A TAXONOMIC RE-EVALUATION OF THE GENERA AMPHIACHYRIS, AMPHIPAPPUS, GREENELLA, GUTIERREZIA, GYMNOSPERMA, THUROVIA, AND XANTHOCEPHALUM (COMPOSITAE)

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The Compositae, one of the largest families of vascular plants, are one in which evolutionary modifications are complex and poorly understood. Generic boundaries within many of the groups are obscure and, therefore, controversial. Generic delimitation of *Xanthocephalum*, *Gymnosperma*, *Gutierrezia*, *Amphiachyris*, *Amphipappus*, and *Greenella* (Astereae, subtribe Solidagineae) is confused. As a consequence, I undertook the present investigation, which has three objectives: (a) to reevaluate the taxonomic position of the genera by attempting to quantify and assess the gross morphological variation among the various groups, (b) to conduct a comparative anatomical study to determine whether endomorphic characters support the relationships suggested by gross morphology and cytology, and (c) to determine phylogenetic or evolutionary relationships from anatomical data.

A somewhat detailed historical account of most of these genera is given by Solbrig (1960). The present account adds some additional data.

Xanthocephalum was the first genus of this group to be described—in 1807 by Willdenow, based on material collected and described by Humboldt (Solbrig, 1961).

Gray (1873), recognizing the close similarities between *Xanthocephalum* and *Gutierrezia*, placed both X. *gymnospermoides* and *X. wrightii* in *Gutierrezia*, emphasizing that the line separating the genera was not perfectly clear. Gray also held *Gutierrezia* to comprise *Amphipappus* as well as *Amphiachyris* but later (Gray, 1884) felt that *Amphipappus* should be merged with *Amphiachyris* and kept separate from *Gutierrezia*. This transfer was justified because of the sterile disk florets and the quite setose pappus of both *Amphipappus* and *Amphiachyris*.

Bentham and Hooker (1873) adopted Gray's original treatment for the group. They merged *Amphiachyris* as well as *Amphipappus* with *Gutierrezia* and placed this group near *Gymnosperma* and *Xanthocephalum*.

According to Nelson (1934), *Amphipappus* and *Amphiachyris* should remain distinct genera, since *Amphiachyris* was based upon an annual herb, *A. dracunculoides*, "differing in many respects from *Amphipappus*." Porter (1943), agreeing with Nelson's line of reasoning, considered *Amphipappus* distinct.

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The morphological similarity of *Greenella* Gray to *Gutierrezia* and *Xanthocephalum* is unquestionable, and both Gray (1884) and Shinners (1950) doubted the distinctness of that genus. According to Gray (1884), in the original description of the genus, "if the ray-flowers of this plant were yellow instead of white, it would be referred to the genus *Xanthocephalum*, and the habit is nearly that of *X. linearifolium* and *X. sericocarpum.*"

More recently, further opposing views as to the taxonomic status of these genera have been recorded. According to Shinners (1950), the quite variable features of pappus, size of heads, and number of rays did not constitute differences sufficient to justify maintaining separate genera. To Shinners the fact that they were of one phylogenetic stock was unquestionable, and in view of the slight differences among them, Shinners felt they represented a single genus. Solbrig (1960) conducted a cytological and morphological study and concluded that certain morphological features in combination could be used to delimit the genera but that they often were insufficient when used alone. Chromosome number, however, proved to be a distinguishing character. This criterion, in Solbrig's opinion, was sufficient to delimit the genera satisfactorily.

Howe (1970) reported on megagametogenesis for *Gutierrezia microcephala* and *G. texana* and compared it with that of *Amphiachyris dracunculoides*. According to Howe, the differences in the female gametophytes supported the retention of *Amphiachyris* as a genus distinct from *Gutierrezia*, thus agreeing in part with Solbrig.

While Solbrig's cytological conclusion seems tenable, recent inconsistencies in chromosome numbers in the various genera, not reported in Solbrig's work, raise questions as to the placement of the groups and warrant reassessment of their status.

