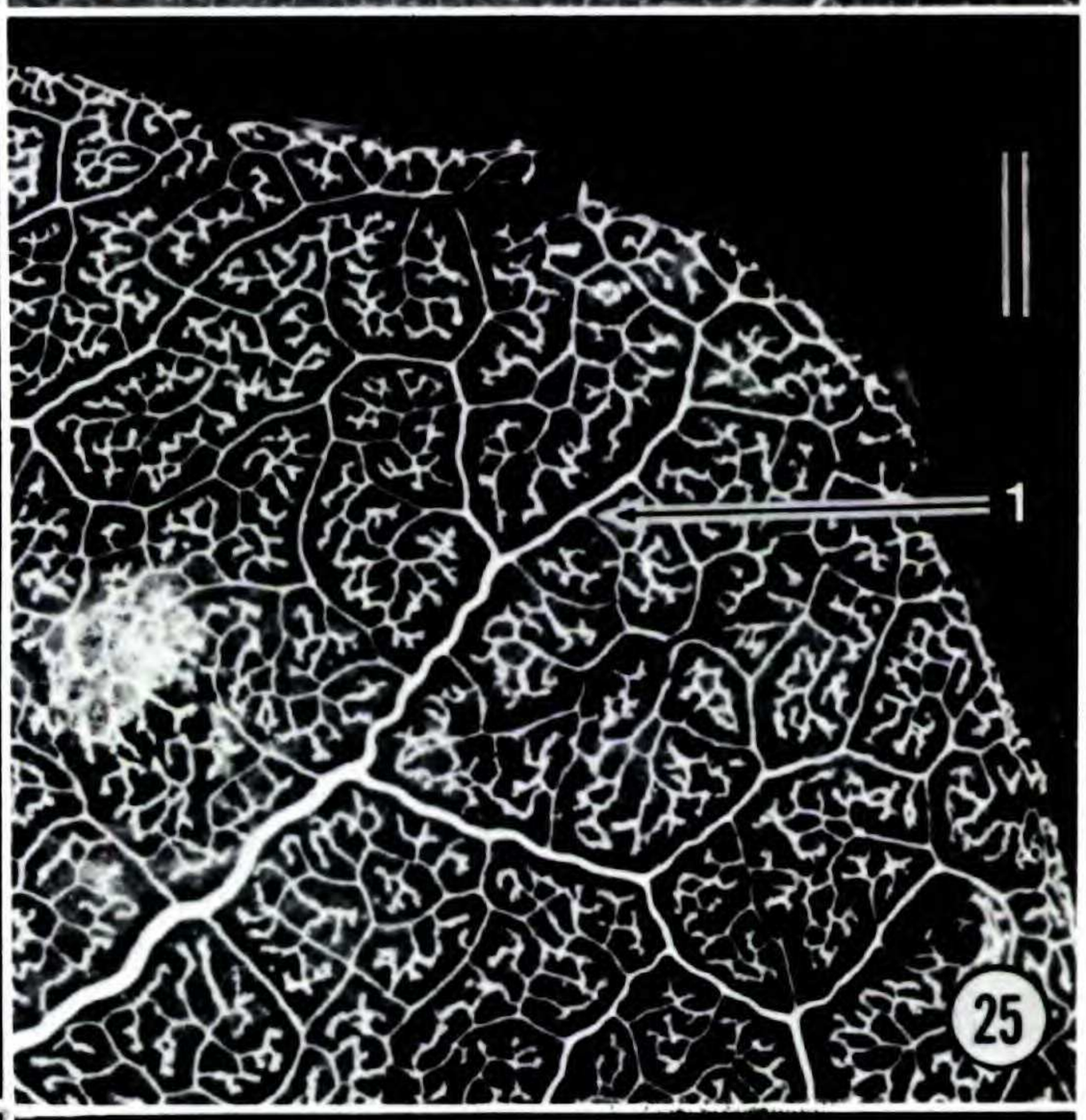


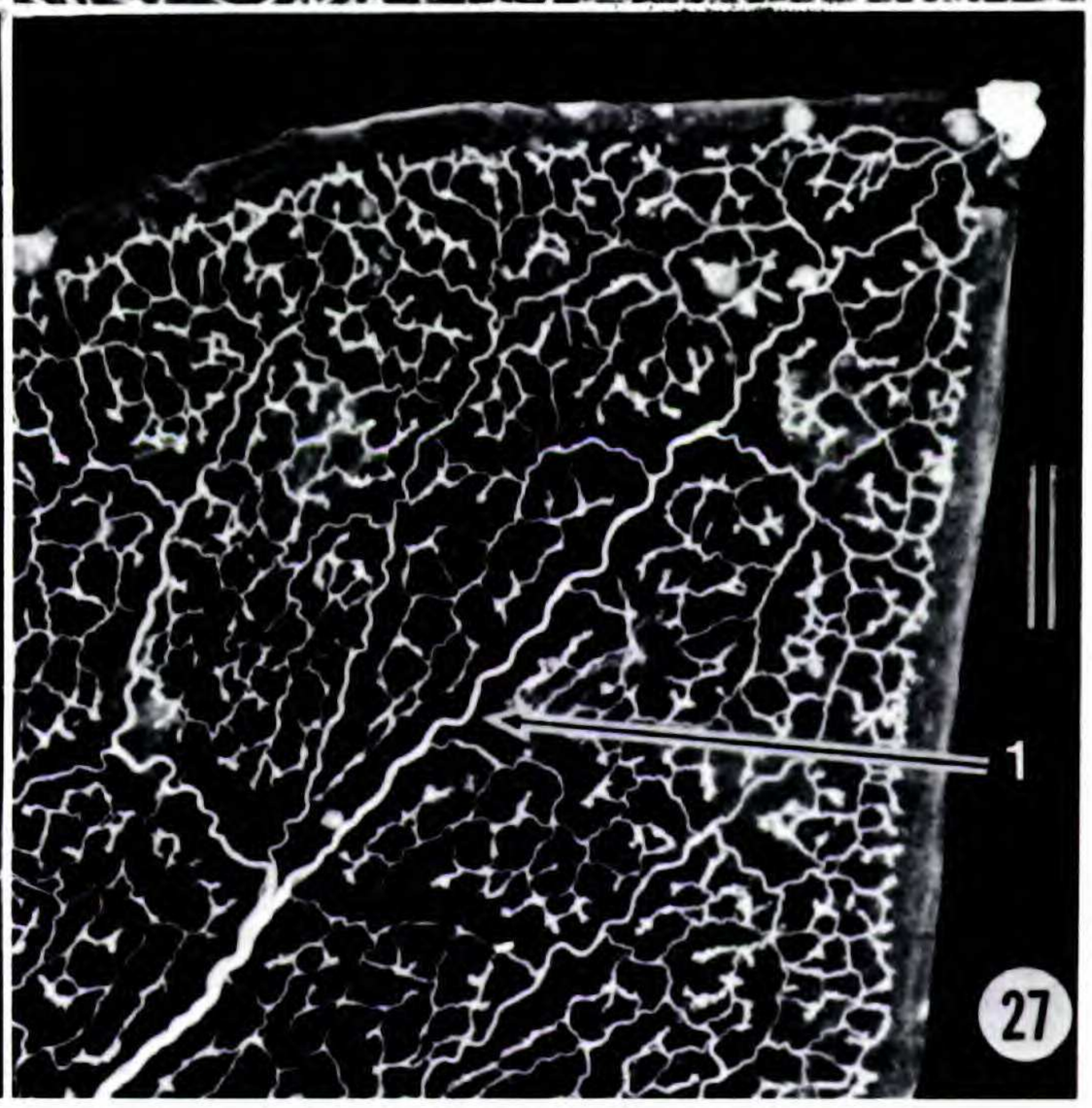
FIGURES 18–21. Cleared whole leaves of *Cistanthe* sects. *Amarantoideae* (18–20) and *Philippiamra* (21).—18. *C. ambigua* (*Nelson & Nelson 3287*).—19. *C. calycina* (*Johnston 5318*).—20. *C. salsoloides* (*Werdermann 1048*).—21. *C. celosioides* (*Worth & Morrison 15820*). Scale bars are (mm) ca. 3.0, 1.3, 2.4, and 1.5, respectively.