Shinners (personal communication), Spencer Tomb (personal communication), and Correll and Johnston (1970) suggested that the monotypic genus *Thurovia* Rose is also closely related to the *Xanthocephalum* complex. Rose (1895), in the original description, noted that, from the head structure and the general habit, *Thurovia* apparently belonged to the tribe Astereae and that the habit of *Thurovia* was like that of *Gutierrezia* or *Greenella*. Thus, my investigation also includes a study of *Thurovia*.

MATERIALS AND METHODS

Fresh plant material for anatomical studies was killed and fixed in either chromic-acetic-formalin or formalin-propionic-alcohol (CRAF and FPA, respectively; Sass, 1958), dehydrated through a graded tertiary butyl-alcohol series, infiltrated, embedded, and sectioned in paraffin. Dried material judiciously taken from herbarium sheets was restored by immersion in 3% aqueous sodium hydroxide and then was dehydrated and processed as described above.

Many of the data on gross morphology were obtained by measuring 15 characters on each of 10 plants per collection. To reduce error variation, only plants in anthesis (showing pollen shedding) were chosen for measurements.

To standardize leaf measurements, the maximum length of the current year's growth was first measured from the base of the year's growth (or base of the plant, for annuals) to the tip of the longest branch. Measurements were made on the leaf nearest the midpoint of the current year's growth. For involucral and floral characters one flower head was chosen from each plant, placed in 50% ethyl alcohol, and measured later. To standardize this procedure and choose heads of the same relative maturity, the flower head nearest the terminal head on the branchlet nearest the midpoint of the current year's growth was chosen.

Whole leaves and flowers for venation studies were cleared and stained as described by Fuchs (1963).

Table 1 shows the sources of the materials used in my morphological studies.

OBSERVATIONS

Involucre and receptacle. Comparative morphological and histological studies of the involucre and phyllaries (involucral bracts) show few major differences and are not useful in delimiting the genera.

Greenella, Gutierrezia, and *Xanthocephalum* possess an involucre varying from narrowly turbinate to broadly campanulate. *Amphiachyris* has a somewhat broadly campanulate involucre, and *Gymnosperma, Amphipappus,* and *Thurovia* possess elongate-turbinate involucres.

Involucral bracts of the genera are glutinous, in two to many rows, imbricated, and dark green at the tips. In all the groups the number of bracts appears to correlate well with the size of the involucre (Table 2).

Histologically, in all species studied the outer phyllaries are four to seven cells thick. In *Greenella, Gutierrezia, Gymnosperma,* and *Xanthocephalum* (except *X. wrightii* and *X. linearifolium*) only one vascular trace enters each bract. Heads of *X. wrightii* have three traces in the outer bracts and one trace in each innermost bract. *Xanthocephalum linearifolium* shows three to five bundles in the outer bracts. In comparison, *Amphipappus* commonly shows three bundles in its bracts, and *Amphiachyris* has as many as five traces in the outer bracts. Heads of *Thurovia,* like *X. linearifolium,* have three to five bundles in the outer bracts.

One to five secretory canals occur in the outer bracts in all species studied. These canals are, for the most part, conspicuous on the adaxial side of the vascular bundles.

All of the species in each genus possess sclerenchyma in the outer bracts. The degree of sclerification is so pronounced that in most species the vascular bundles are usually enveloped in sclerenchyma, which is more abundant near the base of the bracts. Many inner bracts appear to be entirely sclerified except in the epidermal layers. In *Amphipappus* the central area of the larger bracts, six to seven cells thick, consists of a layer of spongy

TABLE 1. Sources of material used in morphological studies of *Amphiachyris*, *Amphipappus*, *Greenella*, *Gutierrezia*, *Gymnosperma*, *Thurovia*, and *Xanthocephalum*

(Voucher specimens are in KSC unless otherwise indicated)