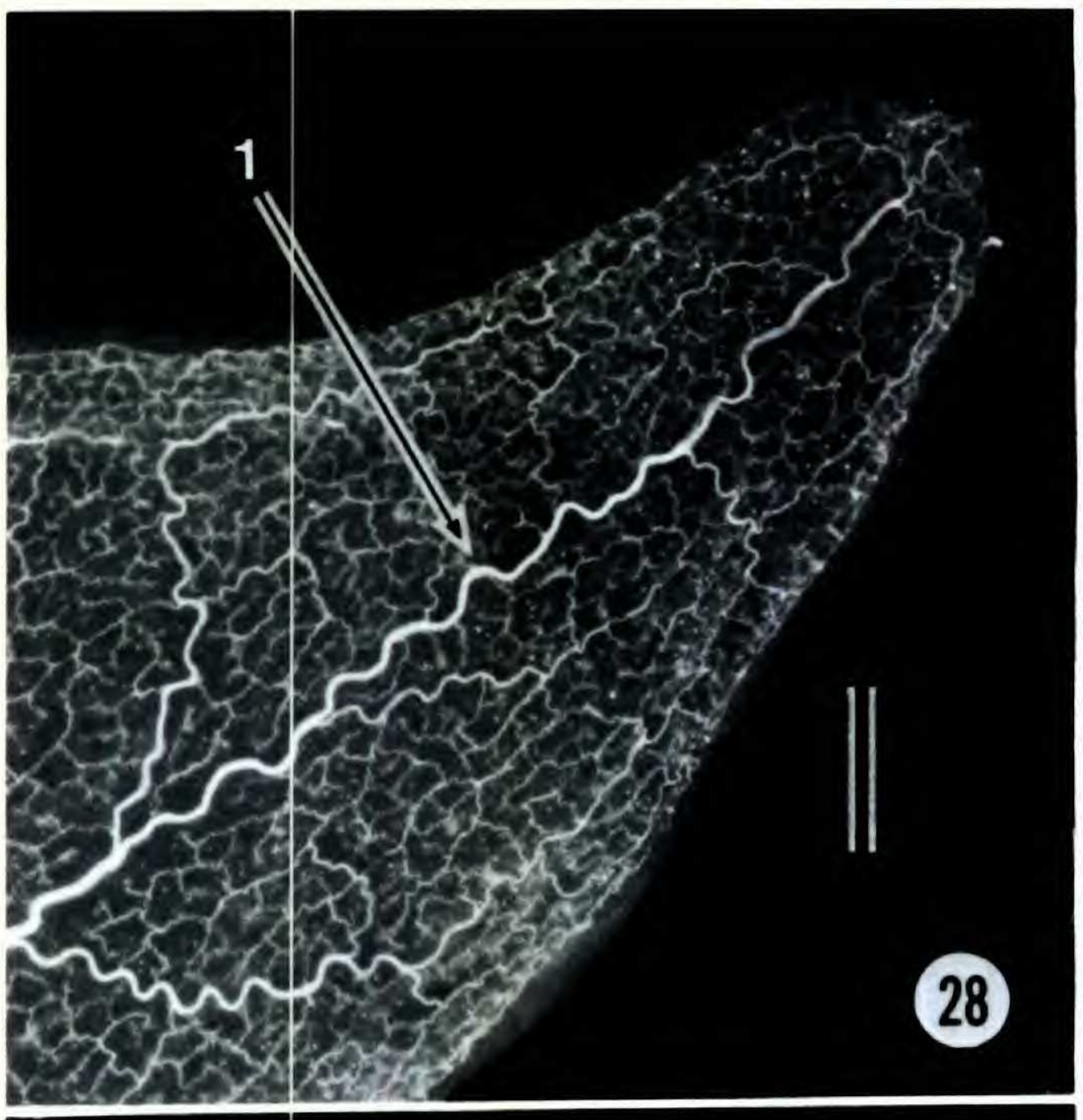


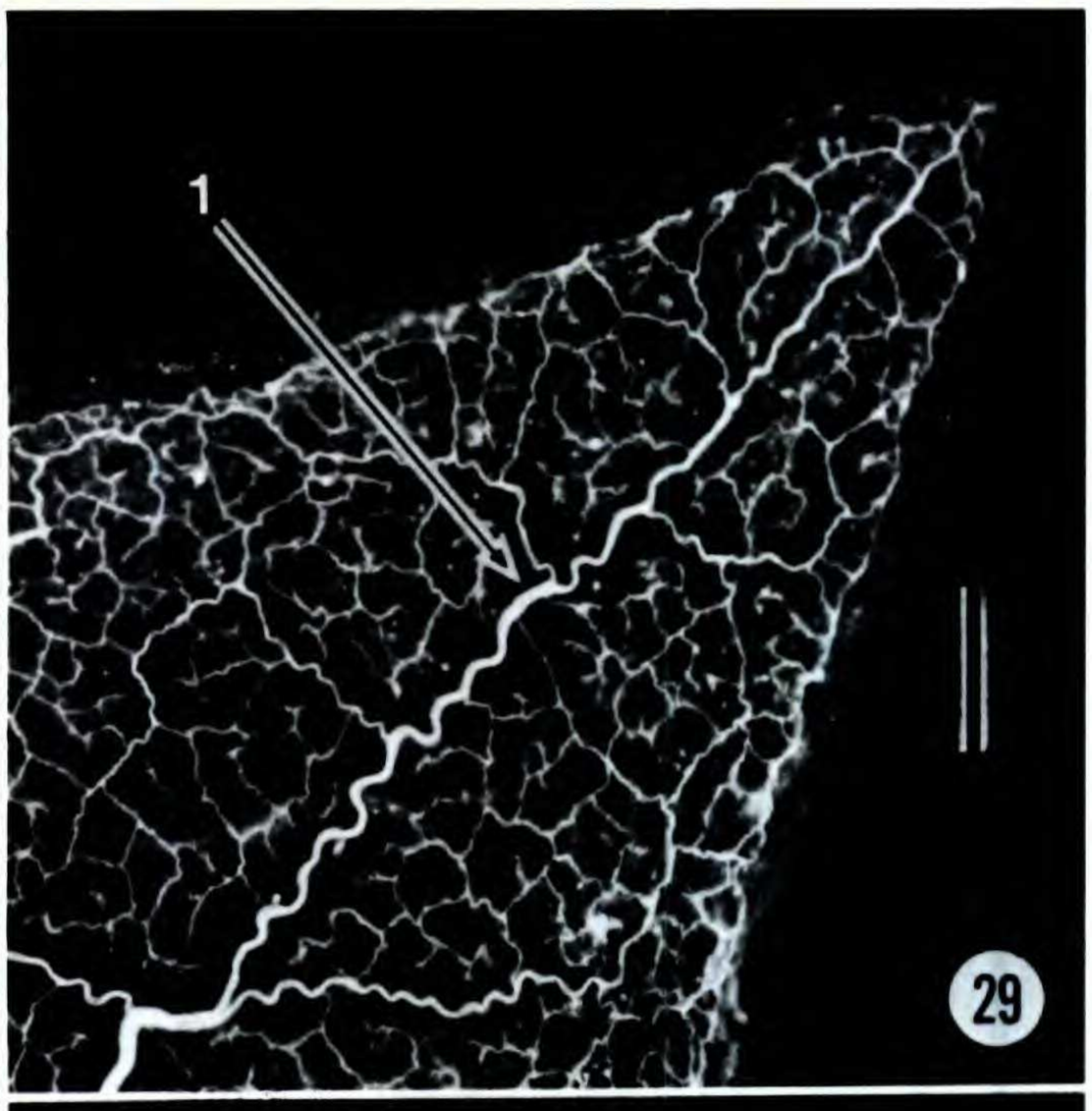


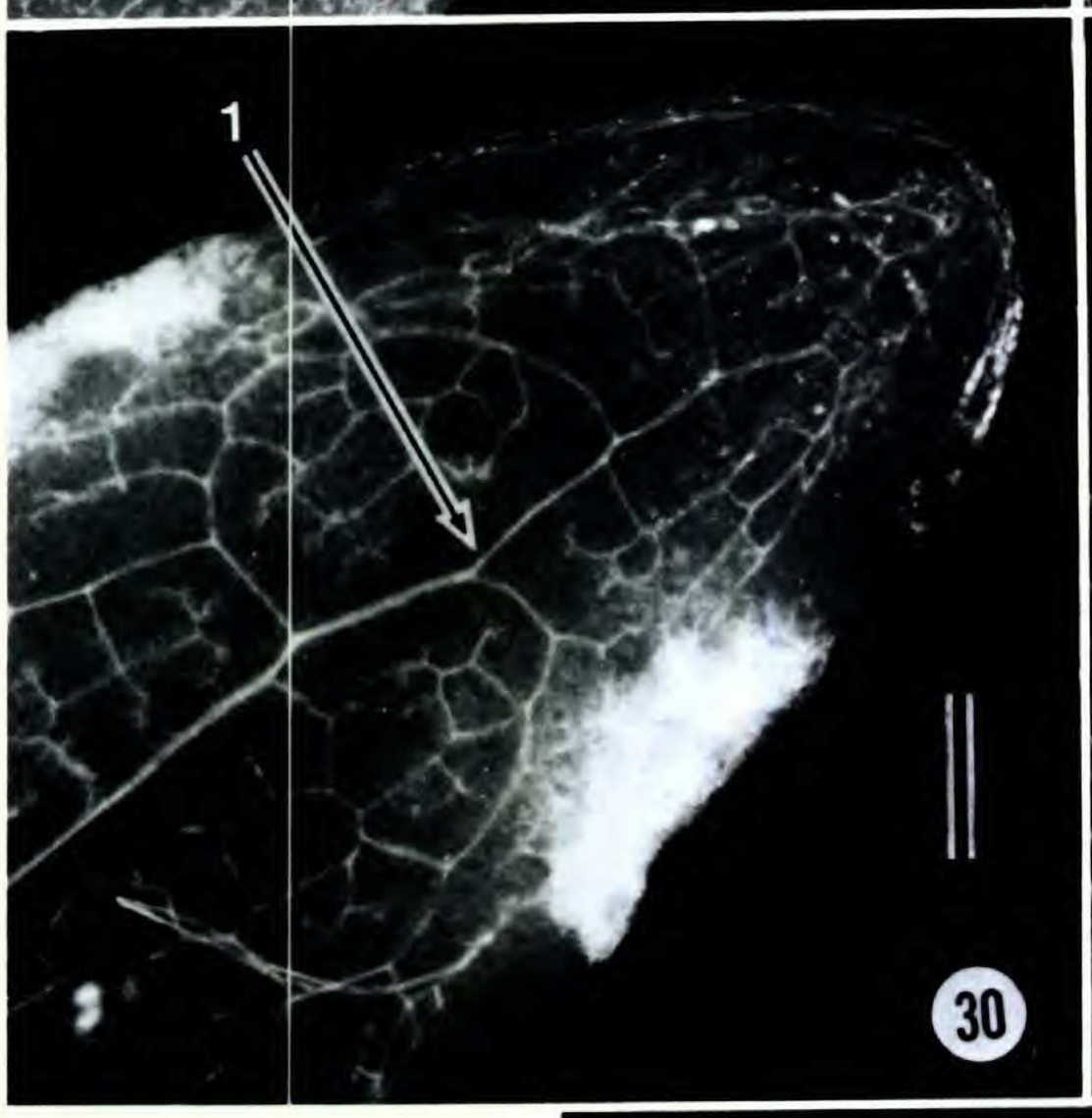


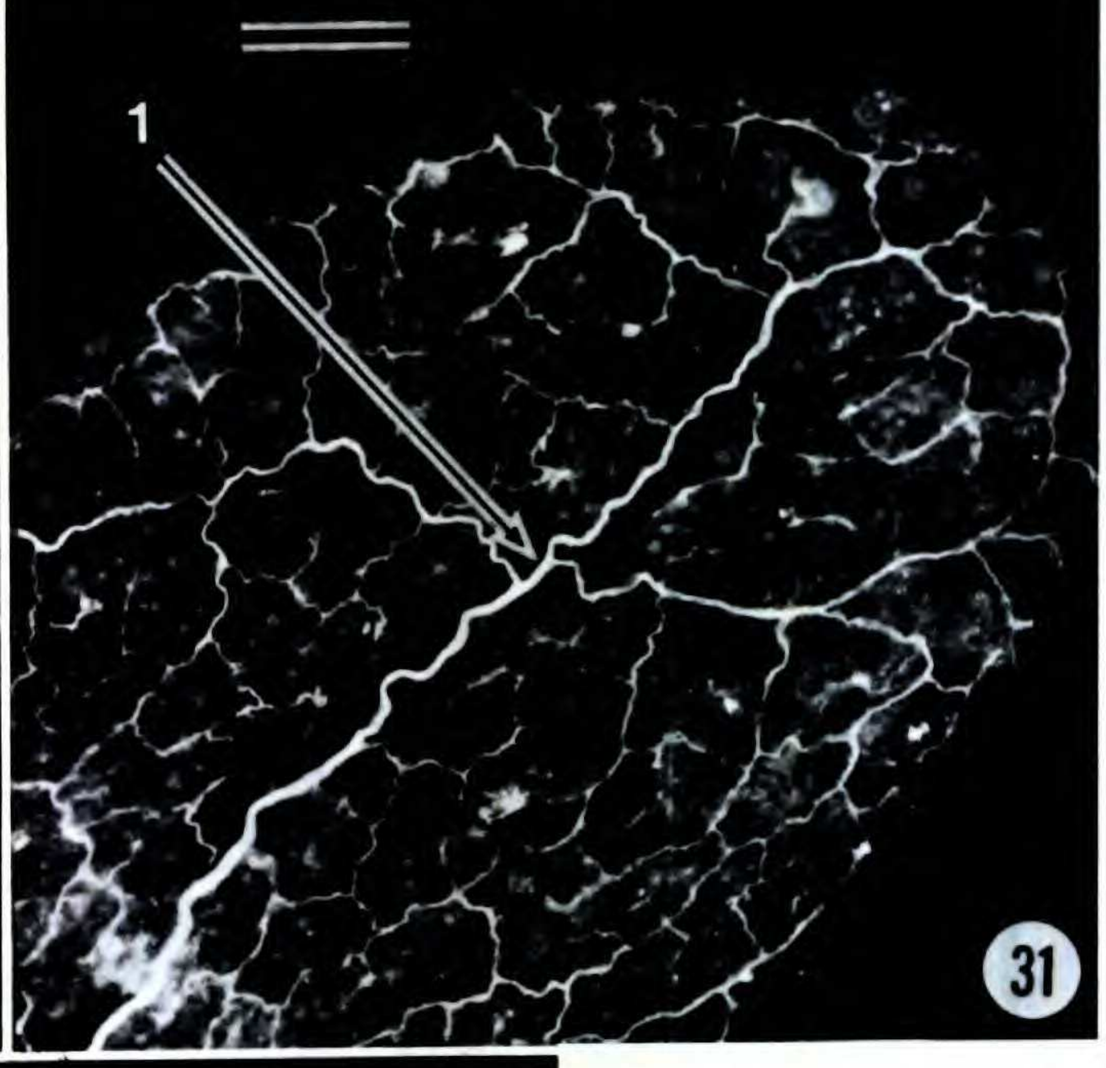


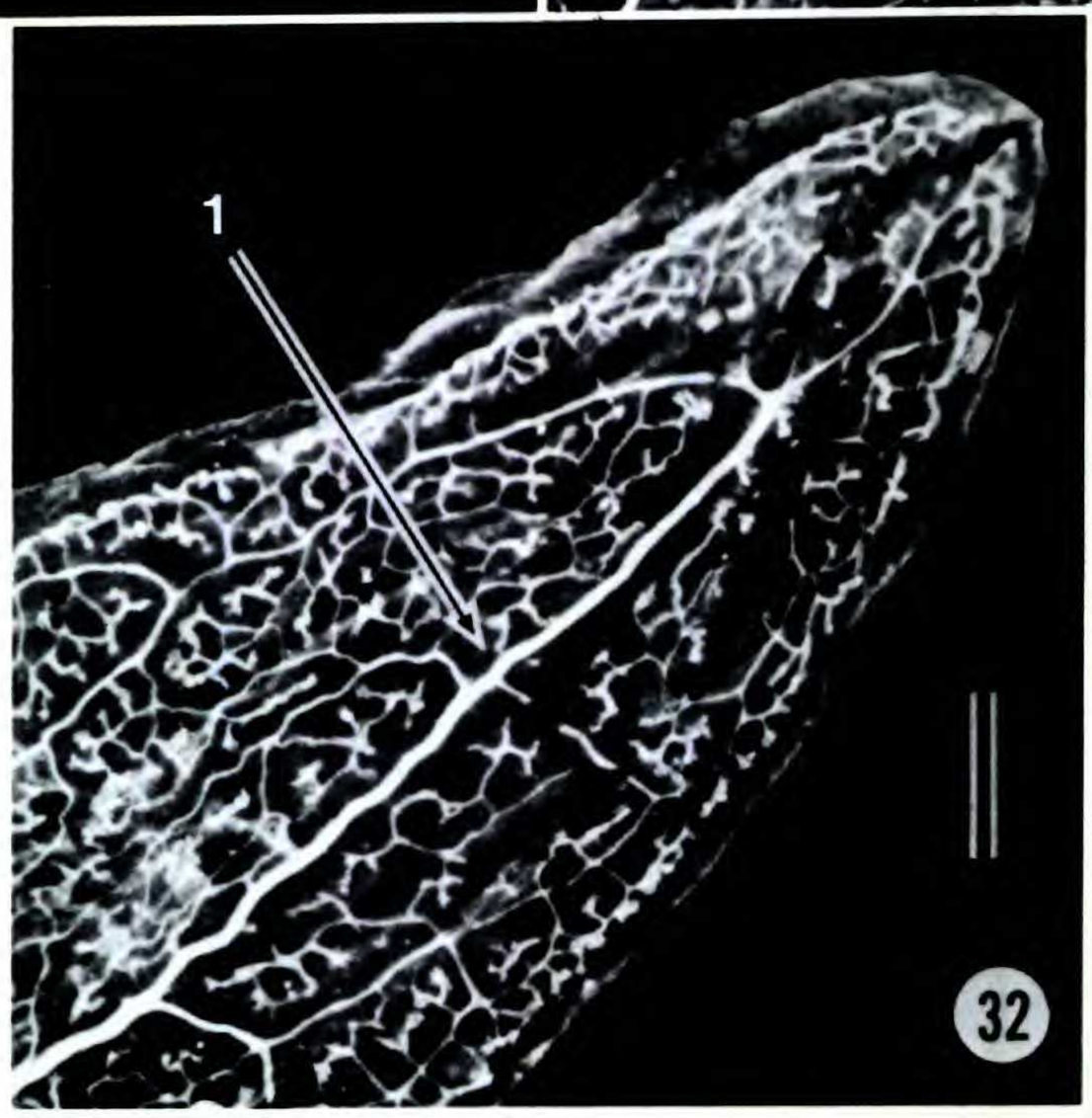
FIGURES 22–27. Cleared leaf apices of *Cistanthe* sect. *Cistanthe*.—22. *C. paniculata*.—23. *C. longiscapa*.—24. *C. guadalupensis*.—25. *C. picta* var. *picta*.—26. *C. coquimbensis*.—27. *C. grandiflora* (*Morrison et al. 16872*). Scale bars are (mm) ca. 2.7, 1.2, 1.7, 0.8, 0.8, and 0.8, respectively.



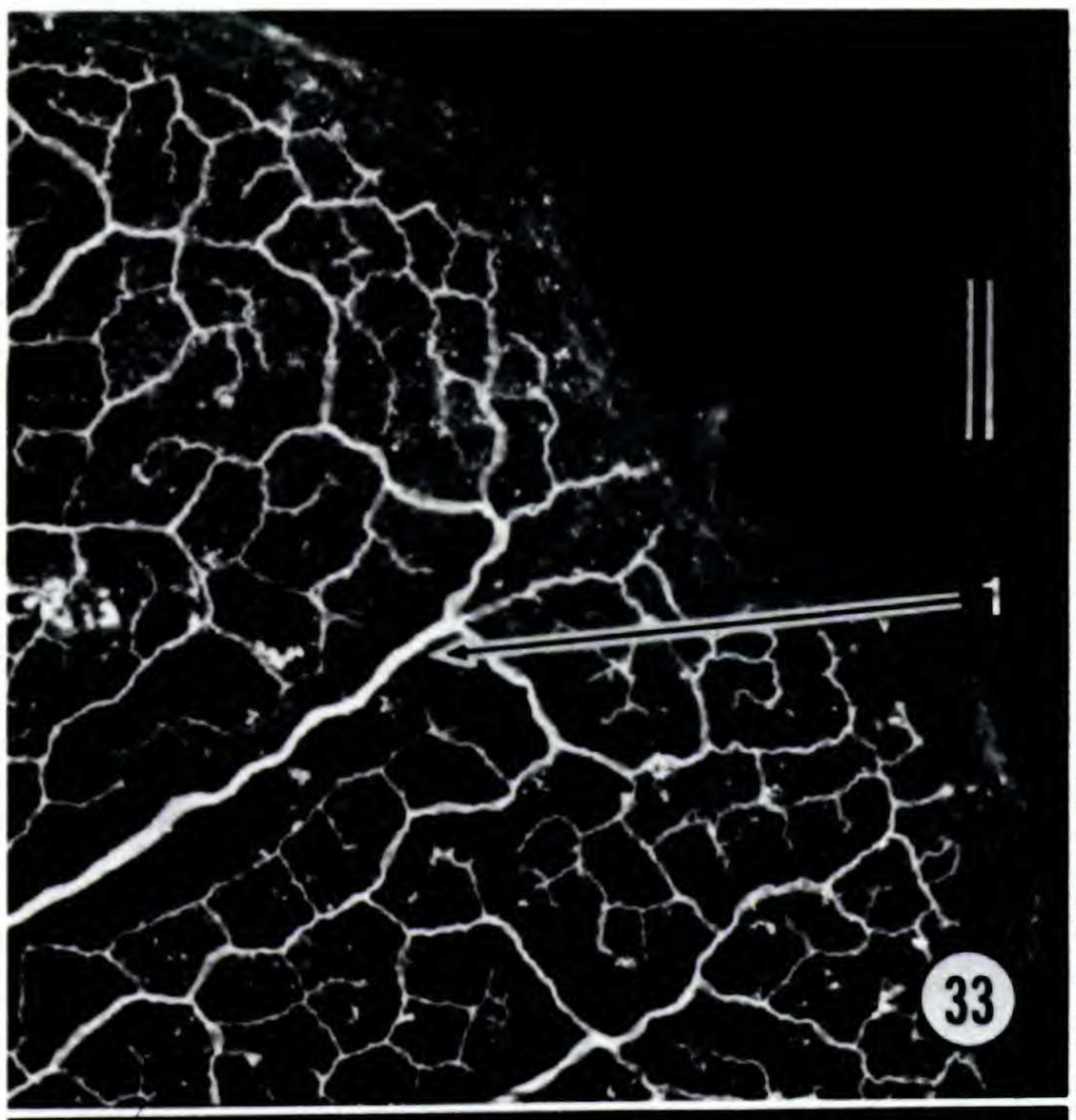


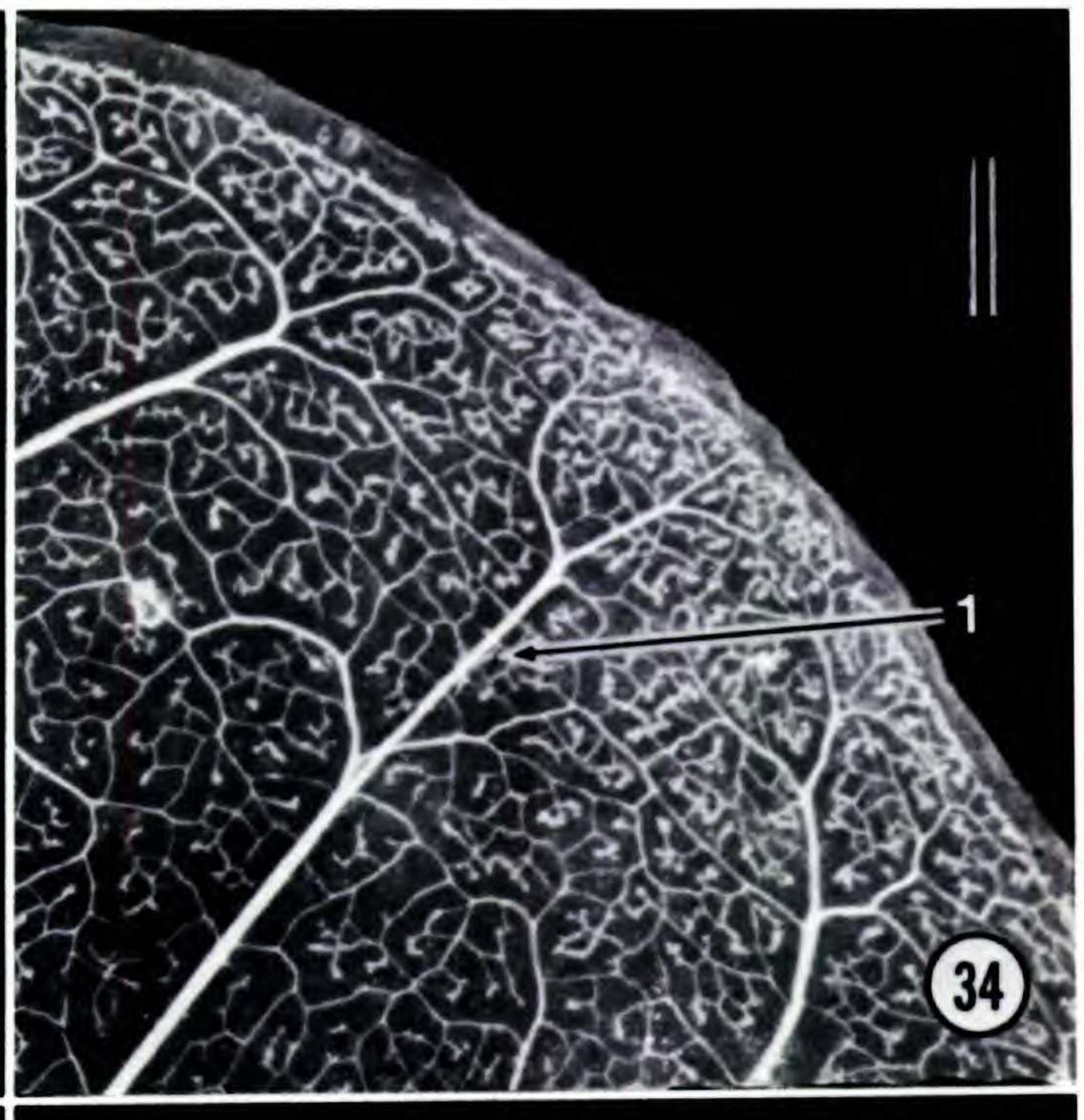


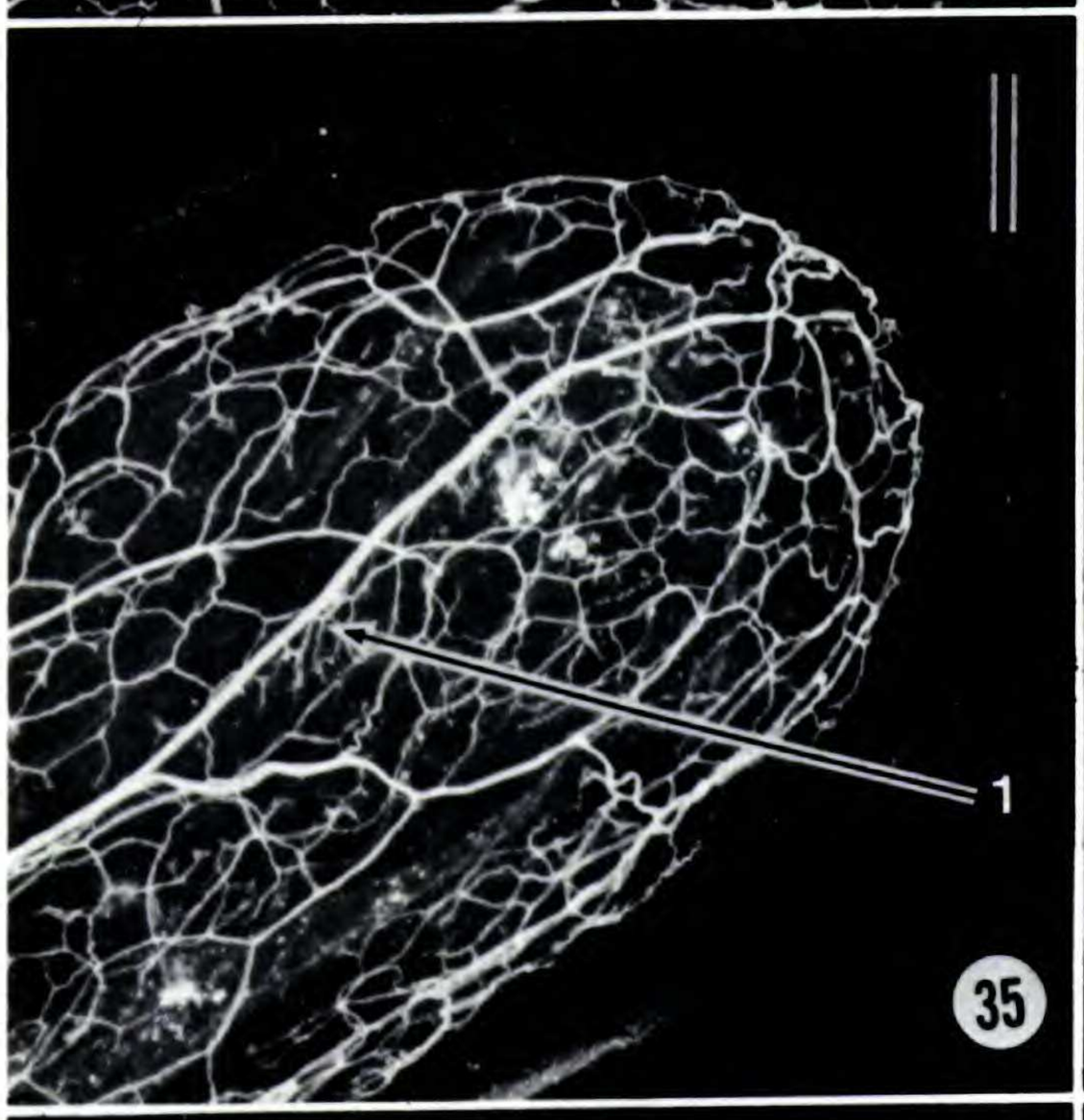


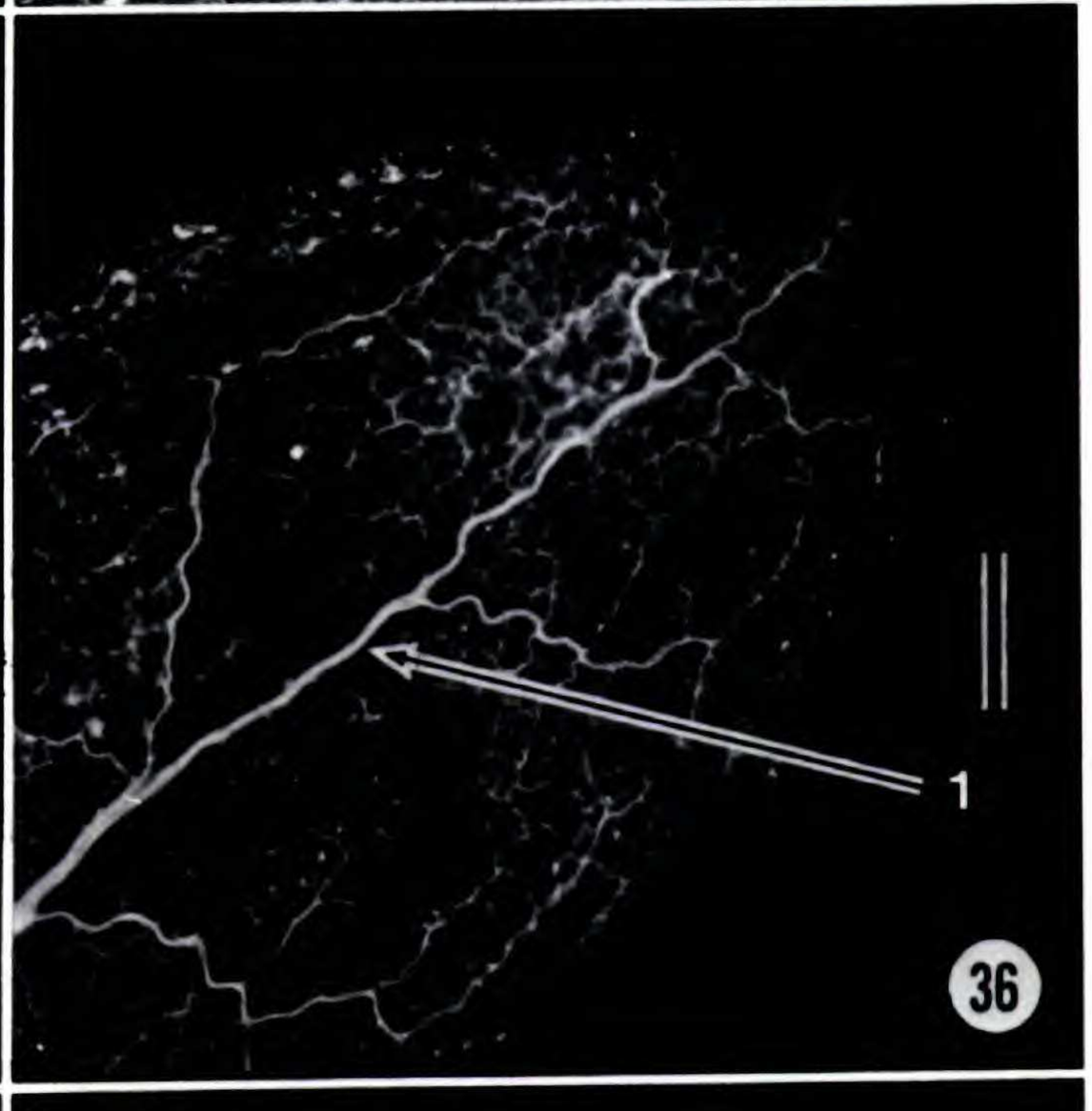


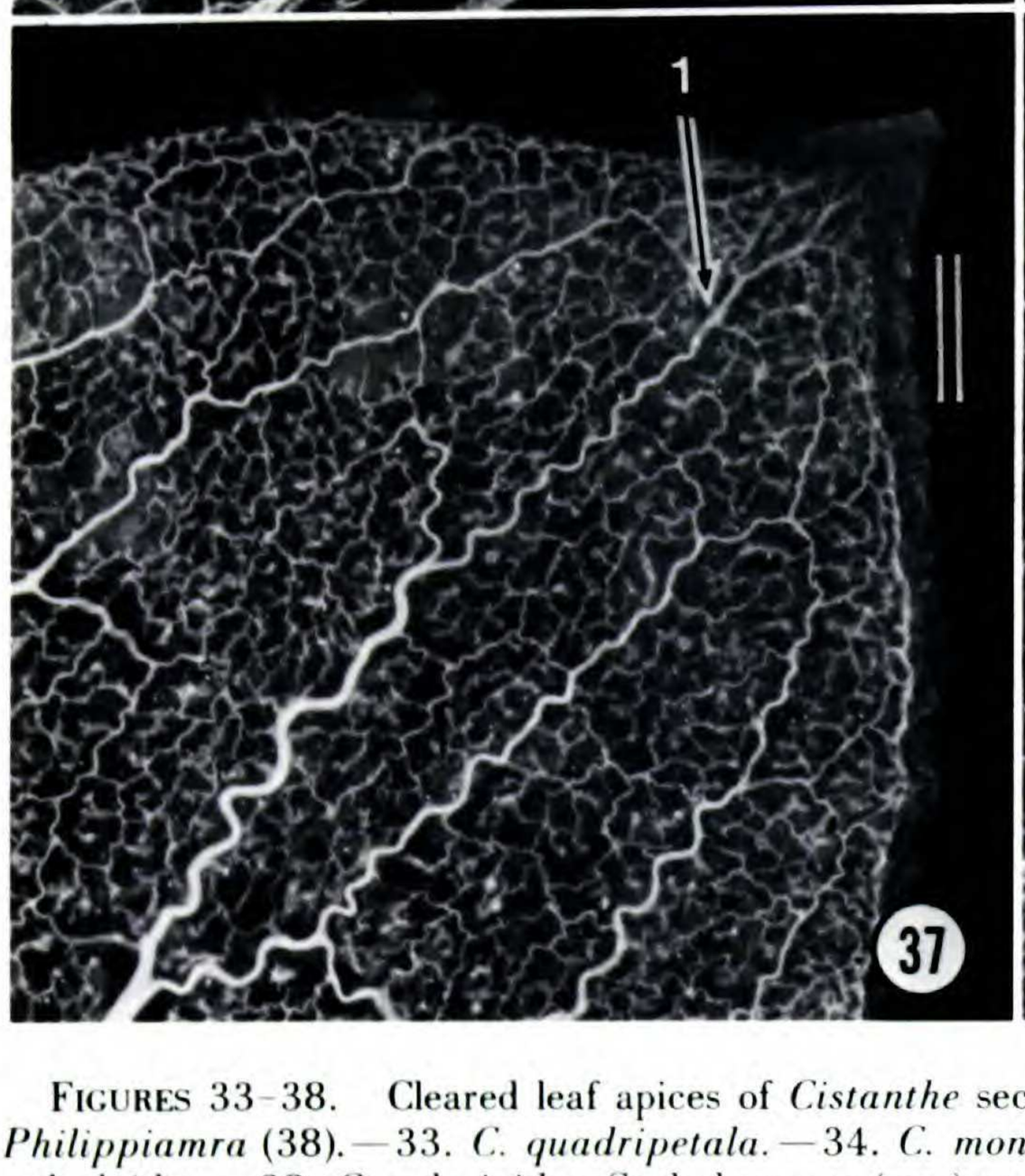
FIGURES 28–32. Cleared leaf apices of *Cistanthe* sect. *Cistanthe*.—28. *C. weberbaueri*.—29. *C.* sp. cf. *arenaria*.—30. *C. lingulata*.—31. *C.* sp. (*Zollner 9807*).—32. *C. fenzlii*. Scale bars are (mm) ca. 0.9, 0.6, 0.7, 0.8, and 0.4, respectively.

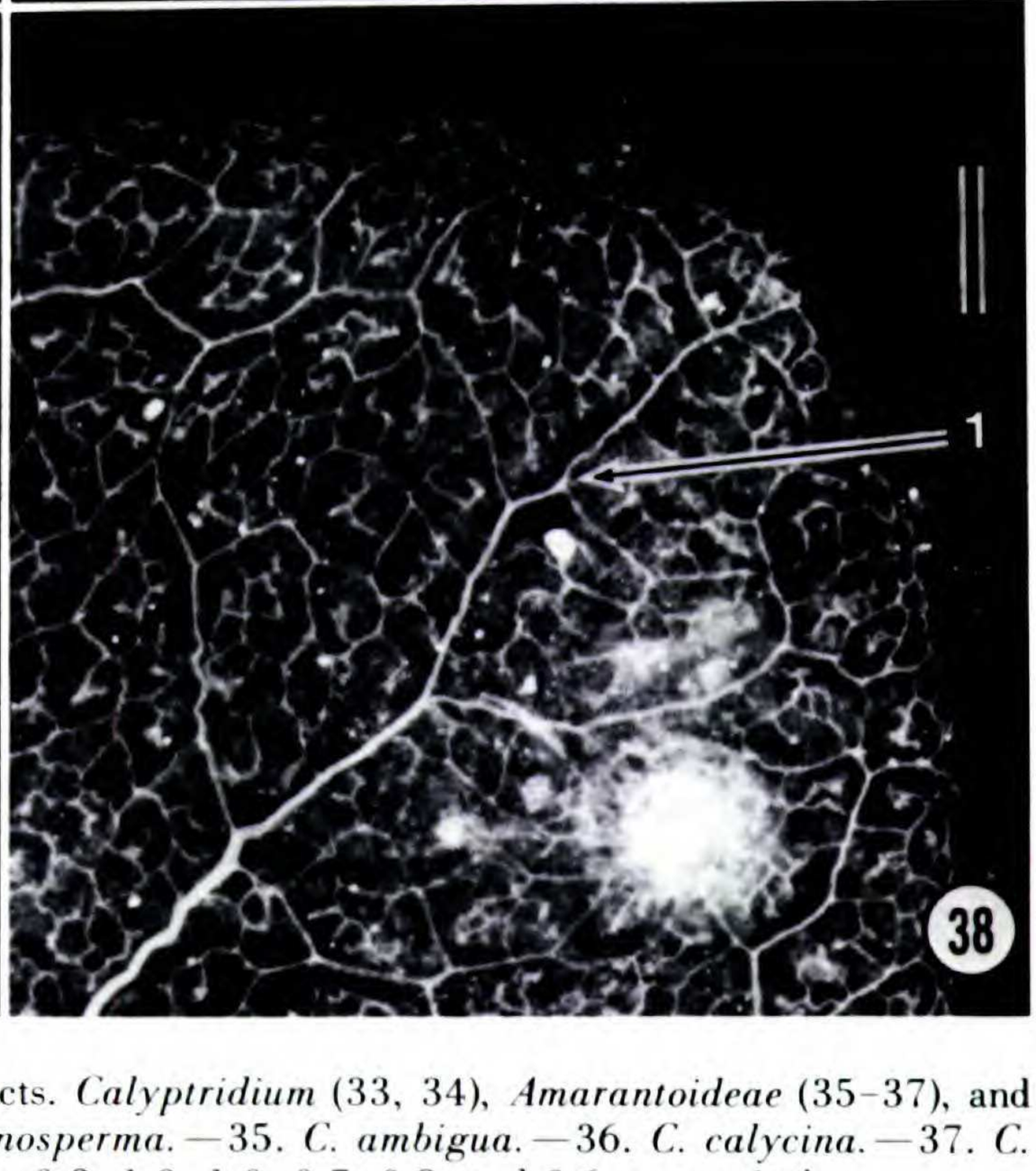




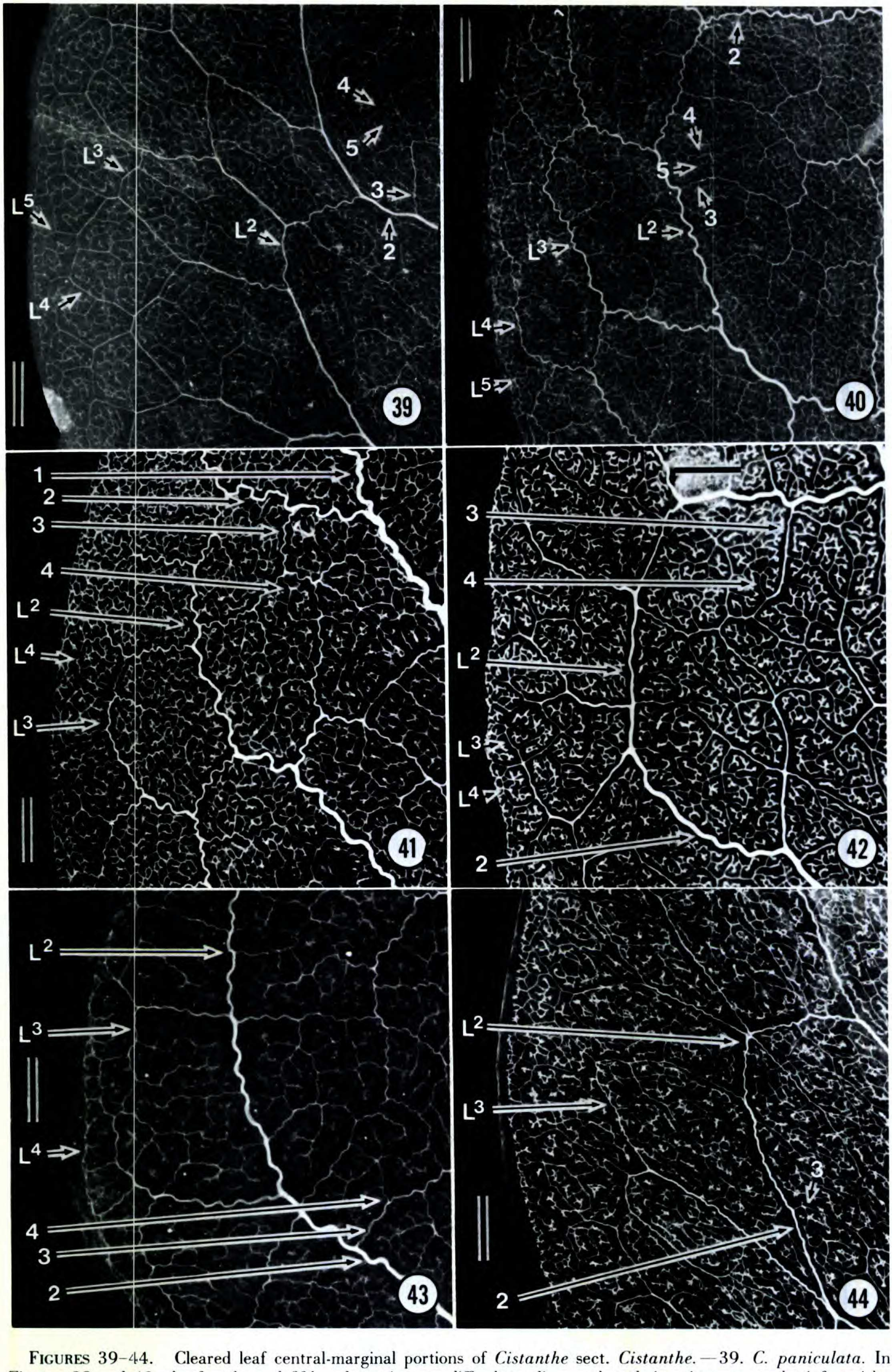




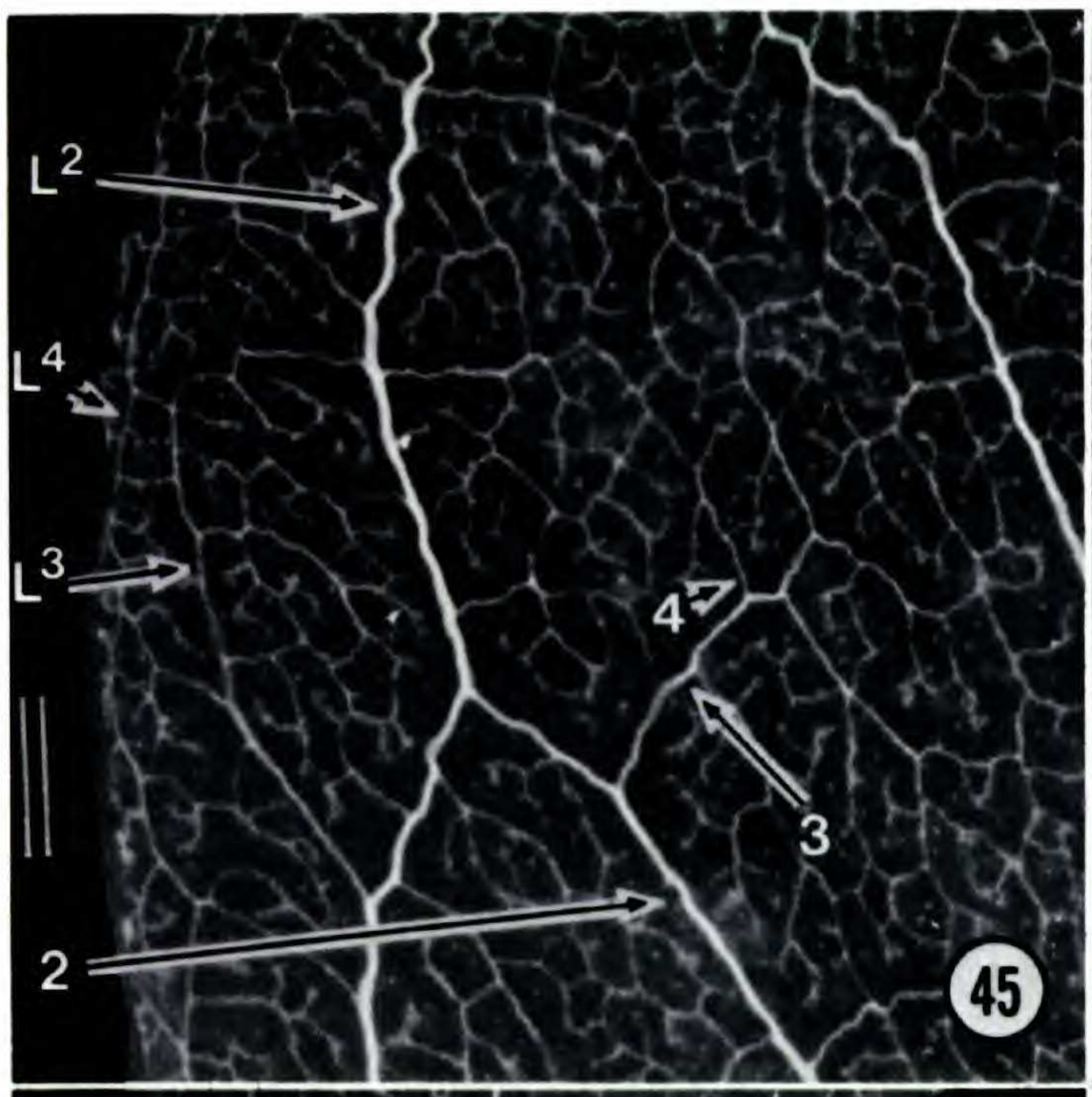


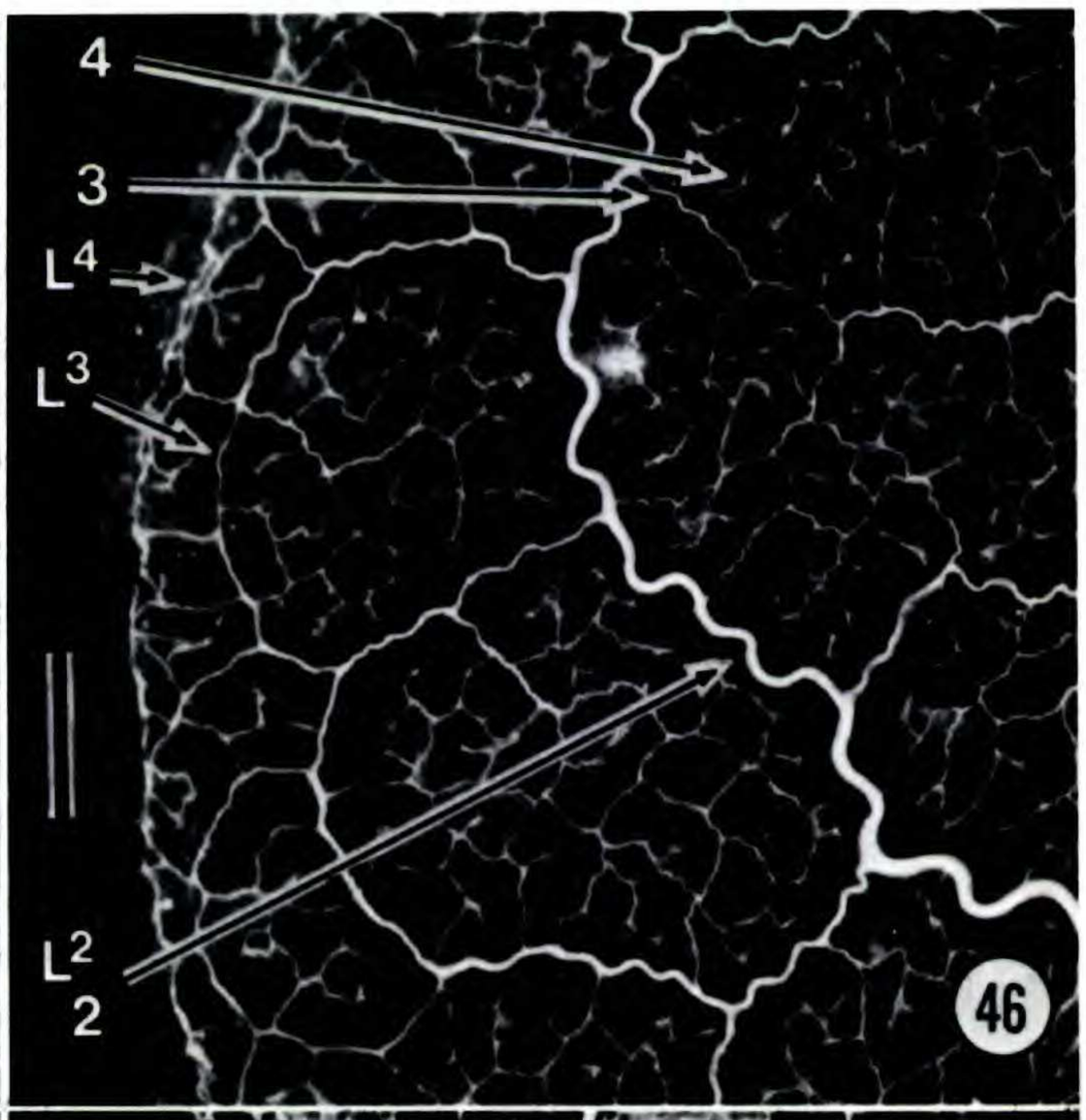


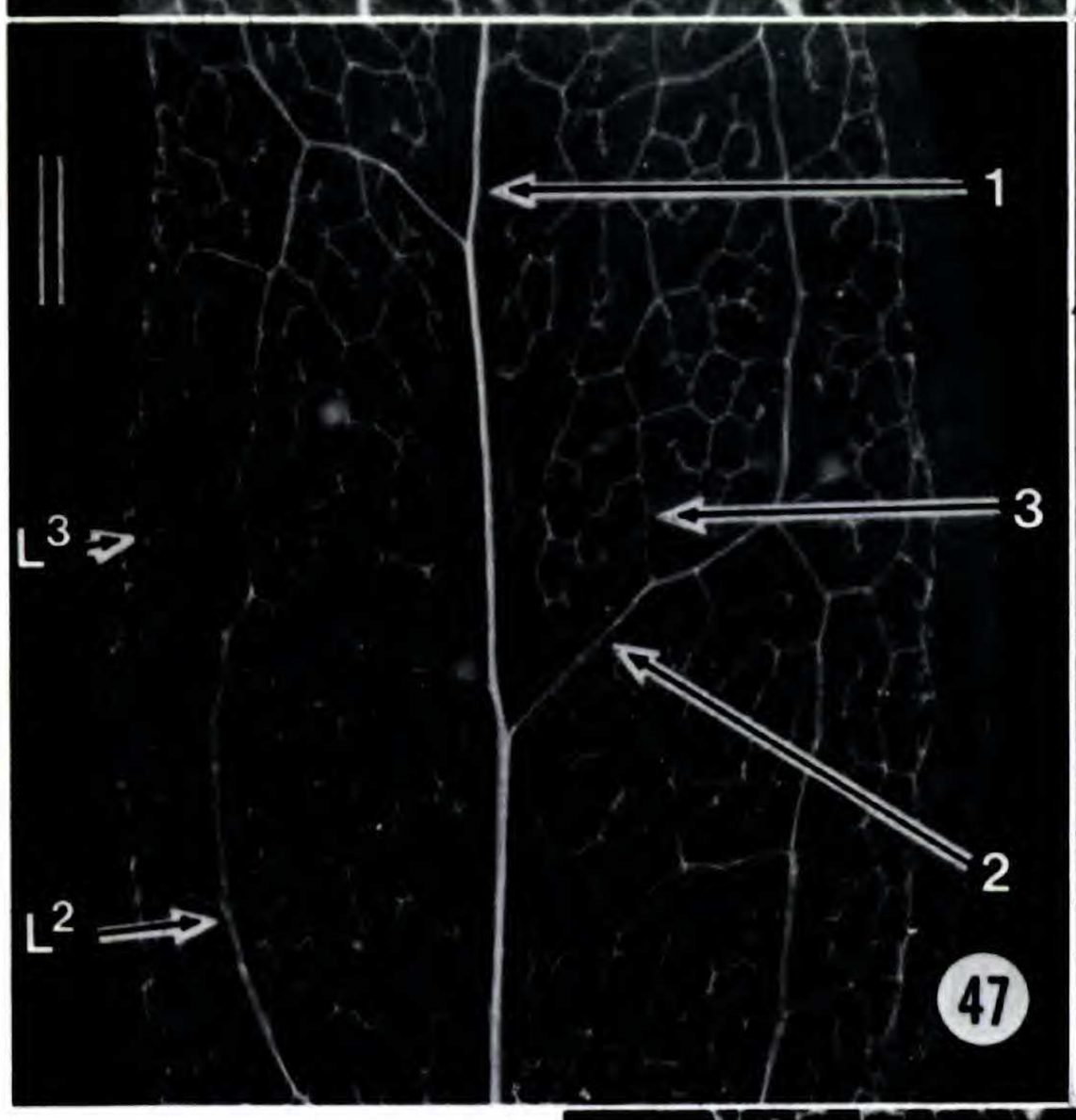
FIGURES 33–38. Cleared leaf apices of *Cistanthe* sects. *Calyptridium* (33, 34), *Amarantoideae* (35–37), and *Philippiamra* (38).—33. *C. quadripetala*.—34. *C. monosperma*.—35. *C. ambigua*.—36. *C. calycina*.—37. *C. salsoloides*.—38. *C. celosioides*. Scale bars are (mm) ca. 0.9, 1.0, 1.0, 0.7, 0.8, and 0.6, respectively.