Species	Collection	Location
Amphiachyris amoenum var. *amoenum* (Shinners) Solbrig	*Ruffin 7033*	Texas: Montague Co., 7 mi NE of Montague.
	Ruffin 7034	Texas: Johnson Co., 13.7 mi SW of Cleburne.
	Ruffin 7035	Texas: Lampasas Co., 3.4 mi NW of Lampasas.
A. amoenum var. *intermedium* (Shinners) Solbrig	*Ruffin 7030*	Texas: Milan Co., N side of Ben Arnold between hwy and railroad.
	Ruffin 7031	Texas: Washington Co., 2½ mi NE of Burton at jct of hwys 390 and 1948.
	Ruffin 7032	Texas: Montague Co., 7 mi NE of Montague.
A. dracunculoides (DC.) Nutt.	*Ruffin 7036*	Kansas: Geary Co., 9 mi W of Junction City along hwy 77.
	Ruffin 7037	Kansas: Riley Co., 13½ mi S of Manhattan along hwy 177.
	Ruffin 7038	Kansas: Chase Co., 25 mi NE of El Dorado.
	Ruffin 7039	Texas: Brewster Co., along hwy 118 S of Alpine.
	Anderson 3005	New Mexico: Chaves Co., 5 mi N of Roswell.
Amphipappus fremontii Torr. & Gray	*Clokey 5962*	Nevada: Clark Co., Glendale Junction, Rocky Hills, Larrea Belt.
Greenella arizonica Gray	*Peebles et al. 3842* (US)	Arizona: Pima Co., Papago Reservation.
G. ramulosa Greene	*Anthony 321* (MO)	Lower California: San Bartolome Bay area.
Gutierrezia californica DC.	*Krikorian s.n.**	California: Fresno Co., Parkfield Grade, NW of Coalinga.
G. mandonii ssp. *mando-*	*Venturi 8156* (US)	Argentina: Prov. Jujuy;

nii (Sch. Bip.) Solbrig		Dept. Rosario de Lerma.
G. microcephala DC.	*Ruffin 7005, 7006*	New Mexico: Grant Co., 15 mi N of Silver City off hwy 25, 6600 ft. (*7005*); 8800 ft. (*7006*).
G. sarothrae Pursh	*Ruffin 7001*	New Mexico: Grant Co., 6 mi N of Silver City along Signal Peak Road.
	Ruffin 7002	Kansas: Logan Co., 20 mi SW of Oakley along hwy 83.
	Ruffin 7003	Kansas: Scott Co., 10 mi E of Scott City.
	Ruffin 7004	Kansas: Ness Co., 13 mi NE of Ness City along hwy 283.
G. texana DC.	*Ruffin 7007* *Anderson 3028*	Texas: Brewster Co., along hwy 118 S of Alpine.
	Ruffin 7008	Texas: Burleson Co., along hwy 290; S of Giddings.
	Ruffin 7009	Texas: Washington Co., 1 mi NE of Burton along hwy 390.
Gymnosperma glutinosum (Spreng.) Less.	*Ruffin 7010*	New Mexico: Grant Co., 5 mi N of Silver City on Cottage Sand Road.
	Ruffin 7011	New Mexico: Hidalgo Co., 1 mi W of Cloverdale on hwy 77.
	Ruffin 7012	Texas: Brewster Co., 21 mi S of Marathon on road to Big Bend National Park.
	Ruffin 7013	Texas: Brewster Co., along hwy 118 S of Alpine.
Thurovia triflora Rose	*Tharp 280* (TEX)	Texas: Jackson Co., Coastal flat near mouth of Lavaca River.
Xanthocephalum centauroides Willd.	*Palmer 501* (MO)	Mexico: City of Durango and vicinity.
X. gymnospermoides (Gray) Benth. & Hook.	*Ruffin 7024, 7025, 7026*	Arizona: Cochise Co., Garden Canyon, Huachuca Mts., 6000 ft (*7024*); 5500 ft (*7025*); 6200 ft (*7026*).
X. humile (HBK.) Sch. Bip.	*Pringle 7422* (US)	Mexico: Distrito Federal; northern puebla.
X. linearifolium (DC.)	*Leavenworth 950*	Mexico: Serrania de Ajusco