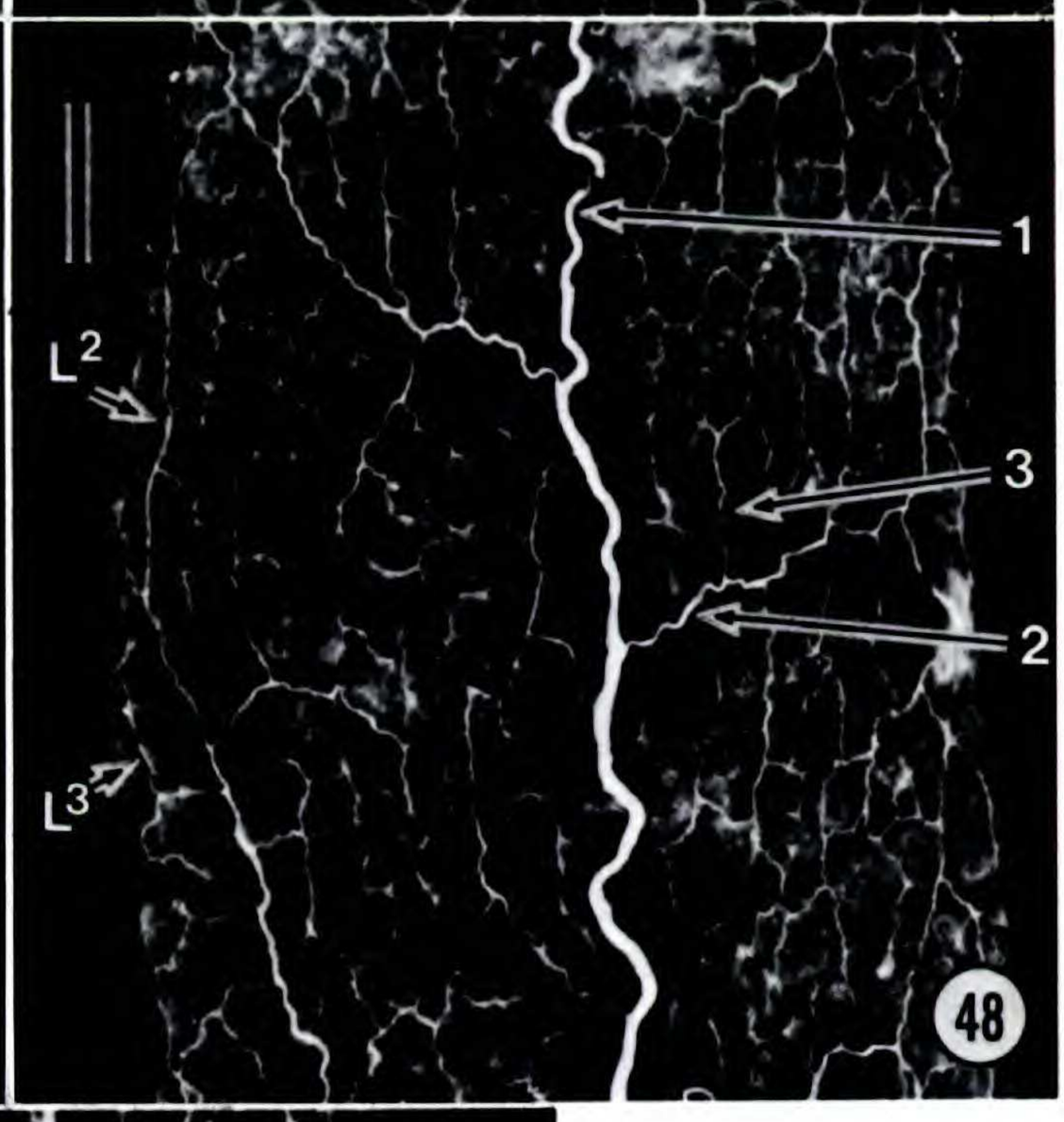


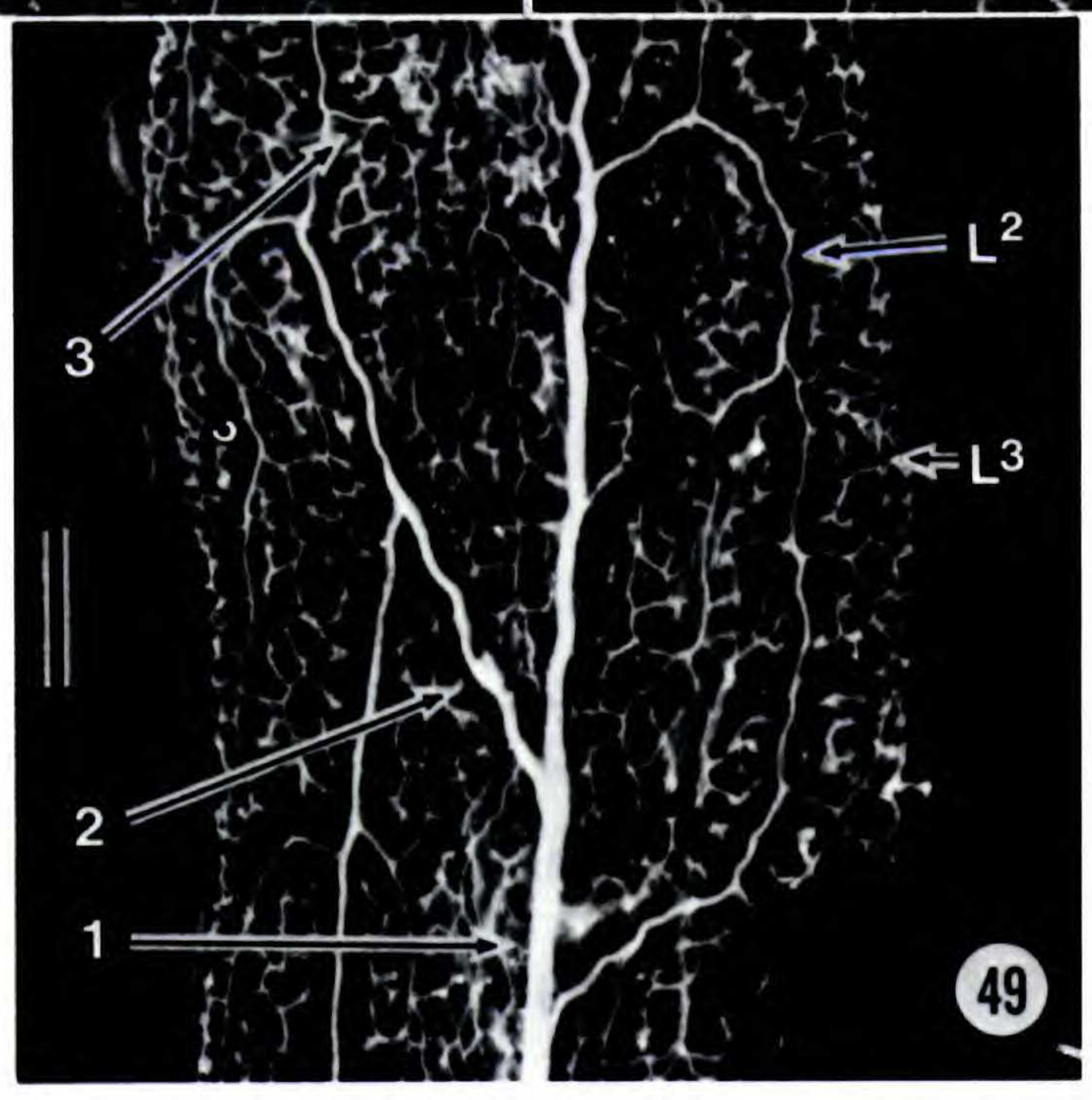
FIGURES 39–44. Cleared leaf central-marginal portions of *Cistanthe* sect. *Cistanthe*.—39. *C. paniculata*. In Figures 39 and 40, the fourth- and fifth-order veins are difficult to discern, but their existence can be inferred by extrapolation from the tertiary veins. The fourth-order veins form the reticulum adjacent to the tertiary veins, and the fifth-order veins traverse the areoles formed by the fourth-order veins and give rise to the free-ending veinlets.—40. *C. longiscapa*.—41. *C. guadalupensis*.—42. *C. picta* var. *picta*.—43. *C. coquimbensis*.—44. *C. grandiflora* (*Werdermann 405*). Scale bars are (mm) ca. 2.2, 1.4, 1.7, 0.9, 0.8, and 1.6, respectively.



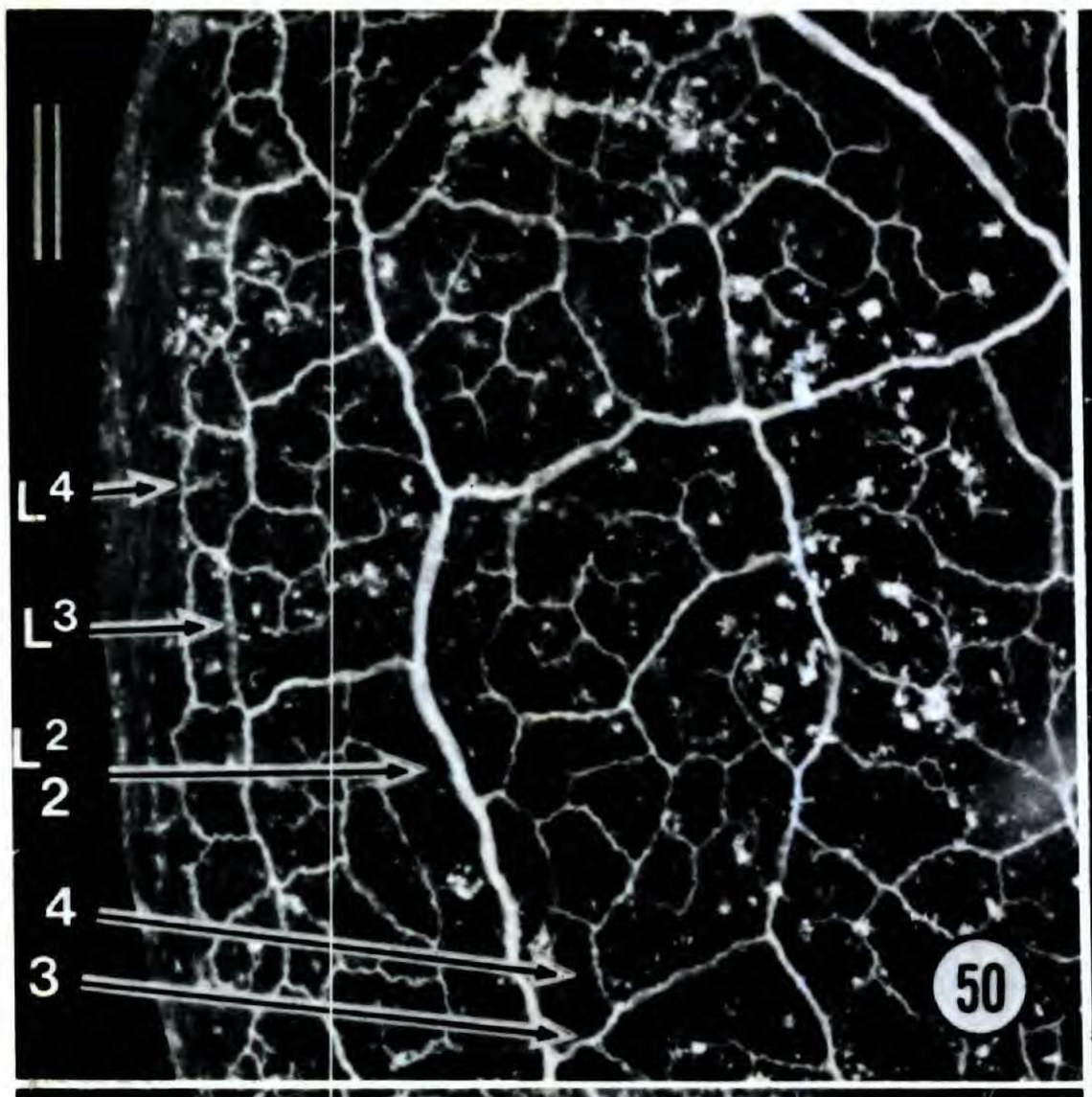


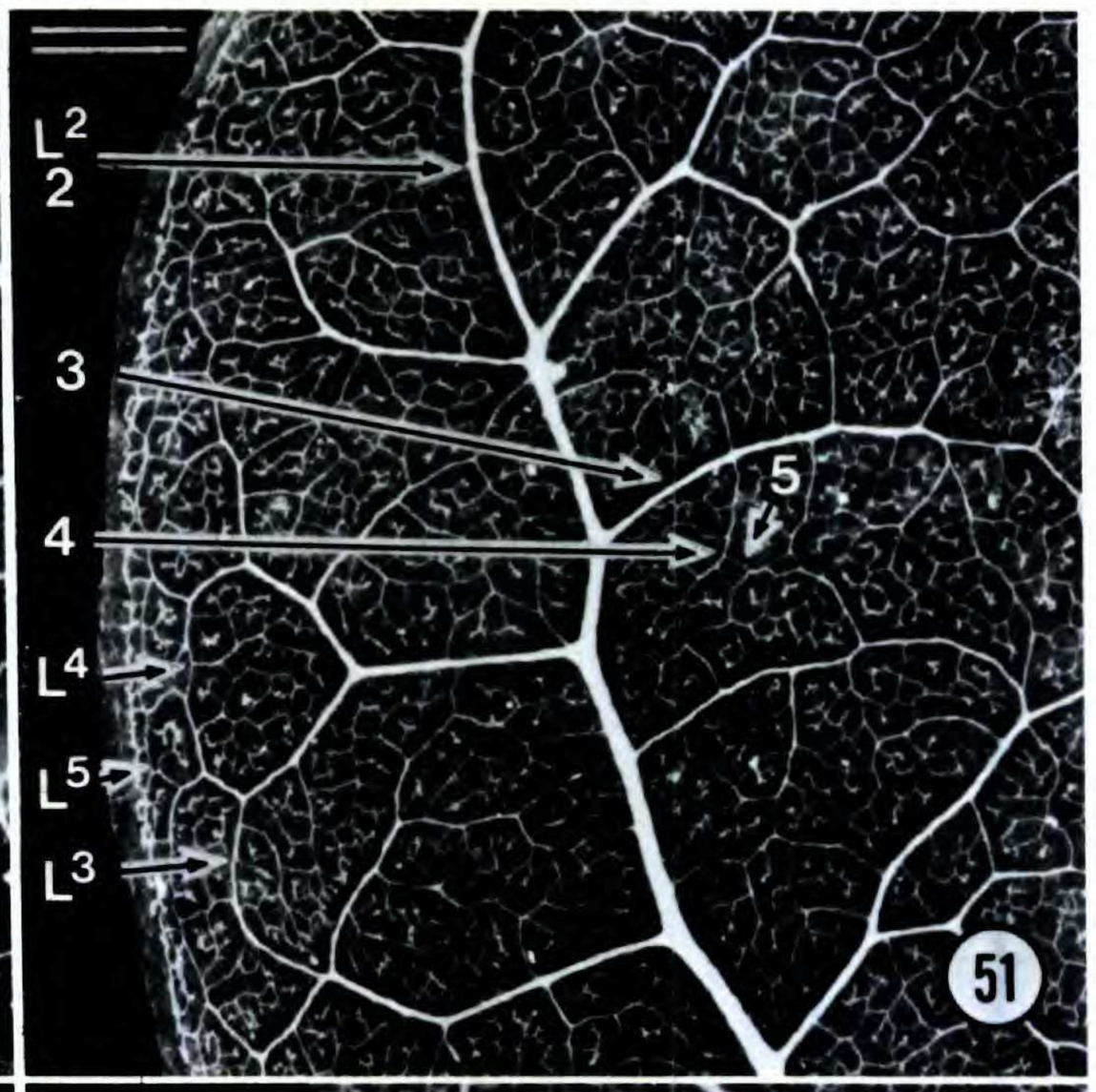


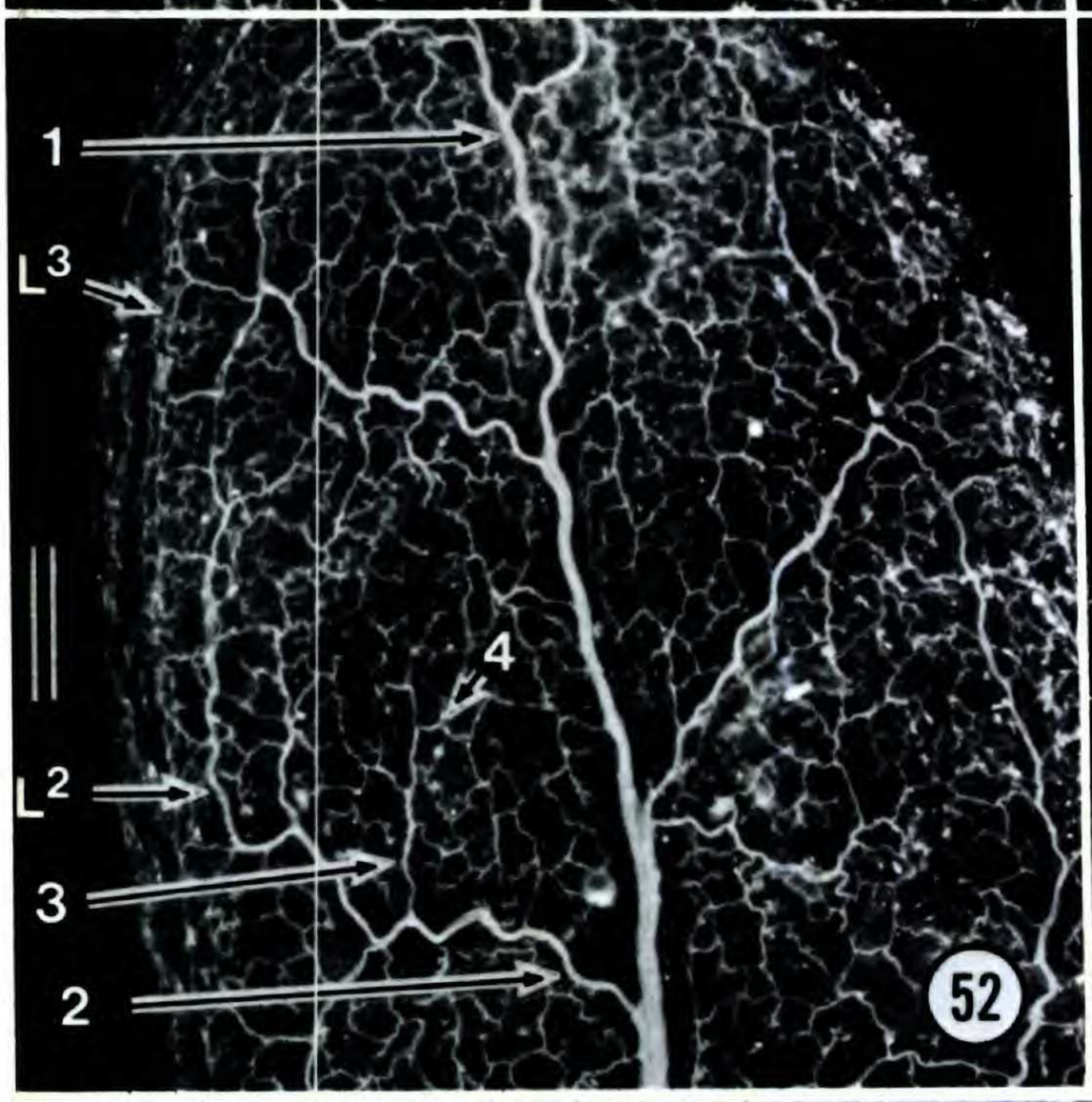


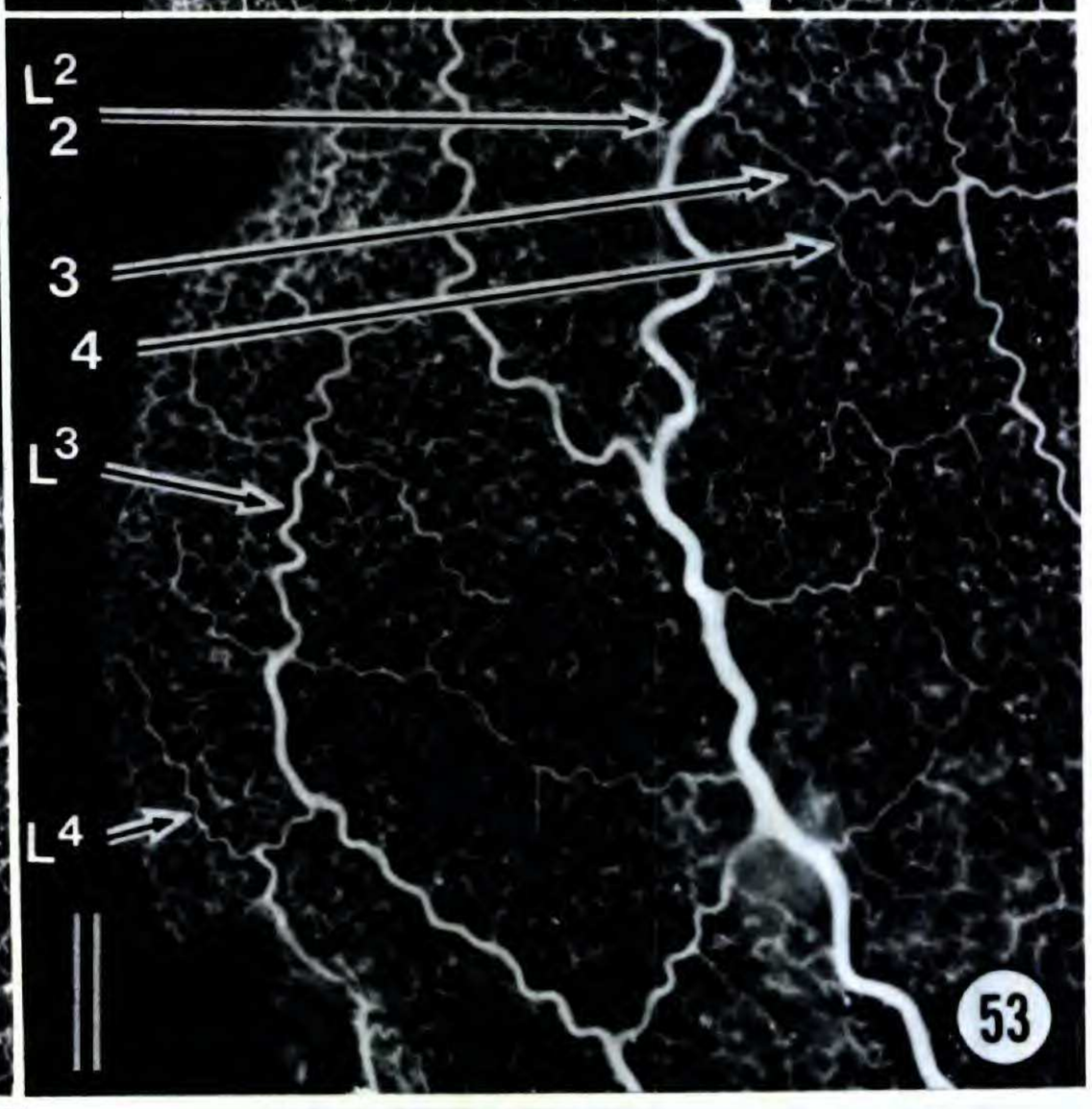


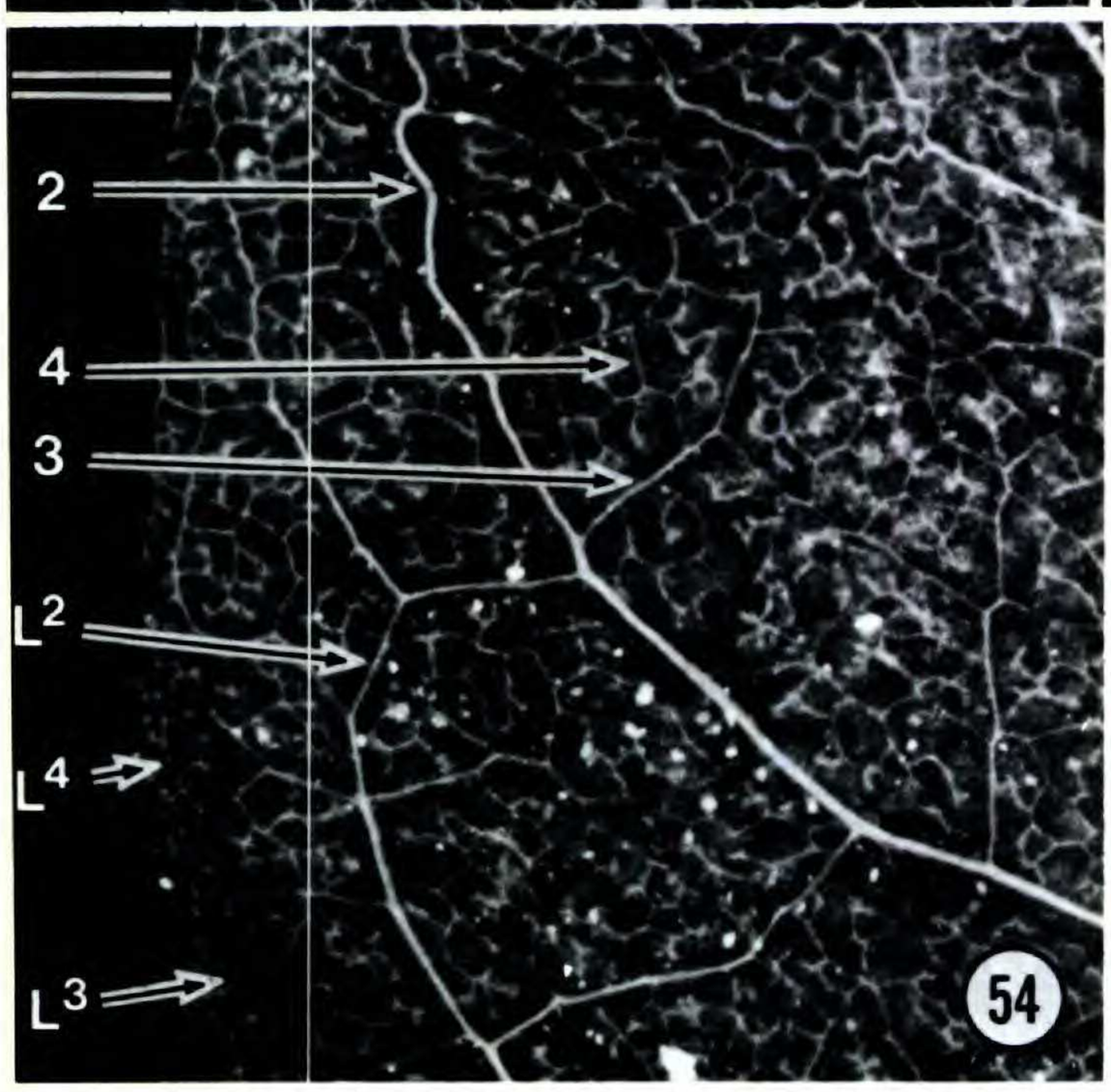
FIGURES 45–49. Cleared leaf central-marginal portions of *Cistanthe* sect. *Cistanthe*.—45. *C. weberbaueri*.—46. *C.* sp. cf. *arenaria*.—47. *C. lingulata*.—48. *C.* sp. (*Zollner 9807*).—49. *C. fenzlii*. Scale bars are (mm) ca. 0.7, 0.5, 1.1, 0.8, and 1.6, respectively.

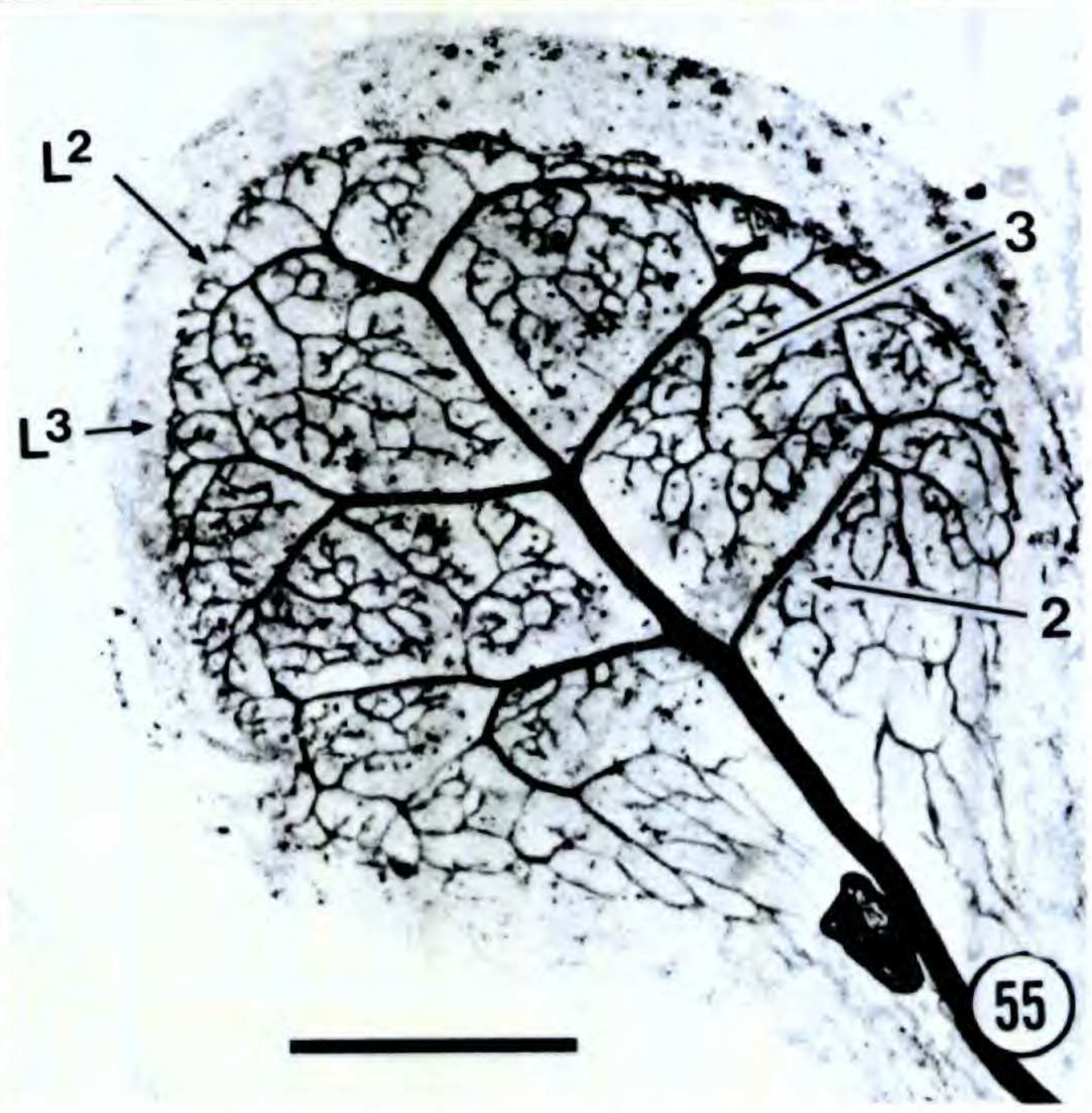




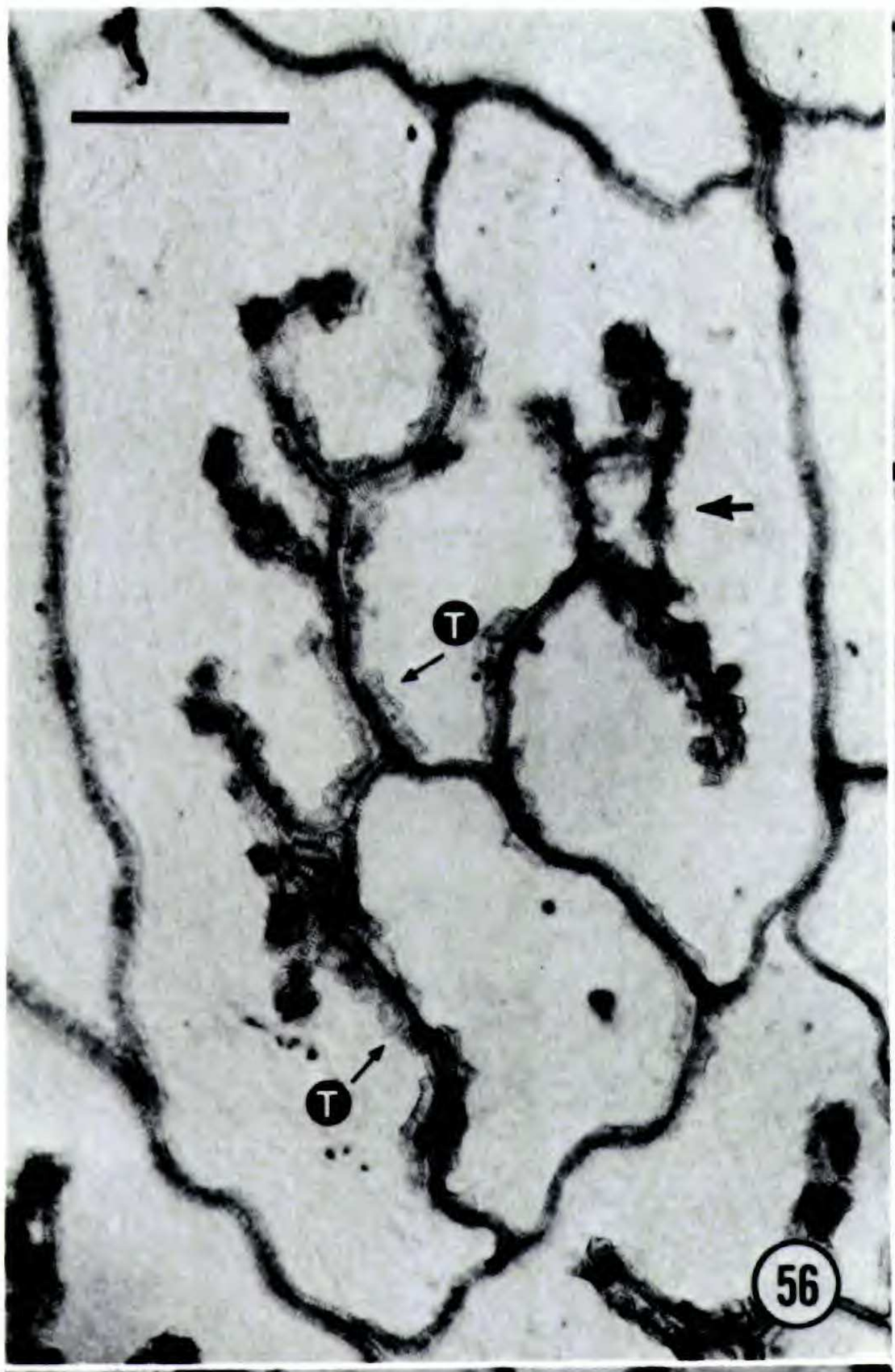


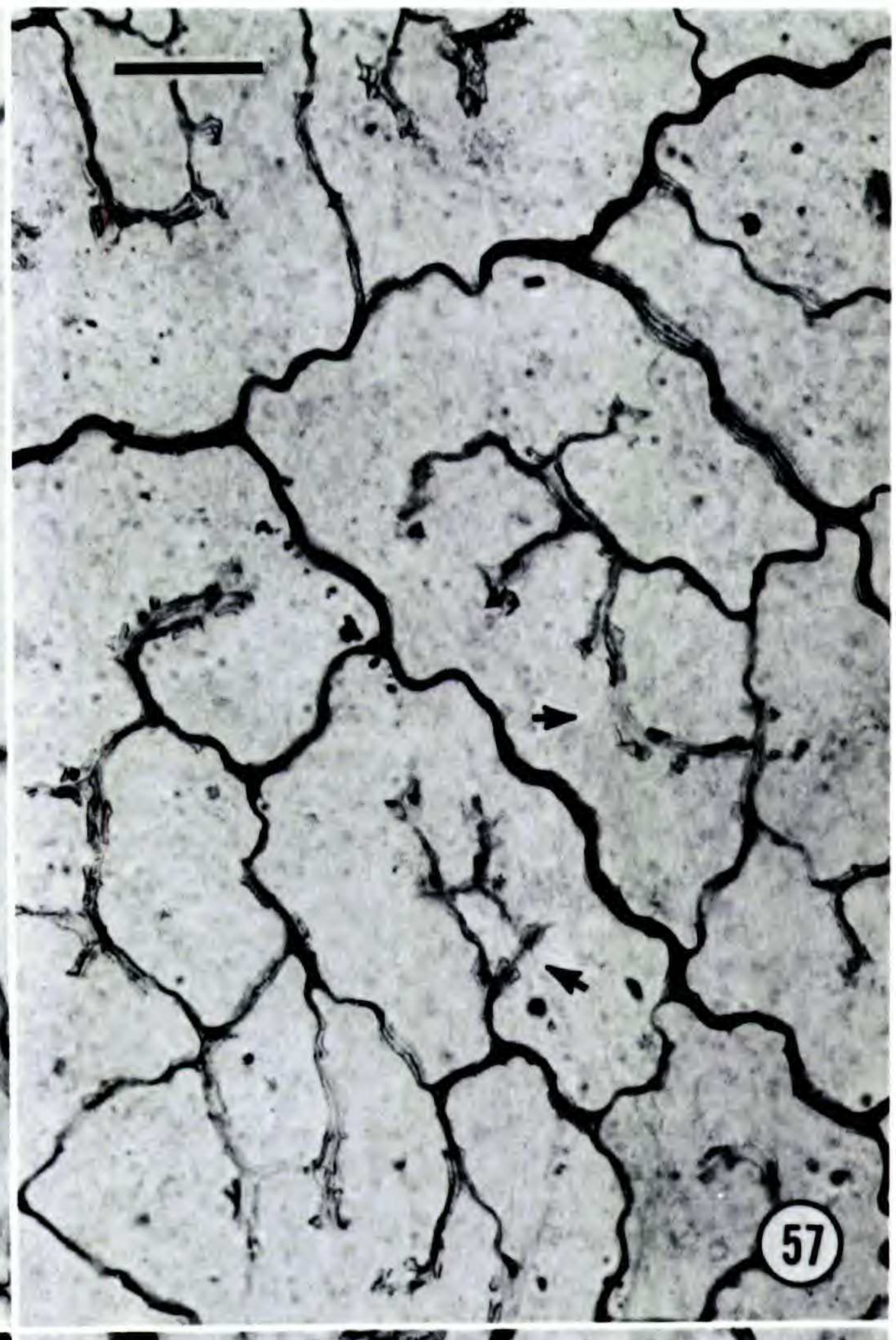


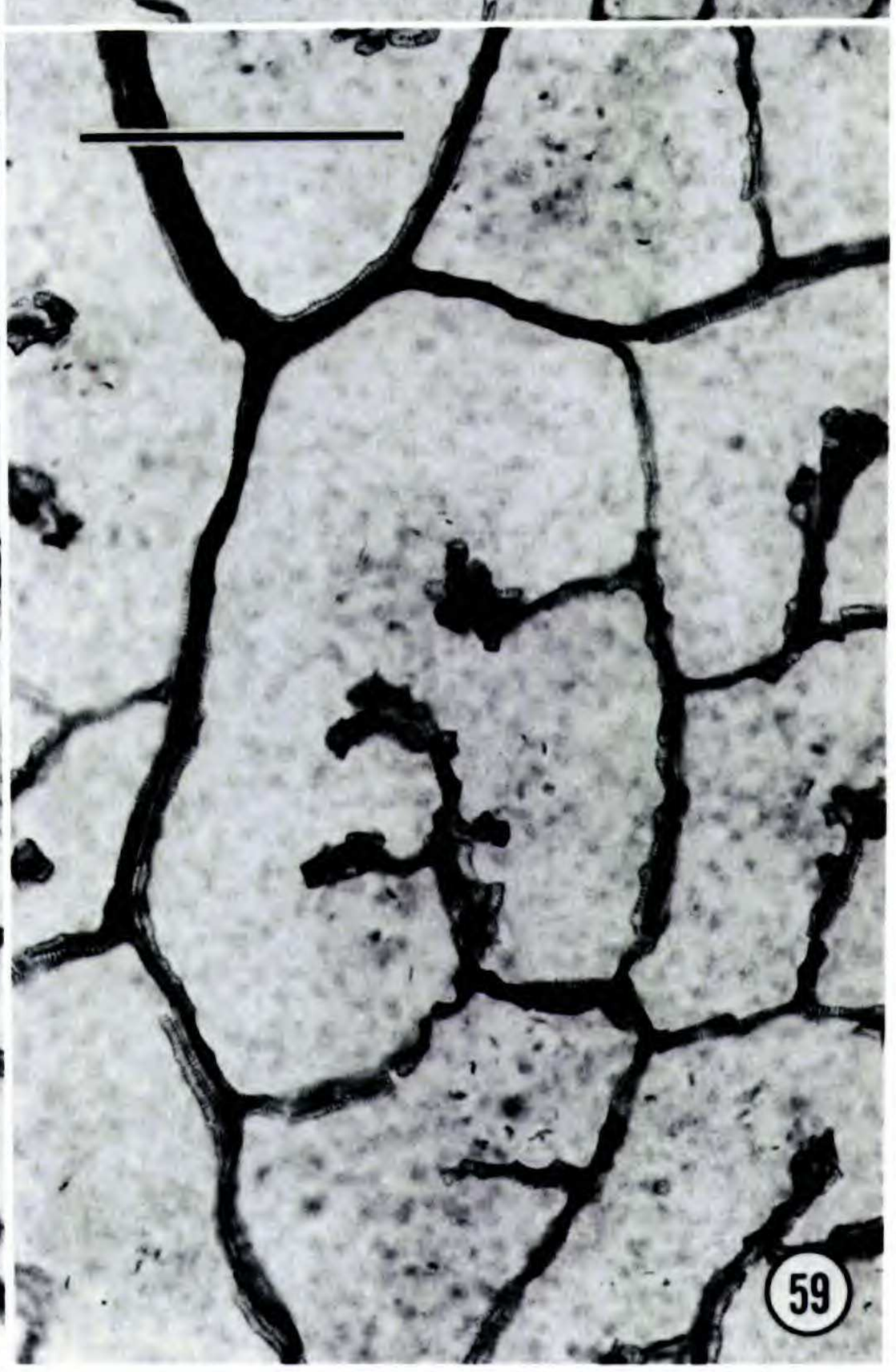




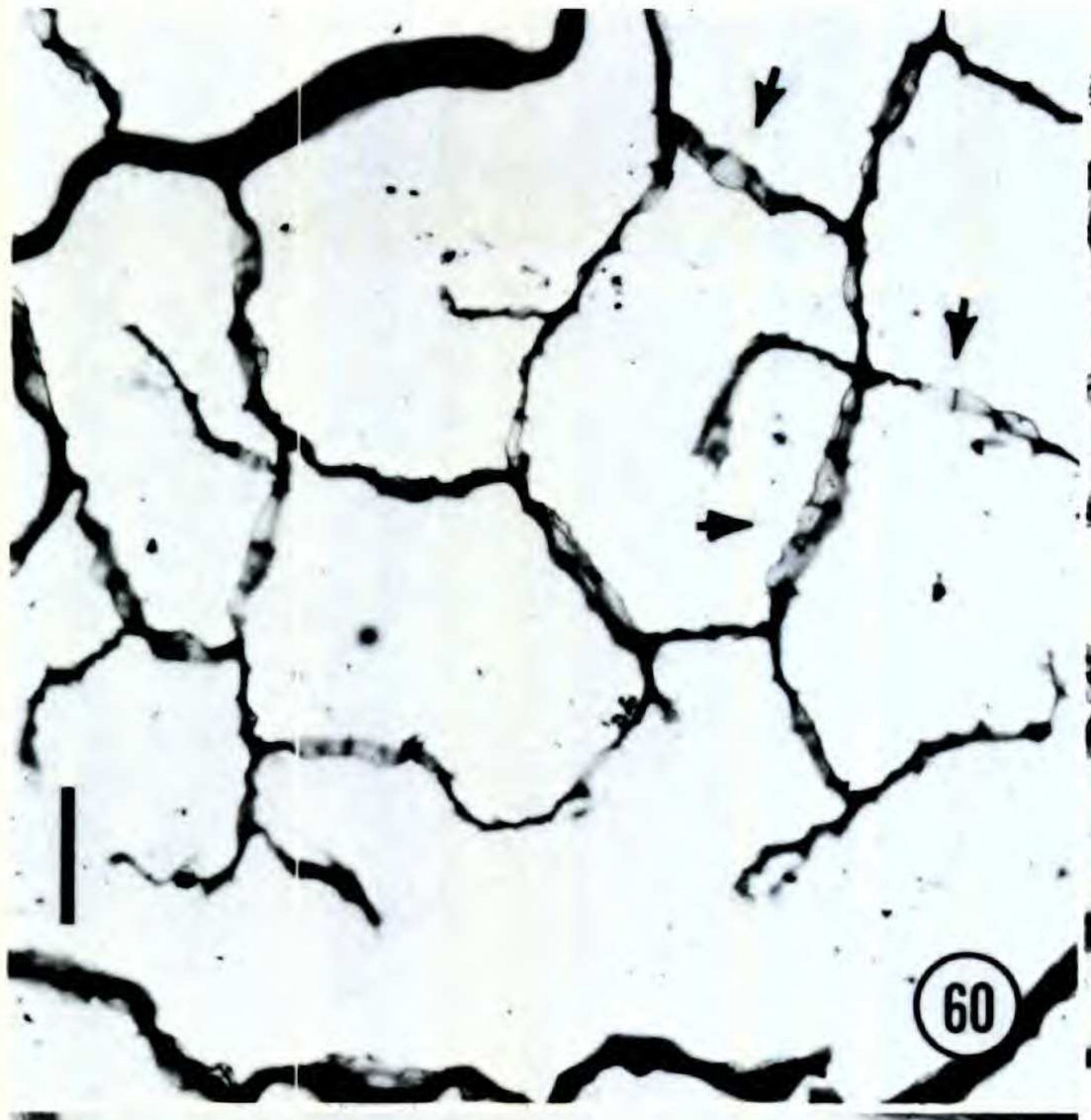
FIGURES 50–54. Cleared leaf central-marginal portions of *Cistanthe* sects. *Calyptridium* (50, 51), *Amarantoideae* (52, 53), and *Philippiamra* (54).—50. *C. quadripetala*.—51. *C. monosperma*.—52. *C. calycina*.—53. *C. salsoloides*.—54. *C. celosioides*. Scale bars are (mm) ca. 0.8, 1.5, 0.6, 0.8, and 0.6, respectively.—FIGURE 55. Cleared whole leaf of *Cistanthe* (*Cistanthe*) *picta* var. *frigida* (*Morrison et al. 16992*). Scale bar = ca. 1 mm.