Greenm.		near Cima Station.
X. sericocarpum Gray	*Palmer 143* (US)	Mexico: city of Durango and vicinity.
X. wrightii (Gray) Gray	*Ruffin 7020*	New Mexico: Catron Co., 18 mi NE of Mogollon on hwy 78.
	Ruffin 7021	New Mexico: Grant Co., 11 mi NE of Silver City at bottom of Cherry Creek Canyon.
	Ruffin 7022, 7023	Arizona: Cochise Co., Garden Canyon, Hauchuca Mts., 6000 ft (*7022*); 5500 ft (*7023*).

**Gutierrezia californica* has been described as being restricted to the area of San Francisco Bay, California (Solbrig, 1960). Material collected by Krikorian places this species about 80 mi S of its previously-known range.

TABLE 2. Averages (in mm) for floral features of *Amphiachyris*, *Amphipappus*, *Greenella*, *Gutierrezia*, *Gymnosperma*, *Thurovia*, and *Xanthocephalum*

		involucre			flowers					
Species	Voucher	length	width	bract number	ray number	disc number	achene length (disc)	achene length (ray)	length of corolla (disc)	width of corolla (disc)
Amphiachyris amoenum var. *amoenum*	*Ruffin 7033*	3.8	3.4	16.2	8.0	26.9	—	1.0	2.4	0.6
	Ruffin 7034	4.0	3.6	16.3	7.9	26.6	—	0.9	2.6	0.6
	Ruffin 7035	3.6	3.3	15.5	8.0	24.2	—	0.9	2.4	0.6
A. amoenum var. *intermedium*	*Ruffin 7030*	3.6	3.3	14.2	8.0	19.4	—	1.0	2.5	0.7
	Ruffin 7031	3.8	3.3	14.7	8.0	20.6	—	0.9	2.6	0.7
	Ruffin 7032	3.7	3.5	15.0	8.0	20.3	—	0.9	2.6	0.7
A. dracunculoides	*Ruffin 7036*	2.7	2.3	14.7	8.0	28.5	—	1.0	2.4	0.5
	Ruffin 7037	2.8	2.5	15.0	8.0	28.1	—	1.0	2.5	0.6
	Ruffin 7038	2.6	2.2	15.4	7.9	25.3	—	1.0	2.4	0.6
	Ruffin 7039	2.9	2.5	14.3	8.0	26.2	—	1.0	2.4	0.6
Amphipappus fremontii	*Clokey 5962*	4.4	2.0	8.0	1.6	4.2	1.0	2.6	3.6	0.7
Greenella arizonica	*Peebles et al. 3842*	3.6	3.4	16.9	13.0	30.4	1.0	1.0	2.9	0.6