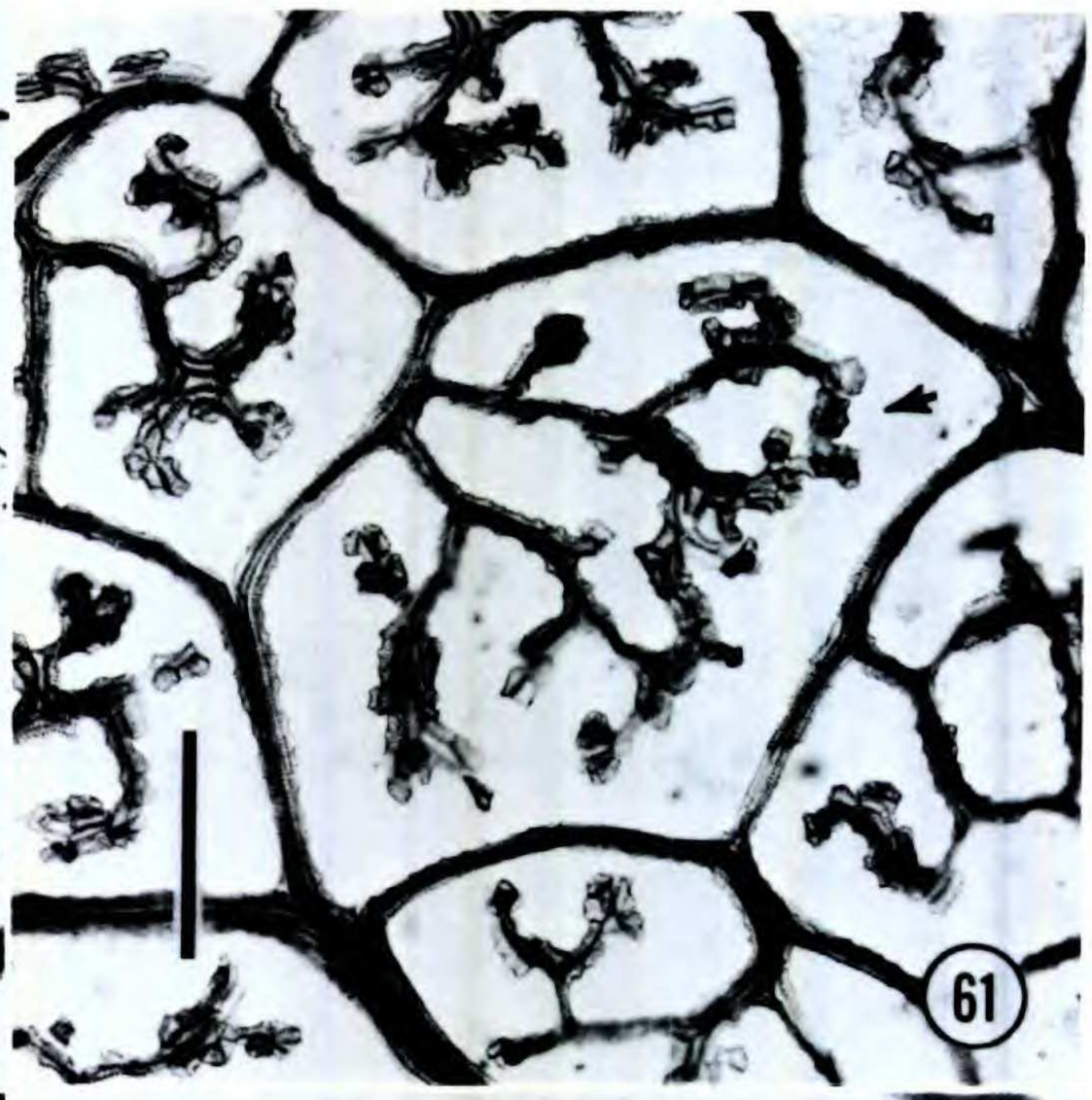


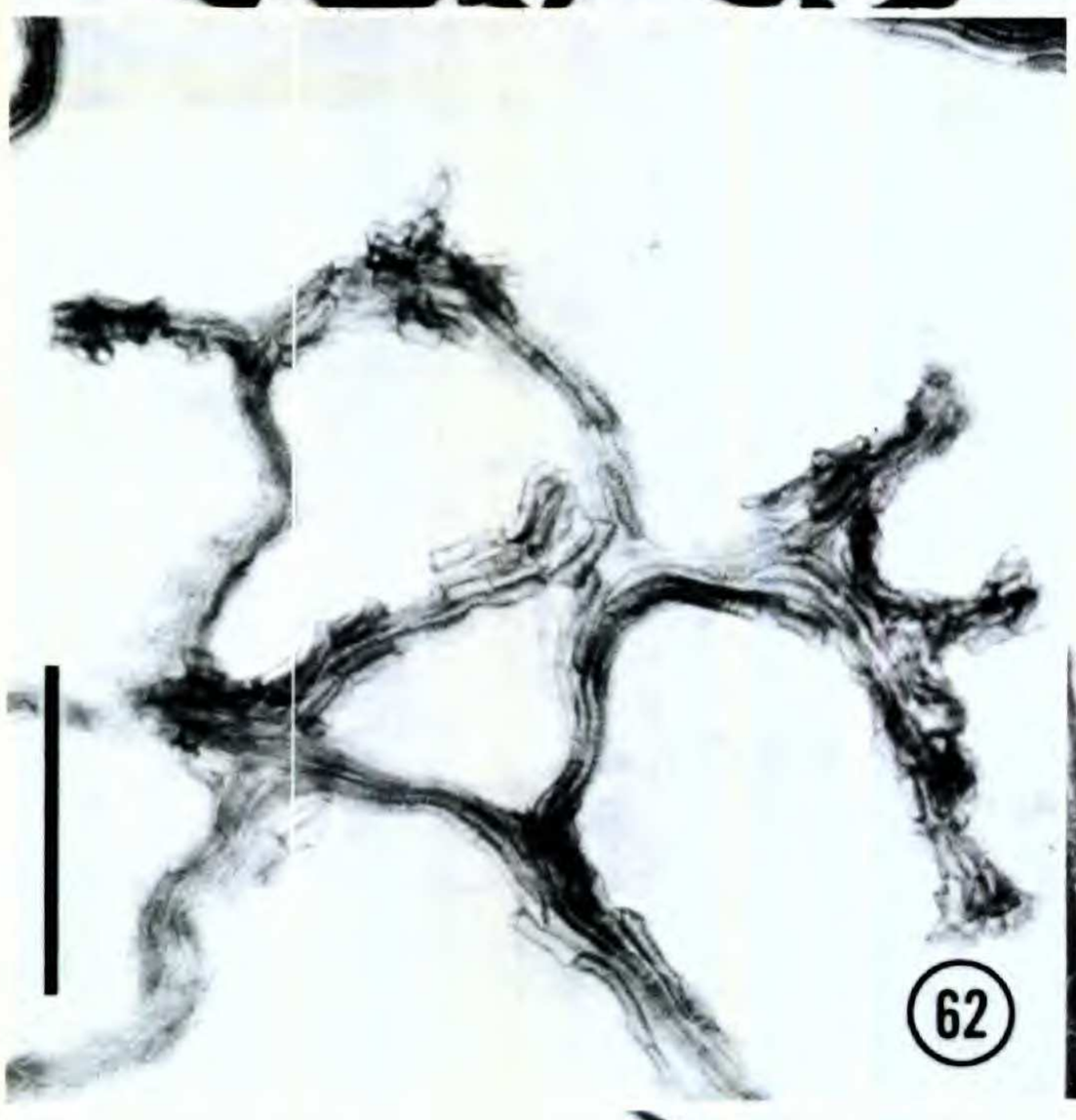


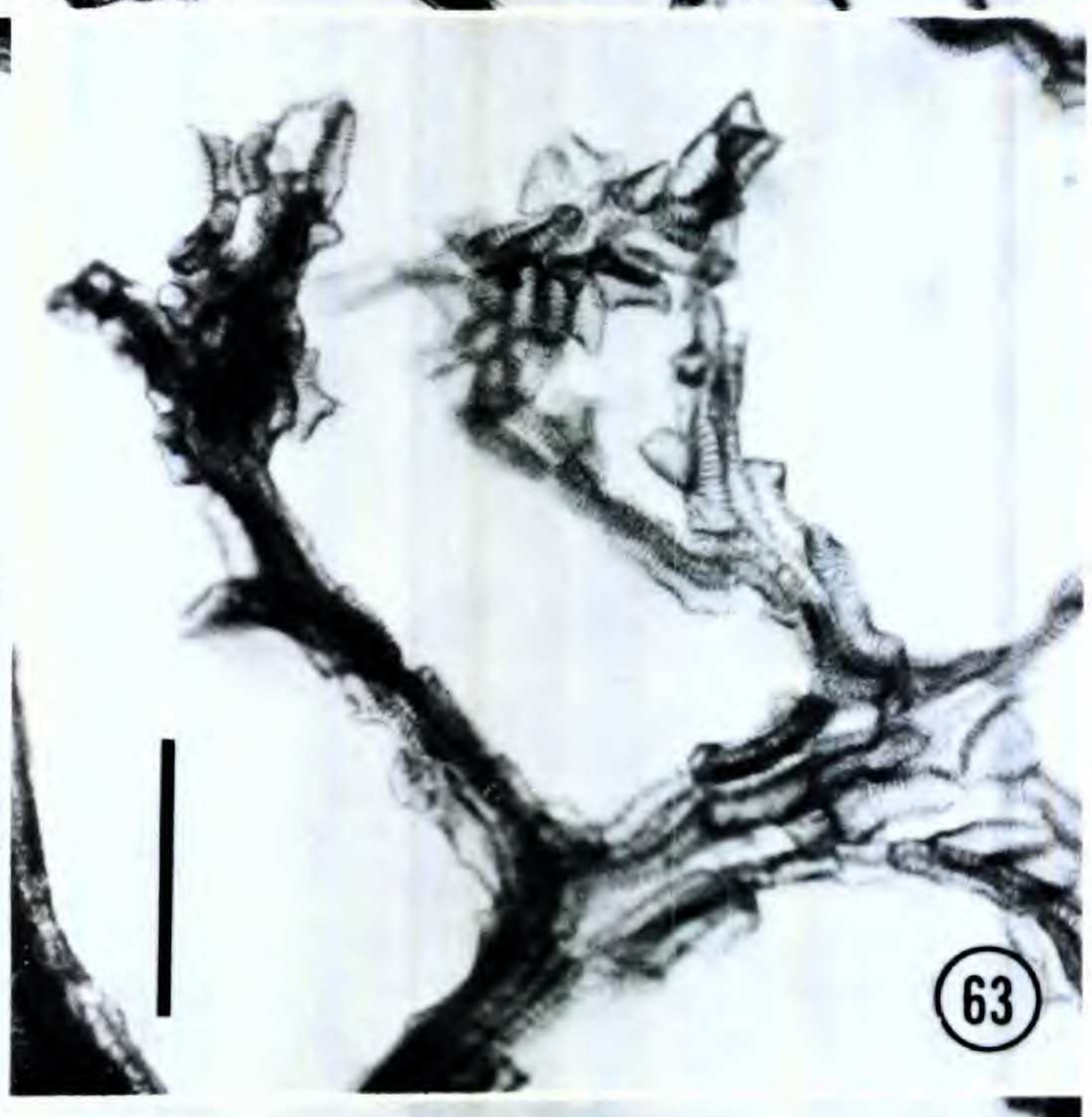


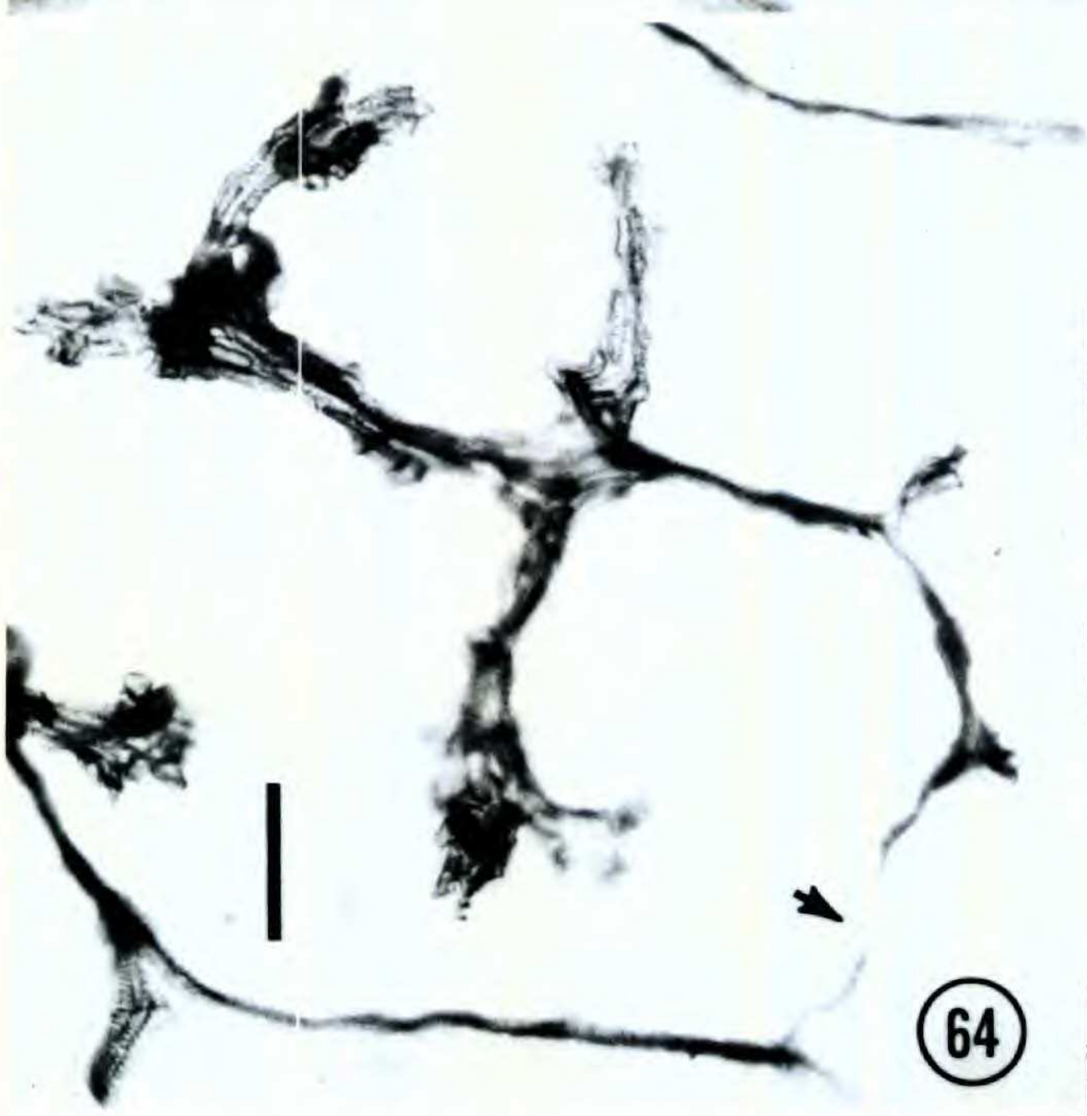
FIGURES 56–59. Fine venation features in *Cistanthe*.—56. Ultimate venation in *C.* (*Cistanthe*) *grandiflora* (*West 3959*). Note the "tracheoids" (T) along the fine veins and the coalescence of veinlet branches (large arrowhead).—57. Ultimate venation and coalesced veinlets (arrows) in *C.* (*Cistanthe*) *coquimbensis* (*Werdermann 881*).—58. Ultimate venation in *C.* (*Cistanthe*) *picta* var. *picta* (*Hutchinson 98*). Note the lack of sinuous veins.—59. Ultimate venation in *C.* (*Philippiamra*) *celosioides* (*Worth & Morrison 15820*). Scale bars = ca. 200 μm.



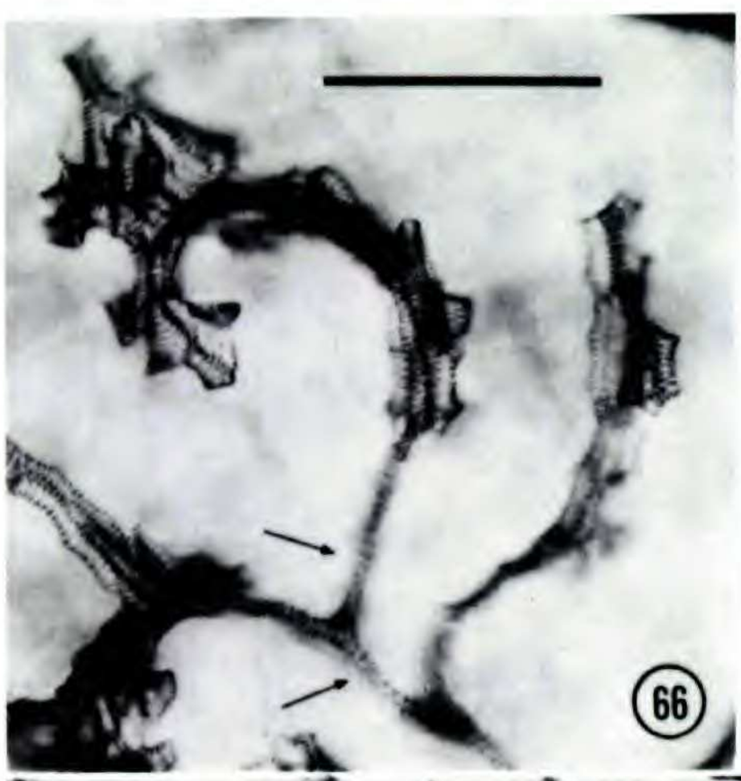


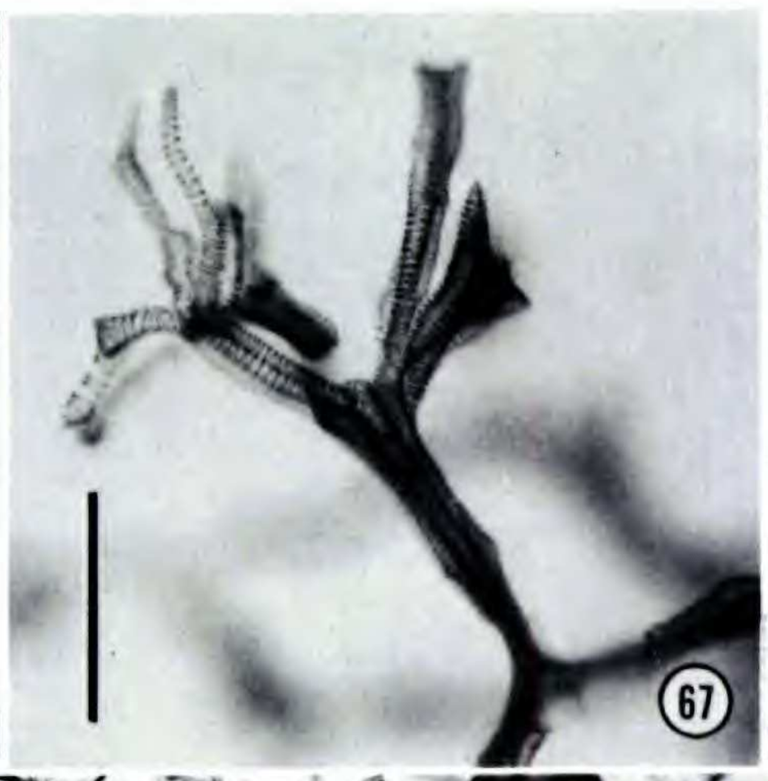


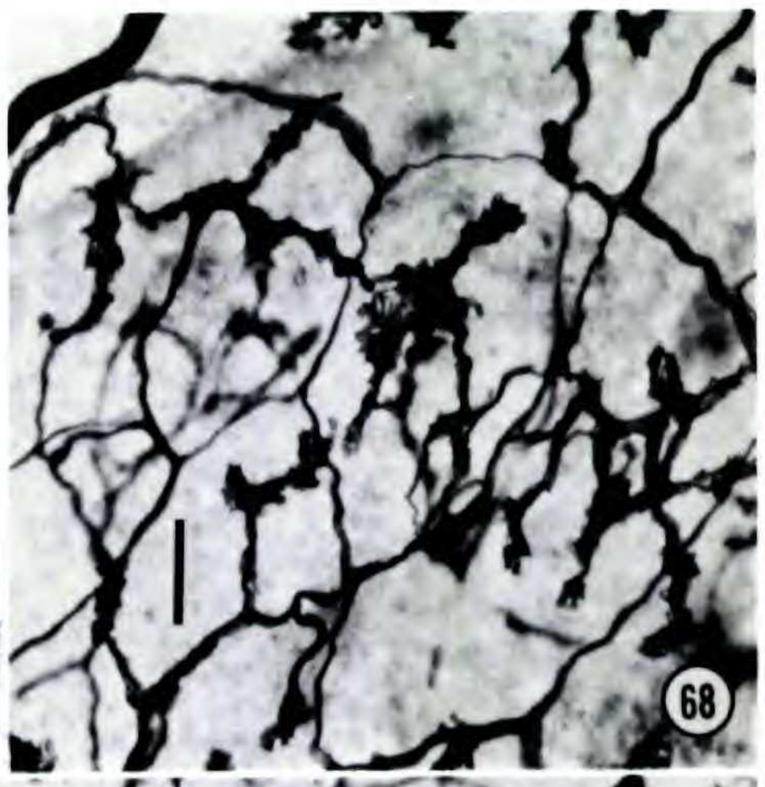


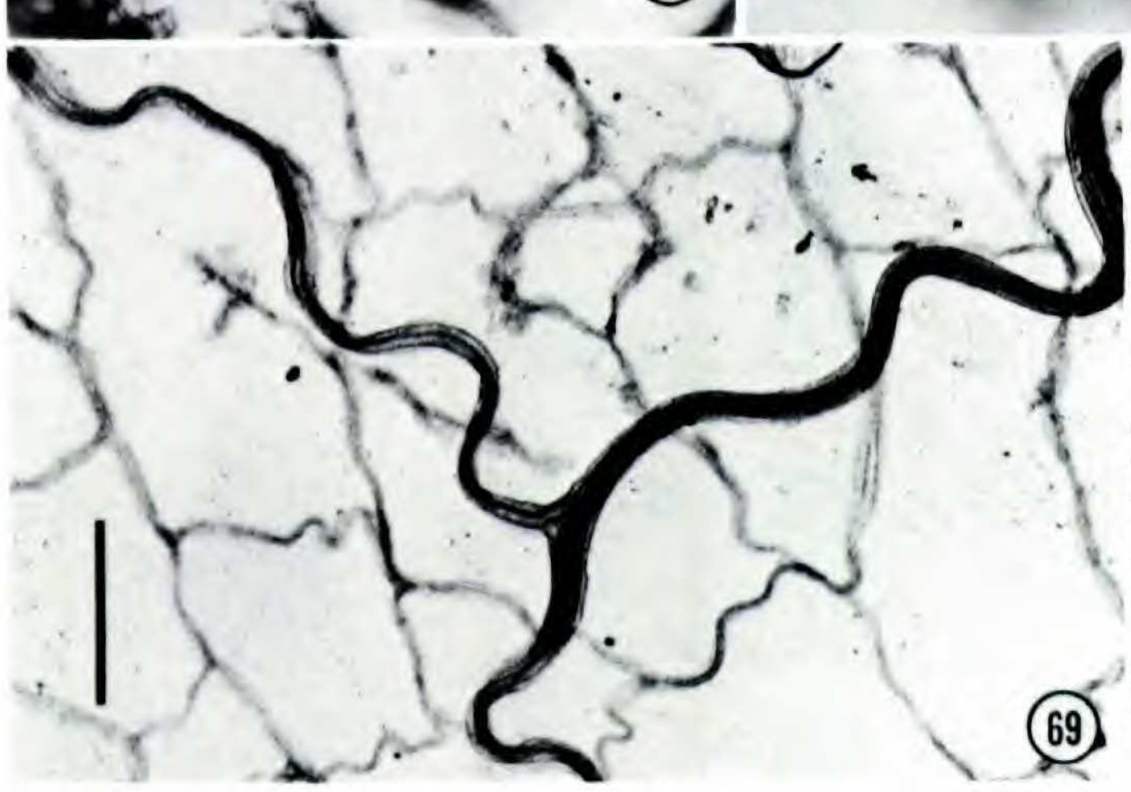


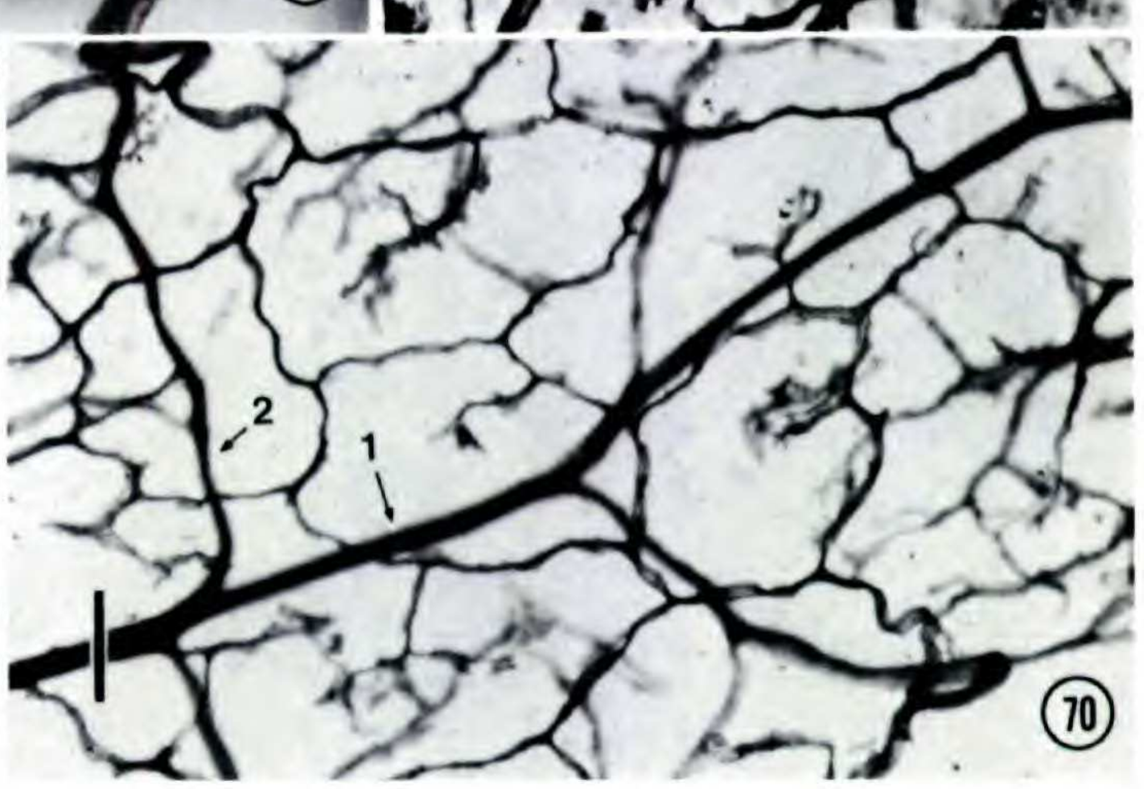
FIGURES 60–65. Fine venation features in *Cistanthe*.—60. Ultimate venation in *C.* (*Calyptridium*) *quadripetala* (*Baker 3075*). Note ribbonlike venation (arrows) and undilated veinlets.—61. Ultimate venation in *C.* (*Calyptridium*) *umbellata* (*Jones 2460*). Note the lack of sinuous veins.—62. Terminal, coalescent veinlets in *C.* (*Cistanthe*) *guadalupensis* (*Wiggins & Ernst 174*).—63. Terminal, coalescent veinlets in *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). Note the numerous densely clustered short tracheary elements.—64. Branched veinlet in *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). Note the fineness of the vein supplying the dilated veinlet (arrow).—65. Multifurcate, dilated veinlet of *C.* (*Cistanthe*) *picta* var. *picta* (*Pennell 12279*). Scale bars are (μm) 200, 200, 200, 100, 100, and 50, respectively.



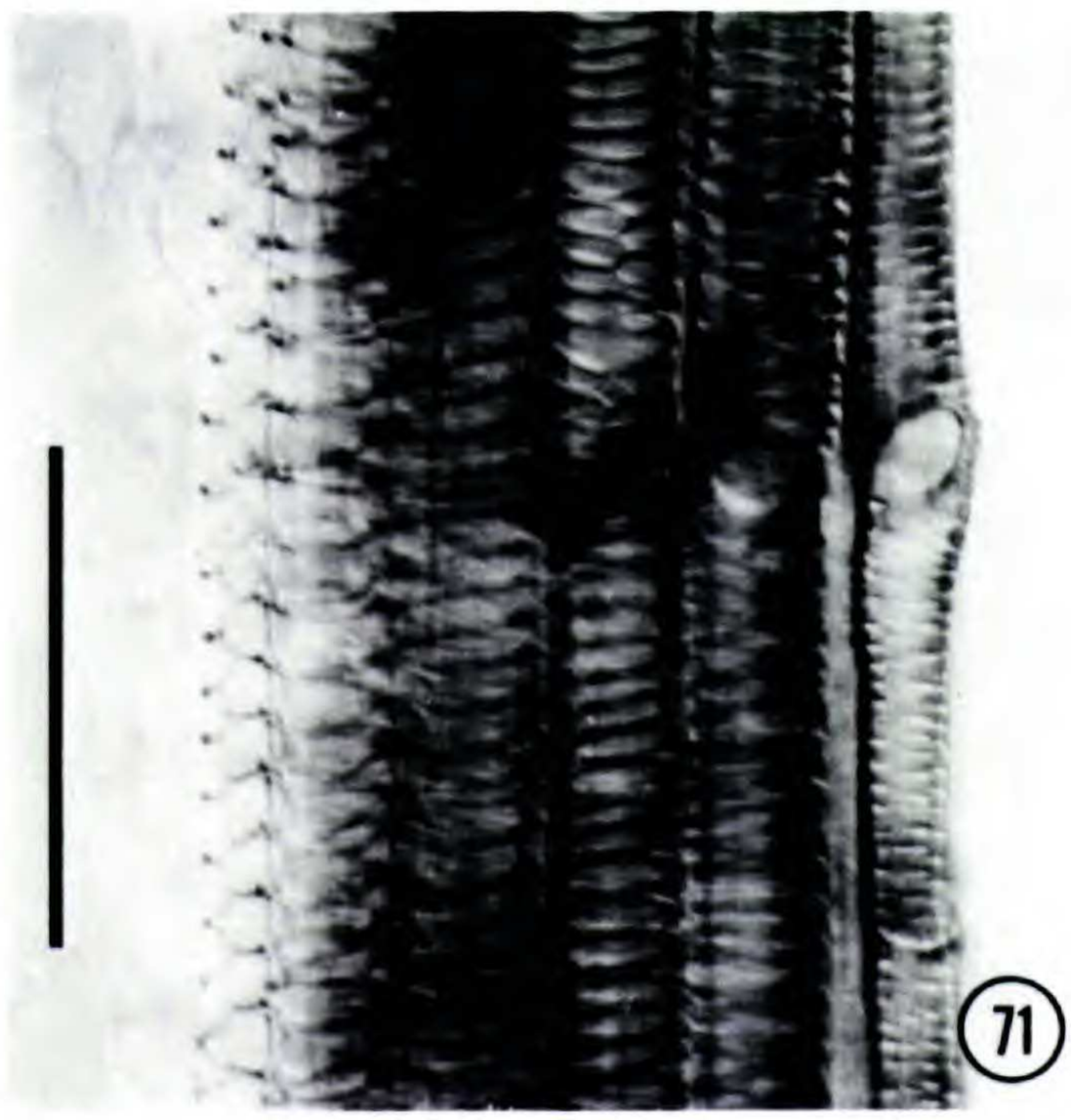


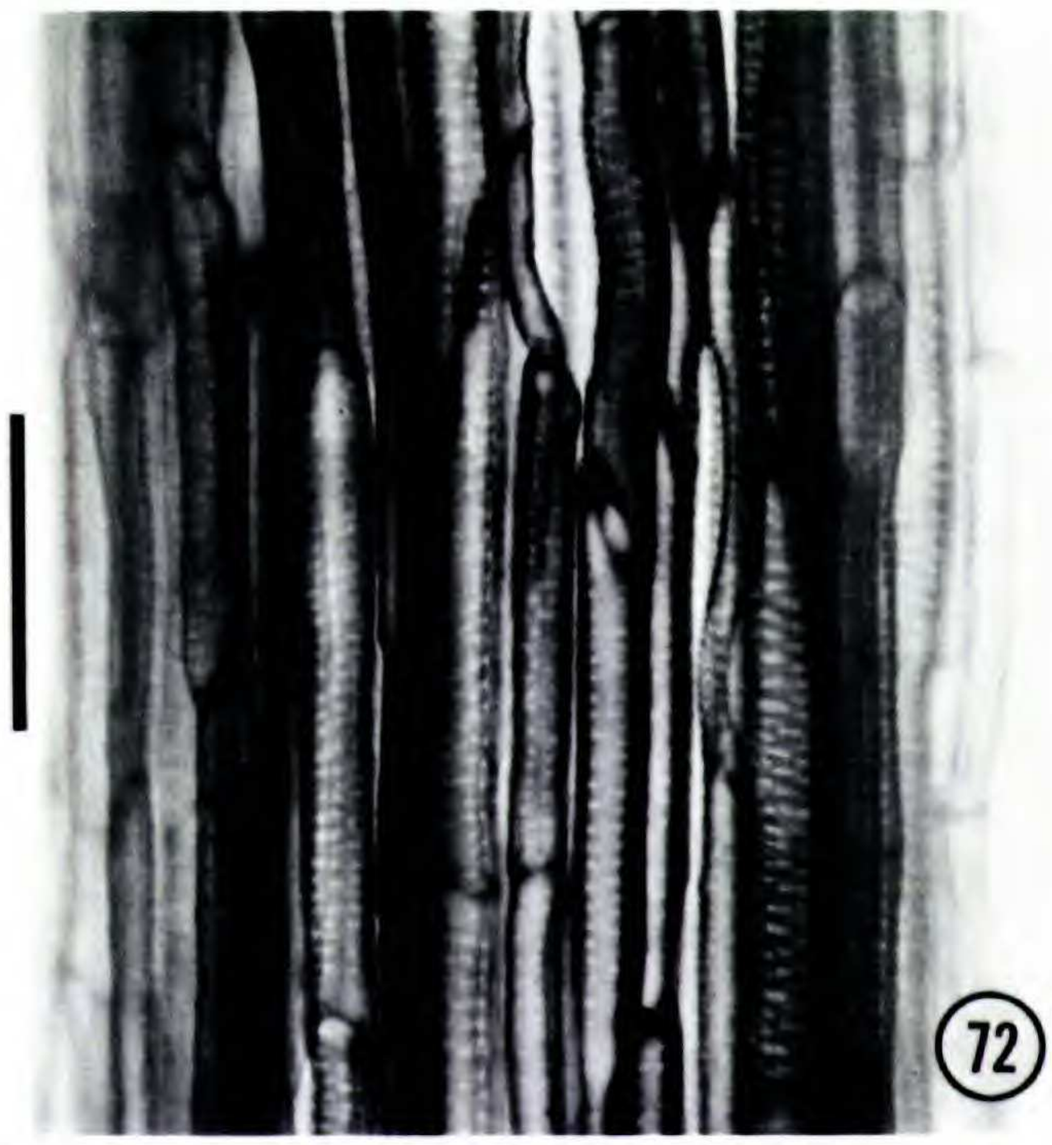




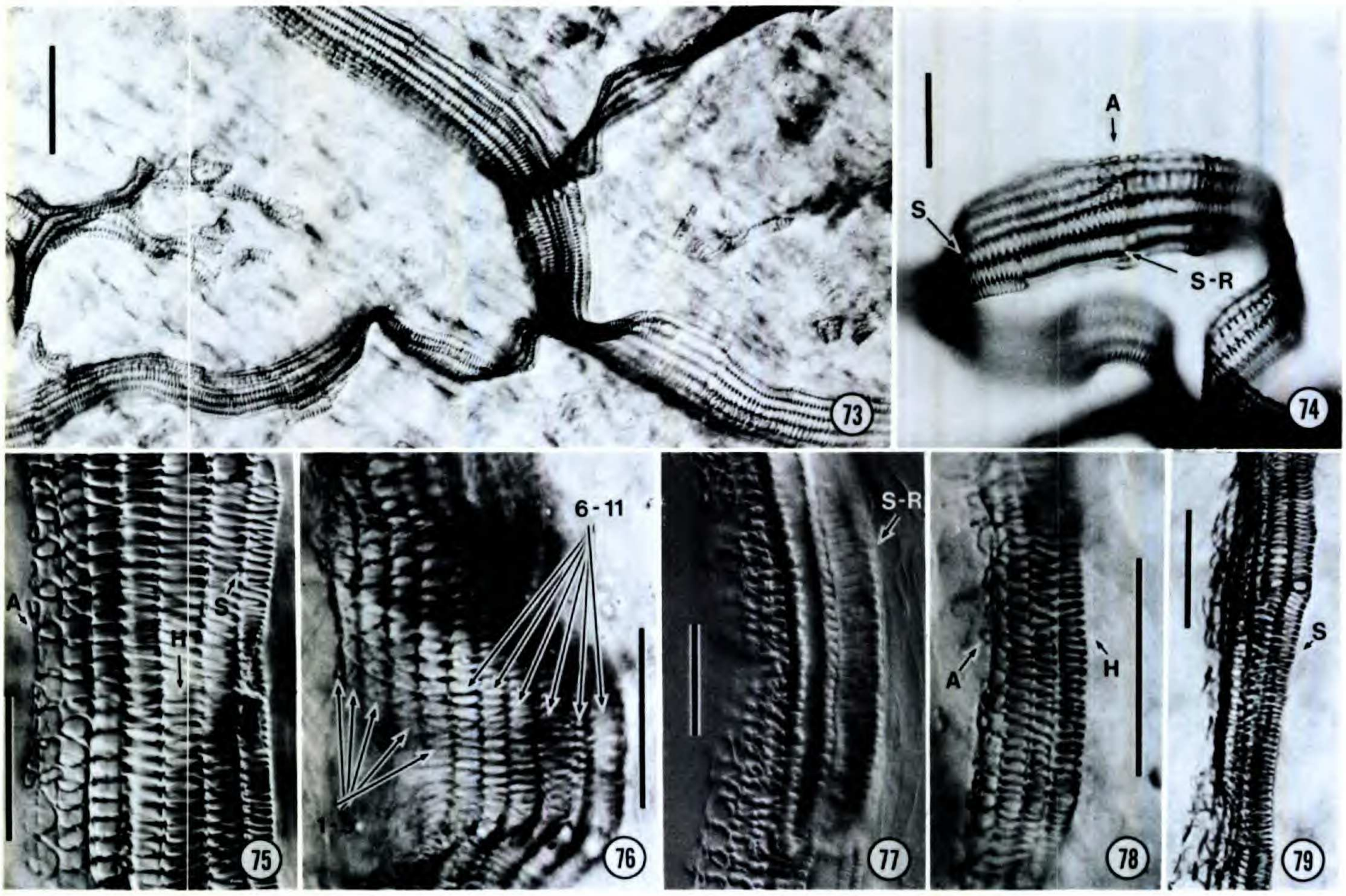


FIGURES 66–70. Fine venation features in *Cistanthe*.—66. Dilated veinlets in *C.* (*Cistanthe*) *fenzlii* (*Philippi s.n.*). Note the fineness of the proximal end of the veinlet and the penultimate vein (arrows).—67. Branched veinlet of *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*). Note the lesser degree of veinlet dilation and more elongate terminal tracheary elements relative to other species.—68. Three-dimensional venation in *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). The veins reticulate freely in more than one plane.—69. Three-dimensional venation in *C.* (*Cistanthe*) *paniculata* (*Ferreyra 12022*). The plane of focus is on the more prominent, lower-order veins, and the finer, higher-order veins form a reticulum in an adaxial plane.—70. Three-dimensional venation in *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*). The finer, higher-order veins form a reticulum in a plane abaxial to the primary (1) and secondary (2) veins. Scale bars are (μm) 100, 100, 200, 200, and 200, respectively.





FIGURES 71–72. Primary veins of *Cistanthe*.—71. *C.* (*Cistanthe*) *lingulata* (*Lopez 374*) showing helical thickenings of the vessel element walls toward the adaxial side and scalariform to reticulate thickenings toward the abaxial.—72. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*) showing reticulate thickenings of the vessel element walls. Scale bars = 100 μm.



FIGURES 73–79. Ribbonlike veins in *Cistanthe*.—73. *C.* (*Cistanthe*) *weberbaueri* (*Weberbauer 5321*), showing vein branching, sinuousness of the veins, and a free-ending veinlet (left).—74. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*) showing sinuousness of the vein.—75. *C.* (*Cistanthe*) *lingulata* (*Lopez 374*).—76. *C.* (*Calyptridium*) *quadripetala* (*Baker 3075*) showing ribbonlike vein 11 tracheary elements wide.—77. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*) showing scalariform to reticulate vessel element wall thickenings on the abaxial side of the ribbon.—78. *C.* (*Philippiamra*) *celosioides* (*Worth & Morrison 15820*).—79. *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). A = annular wall thickenings; H = helical wall thickenings; S = scalariform wall thickenings; S–R = scalariform to reticulate wall thickenings. Scale bars are (μm) 1,000, 50, 50, 50, 50, 50, and 50, respectively.

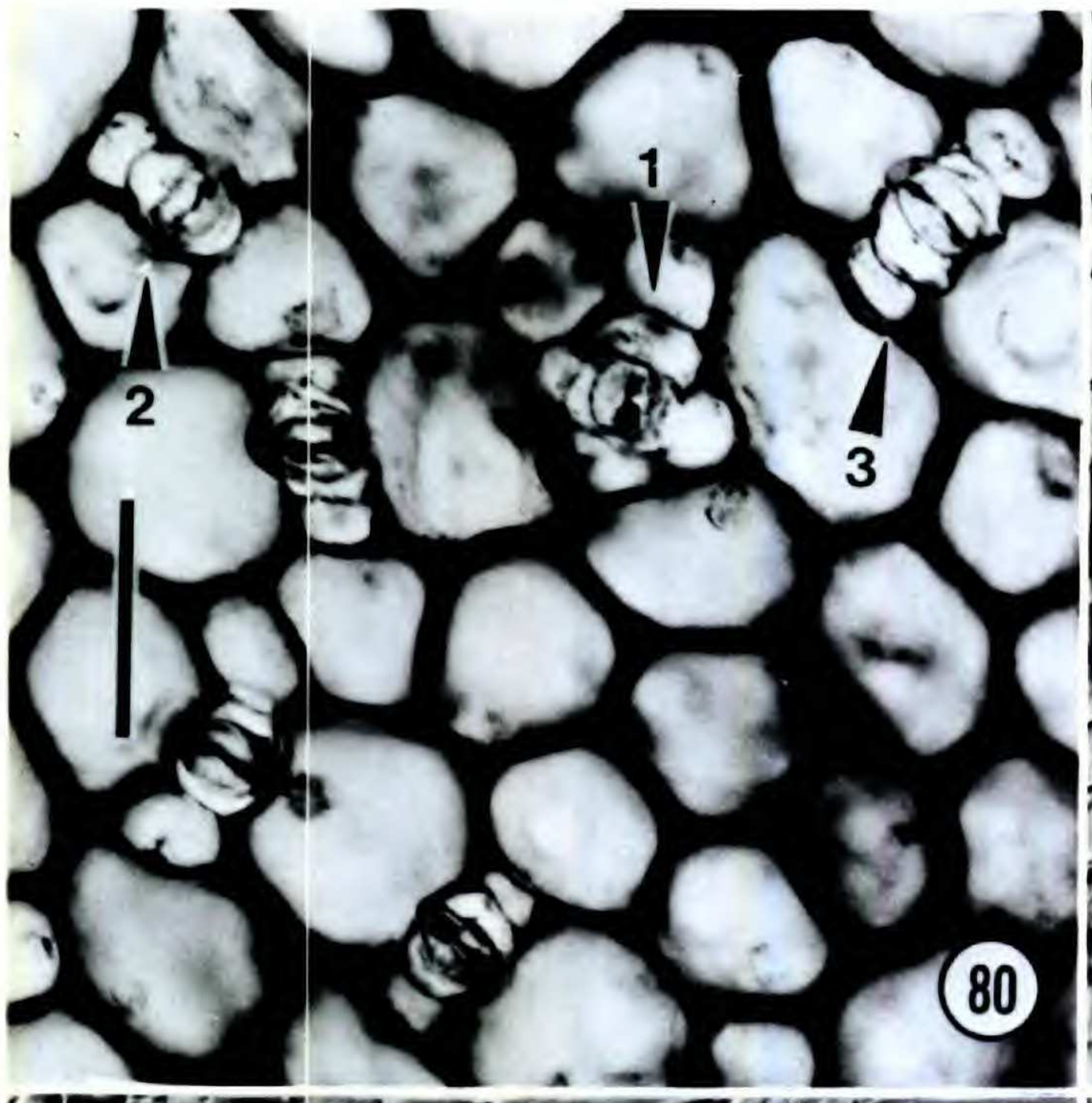
→

FIGURES 80–94. Epidermal morphology in *Cistanthe*. Labels, except where noted, refer to specific features diagrammed in Figure 95 evident in particular stomatal complexes.

FIGURES 80–85. Epidermal morphology in *Cistanthe* sect. *Cistanthe*. All scale bars = ca. 100 μm.—80. *C. grandiflora* (*Werdermann 405*). The plane of focus is subsurface—the stomata are somewhat sunken. 1, more or less hexacytic stoma; 2, hemi-amphibrachyparacytic stoma; 3, amphibrachyparacytic stoma.—81. *C. longiscapa* (*Johnston 5034*). The stomata are slightly sunken. 1, brachyparacytic stoma with four contact cells, cf. Figure 95M and P; 2, amphibrachyparacytic stoma with six contact cells, cf. Figure 95N; 3, similar to 1 above but with five contact cells; 4, more or less brachyparacytic stoma with very broad lateral subsidiary cells; 5, hemibrachyparacytic stoma with three contact cells; 6, stoma with a split lateral subsidiary cell, cf. Figure 95R; 7, amphibrachyparacytic stoma. 82, 83. *C. picta* var. *picta* (*Kuntze s.n.*).—82. 1, brachyparacytic stoma with polygonal subsidiary cells, cf. Figure 95P; 2, hemi-amphibrachyparacytic stoma, cf. Figure 95P and Q; 3, brachyparacytic stoma, cf. Figure 95M and O; 4, brachytetracytic stoma; 5, brachyparacytic stoma, cf. Figure 95I; 6, anomocytic stoma with three contact cells.—83. 1, brachyparacytic stoma, cf. Figure 95I and P; 2, stoma with five contact cells, cf. Figure 95S; 3, stoma with five contact cells, cf. Figure 95R; 4, amphibrachyparacytic stoma; 5, unclassifiable stoma with five contact cells.—84. *C. fenzlii* (*Neger s.n.*). 1, staurocytic stoma with four contact cells, cf. Figure 95G; 2, hemi-amphibrachyparacytic stoma; 3, brachytetracytic stoma; 4, amphibrachyparacytic stoma; 5, stoma with six contact cells but showing essentially the characteristics of Figure 95R.—85. *C. lingulata* (*Ferreyra 10486*). 1, hemi-amphibrachyparacytic stoma; 2, stoma with five contact cells, cf. Figure 95N and R; 3, amphibrachyparacytic stoma, cf. Figure 95K; 4, stoma with five contact cells, cf. Figure 95J and S.

FIGURES 86–90. Epidermal morphology in *Cistanthe* sects. *Cistanthe* and *Amarantoideae*. All scale bars = ca. 100 μm. 86, 87. *C.* (*Cistanthe*) sp. cf. *longiscapa* (*Worth & Morrison 16184*).—86. Epidermal papillae (P).—87. 1, brachyparacytic stoma, cf. Figure 95I and L; 2, hemi-amphibrachyparacytic stoma, cf. Figure 95J and N.—88. *C.* (*Cistanthe*) *cymosa* (*Werdermann 853*). The largest epidermal cells are more or less papillar. The stomata are somewhat sunken. 1, double stoma; 2, hemibrachyparacytic stoma, cf. Figure 95M; 3, anomocytic stoma with four contact cells; 4, brachyparacytic stoma, cf. Figure 95L.—89. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*). 1, brachyparacytic stoma, cf. Figure 95L and O; 2, stoma with five contact cells, cf. Figure 95L and R; 3, amphibrachyparacytic stoma, cf. Figure 95Q; 4, brachyparacytic stoma, cf. Figure 95L.—90. *C.* (*Amarantoideae*) *salsoloides* (*Werdermann 1048*). 1, amphibrachyparacytic stoma; 2, hemi-amphibrachyparacytic stoma with a polar subsidiary cell, cf. Figure 95T; 3, brachyparacytic stoma with a polar subsidiary cell, cf. Figure 95T.

FIGURES 91–94. Epidermal morphology in *Cistanthe* sects. *Calyptridium* and *Philippiamra*. All scale bars = ca. 100 μm.—91. *C.* (*Calyptridium*) *quadripetala* (*Sharsmith 4345*). 1, brachyparacytic stoma with five contact cells; 2, anomocytic stoma with four contact cells; 3, anomocytic stoma with three contact cells; 4, double stoma; 5, hemibrachyparacytic stoma.—92. *C.* (*Calyptridium*) *umbellata* (*Abrams 11351*). The stomata are slightly to markedly sunken. 1, stoma with five contact cells, cf. Figure 95N and S; 2, brachytetracytic (but nearly hexacytic) stoma, cf. Figure 95E and F; 3, hemi-amphibrachyparacytic stoma with one especially narrow polar subsidiary cell; 4, staurocytic stoma with four contact cells; 5, amphibrachyparacytic stoma.—93. *C.* (*Calyptridium*) *rosea* (*Duran 2805*). The stomata are sunken. 1, anomocytic stoma; 2, hemibrachyparacytic stoma, cf. Figure 95N; P, epidermal papillar cell.—94. *C.* (*Philippiamra*) *celosioides* (*Werdermann 862*). 1, hemi-amphibrachyparacytic stoma (the epidermis is torn on the left side between the subsidiary cell and the guard cell pair); 2, amphibrachyparacytic stoma with five contact cells; 3, amphibrachyparacytic stoma with four contact cells.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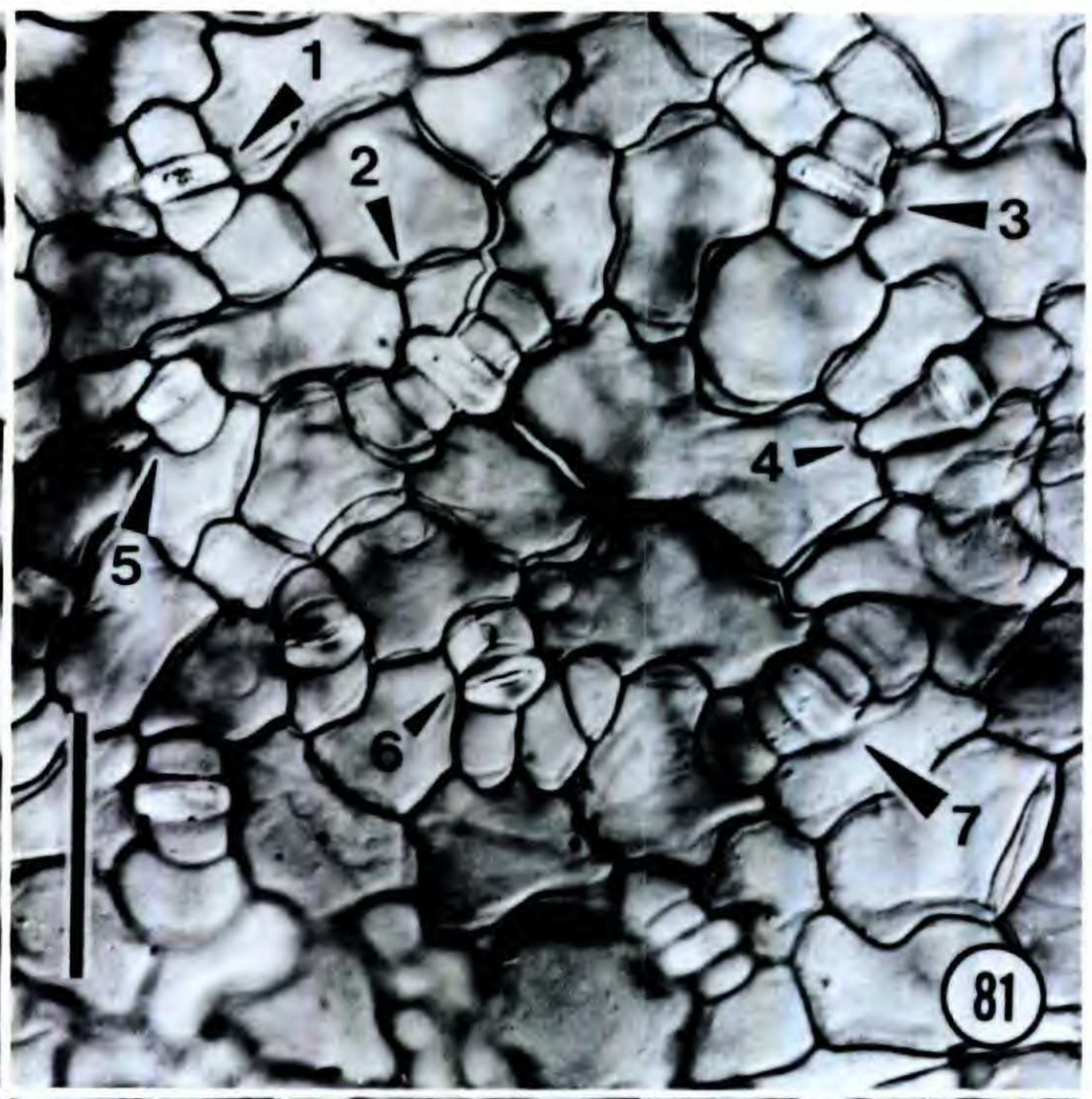
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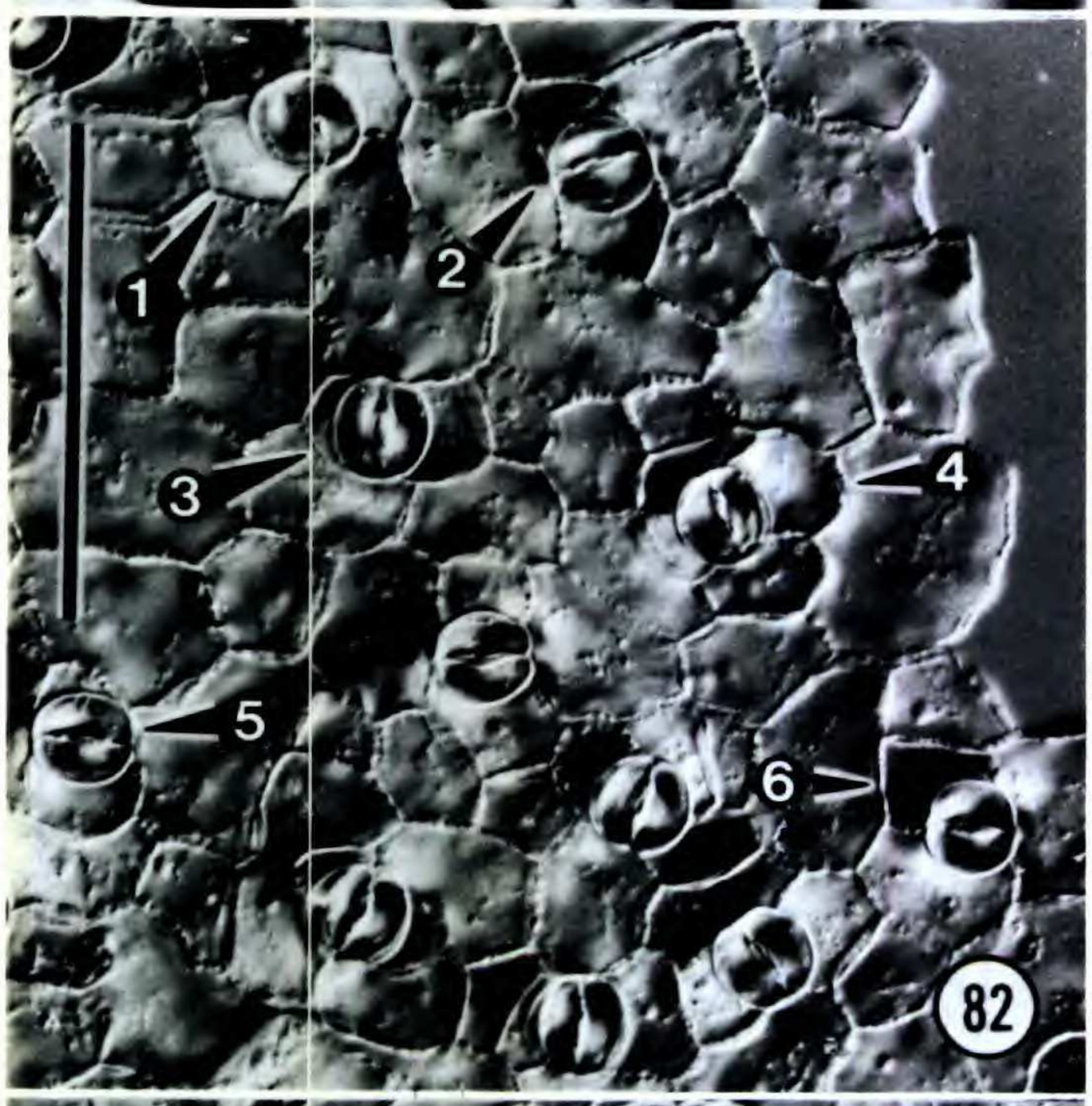
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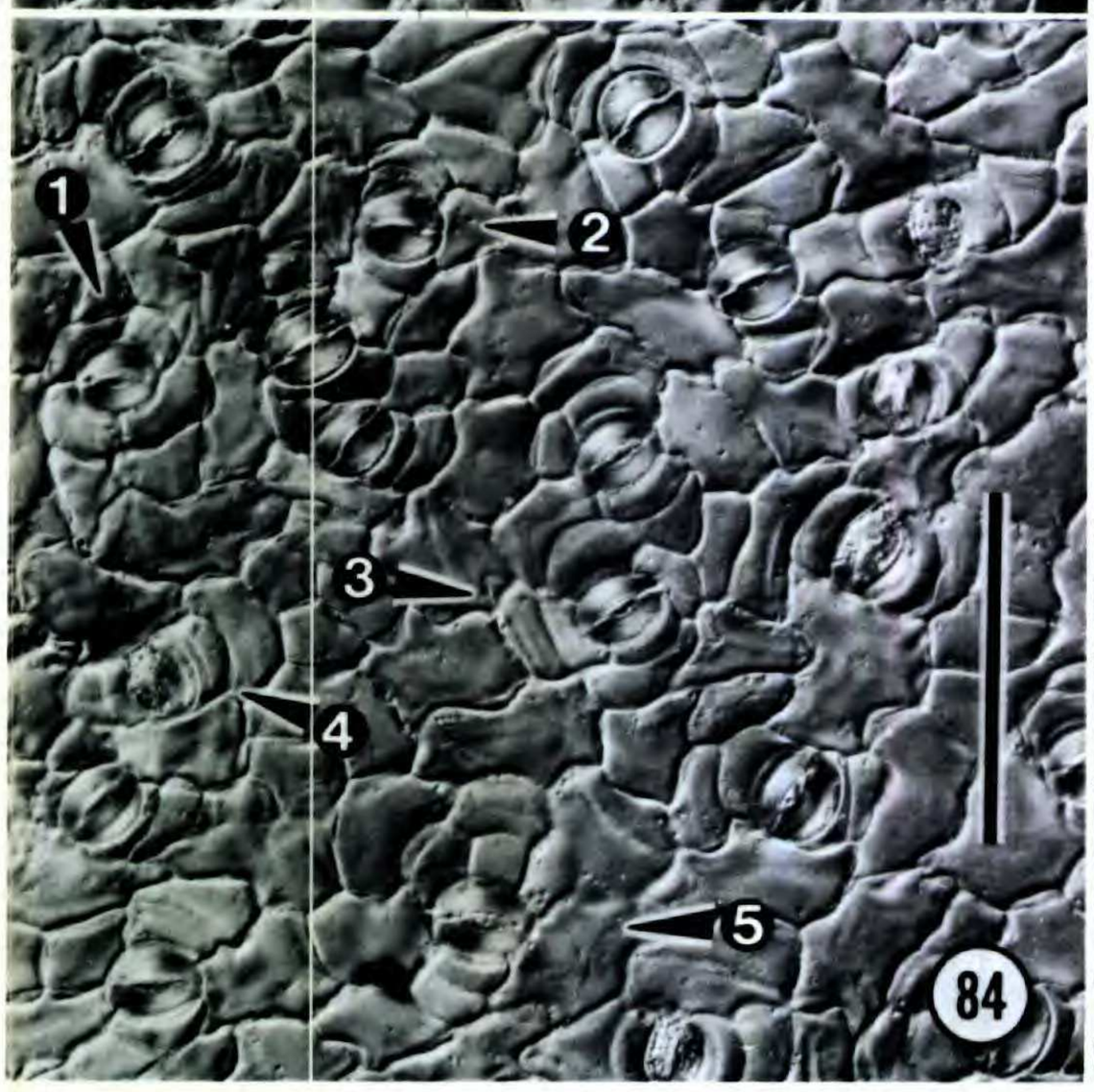
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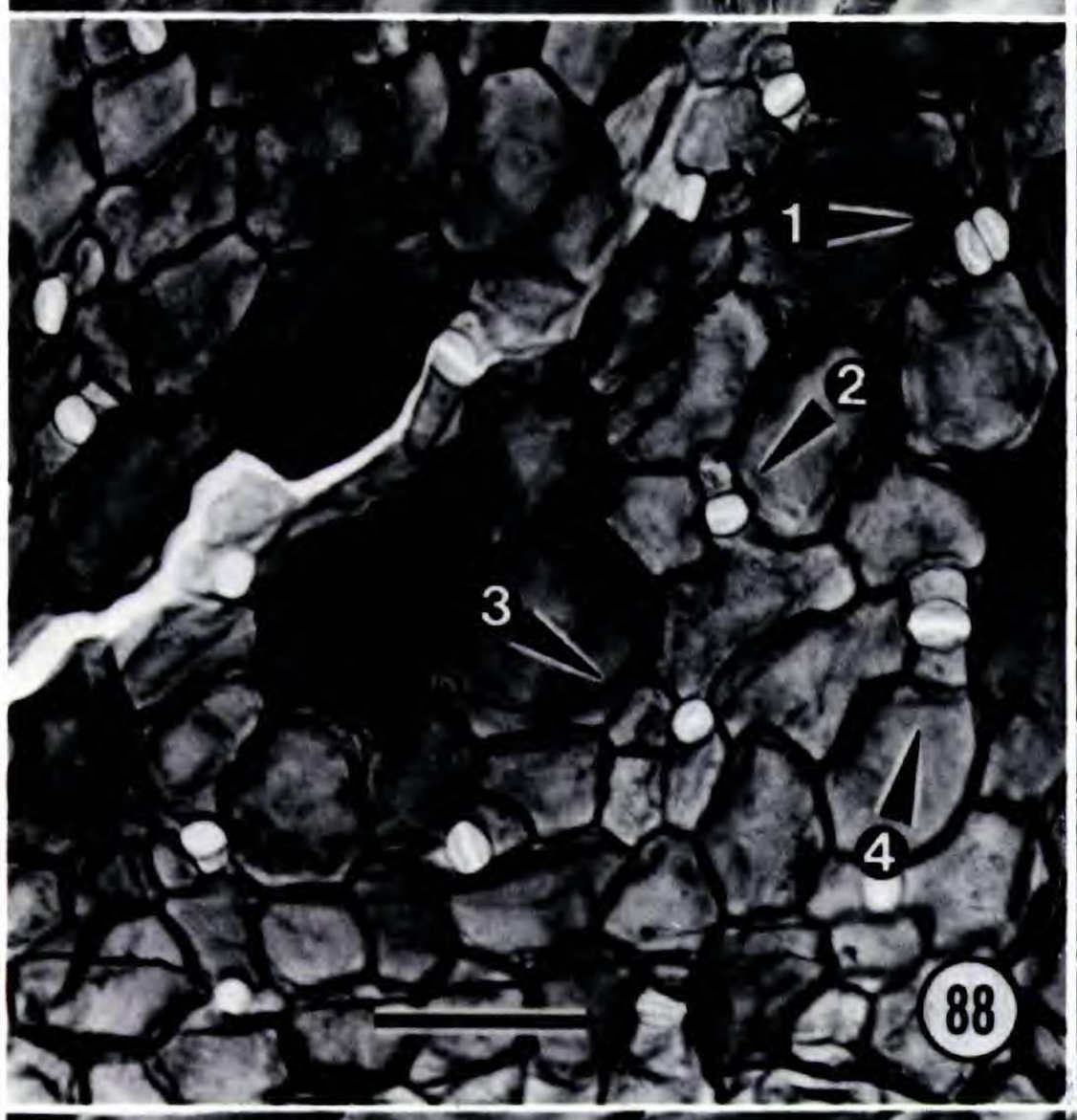
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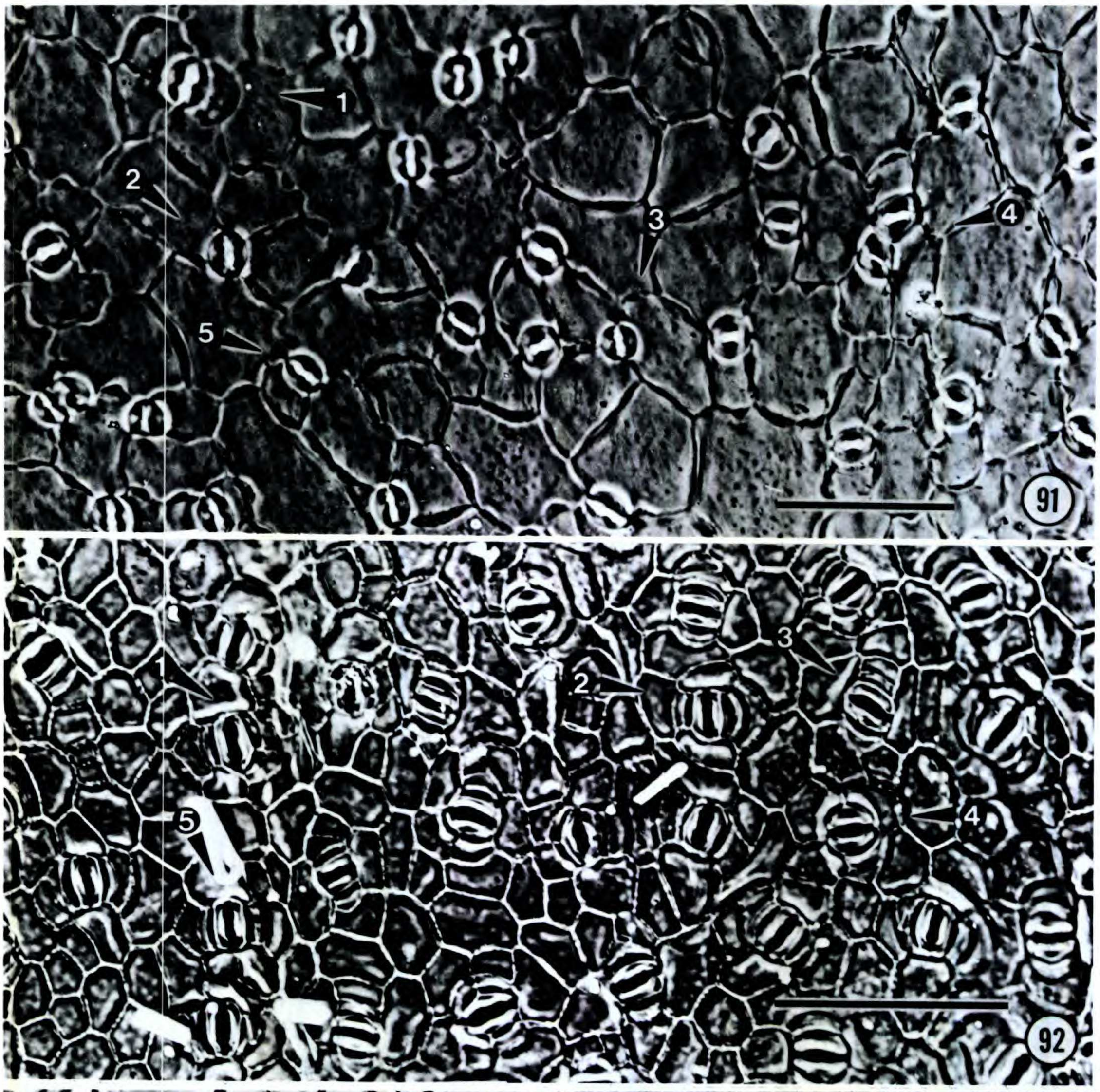
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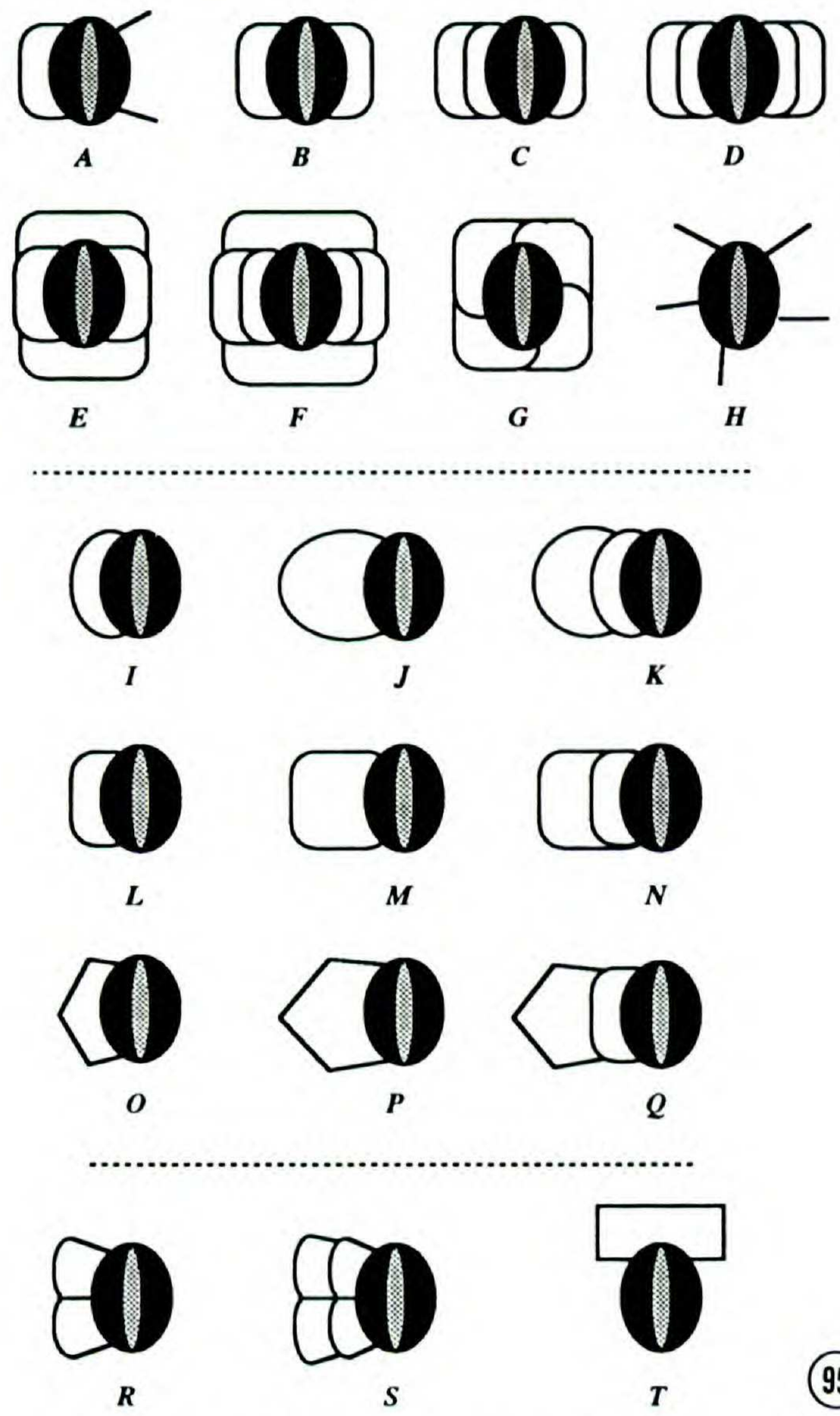

FIGURE 95. Stomatal complex configurations in *Cistanthe*. A–H, stomatal types, cf. Wilkinson (1979).—A. Hemibrachyparacytic.—B. Brachyparacytic.—C. Hemiamphibrachyparacytic (see text).—D. Amphibrachyparacytic.—E. Tetracytic.—F. Hexacytic.—G. Staurocytic.—H. Anomocytic. I–Q. Examples of morphological variation of lateral subsidiary cells.—I. Contoured, narrow.—J. Contoured, broad.—K. Contoured, double.—L. Rectangular, narrow.—M. Rectangular, broad.—N. Rectangular, double.—O. Polygonal, narrow.—P. Polygonal, broad.—Q. Double, the outer polygonal. R–T. Other subsidiary cell types.—R. Lateral cell divided transversely.—S. Two lateral cells, both divided transversely.—T. Polar, elongate cell perpendicular to the guard-cell axis.