Gutierrezia californica	*Krikorian s.n.*	6.1	2.5	19.4	8.8	10.6	1.2	1.0	3.2	0.9
G. microcephala	*Ruffin 7005*	3.1	1.0	4.5	1.2	1.3	—	1.0	2.3	0.5
	Ruffin 7006	3.2	1.0	4.4	1.1	1.5	—	1.0	2.4	0.5
G. sarothrae	*Ruffin 7001*	3.4	1.5	11.6	5.0	3.6	1.0	1.1	2.7	0.6
	Ruffin 7002	3.2	1.5	12.1	5.0	3.4	1.0	1.1	2.6	0.6
	Ruffin 7003	3.3	1.4	11.2	4.9	3.2	1.0	1.1	2.6	0.7
	Ruffin 7004	3.2	1.5	11.8	5.0	3.4	1.0	1.0	2.6	0.7
G. texana	*Ruffin 7007*	3.1	3.3	17.2	10.4	17.2	1.0	0.8	1.9	0.8
	Ruffin 7008	3.1	3.5	16.6	10.3	17.4	1.0	0.9	1.7	0.8
	Ruffin 7009	3.3	3.2	17.9	11.8	17.9	1.0	0.9	1.8	0.8
Gymnosperma glutinosum	*Ruffin 7010*	3.8	1.6	10.1	7.1	4.4	1.0	1.3	3.3	0.8
	Ruffin 7011	3.6	1.6	11.0	7.3	4.8	1.0	1.3	3.3	0.8
	Ruffin 7012	3.9	1.7	10.6	7.4	4.9	1.0	1.2	3.2	0.3
	Ruffin 7013	4.0	1.7	10.4	7.1	4.6	1.0	1.3	3.1	0.3
Thurovia triflora	*Tharp 280*	3.5	2.1	7.2	0.0	3.0	1.0	0.0	2.4	0.8
Xanthocephalum centauroides	*Palmer 501*	4.7	5.7	43.2	32.6	49.4	1.0	1.0	4.0	0.7
X. gymnospermoides	*Ruffin 7024*	5.0	5.9	42.9	37.6	160.0	1.0	1.0	4.2	0.6
	Ruffin 7025	4.9	5.5	41.8	34.3	157.8	0.9	1.0	4.1	0.6
	Ruffin 7026	5.2	6.3	43.7	41.5	162.7	1.0	1.1	4.4	0.5
X. linearifolium	*Leavenworth 950*	5.6	6.9	24.6	13.2	67.8	1.0	1.0	3.2	0.6
X. sericocarpum	*Palmer 143*	5.7	6.7	33.2	32.4	120.6	1.0	0.9	3.5	0.3
X. wrightii	*Ruffin 7020*	5.3	5.9	22.2	12.7	47.1	1.0	1.0	3.7	0.8
	Ruffin 7021	4.7	5.6	24.4	12.4	45.6	1.0	1.0	2.9	0.8
	Ruffin 7022	5.3	5.9	20.3	12.0	46.3	1.0	1.0	3.6	0.7
	Ruffin 7023	5.4	6.0	23.4	11.9	47.4	1.0	1.1	3.7	0.6

mesopyhll, three to four rows of sclerenchyma adjacent to the abaxial epidermis, and two to three rows of parenchyma between the sclerenchyma and the adaxial epidermis.

In all species studied, the inner bracts, in contrast to the outer, are relatively longer and narrower. Particularly noteworthy is the strong alignment of bracts in *Greenella ramulosa* (Fig. 15d), a condition not encountered in any other species.

Uniseriate as well as multiseriate glandular trichomes may occur along the outer as well as the inner epidermis of most species of *Gutierrezia*, *Greenella*, *Xanthocephalum*, *Thurovia*, and *Amphipappus*. However, in *G. texana*, *G. sarothrae*, *X. gymnospermoides*, and *Amphipappus*, trichomes about two to three cells high are especially abundant along both surfaces. In *Gymnosperma* and *Amphiachyris*, glandular trichomes occur almost exclusively along the adaxial epidermis.

The receptacles of most species studied appears flat or somewhat convex. However, in *X. sericocarpum*, the receptacle is more conical in form.

Occurring on the receptacle of all species of *Gutierrezia*, *Greenella*, and *Thurovia* and of most species of *Xanthocephalum* are characteristic hook-like glandular trichomes (Fig. 14b-d); these are lacking only in *X. gymnospermoides*, *X. humile*, and *X. centauroides*. They usually are four to eight cells long. The presence of these glands in the above genera appears to be a unifying feature; they are absent in *Amphiachyris*, *Amphipappus*, and *Gymnosperma*.

Achene. In all of the genera both disc and ray achenes show little morphological variation, appearing turbinate and slightly flattened.

A single vascular bundle from the receptacle extends into the base of the disc achene. According to Carlquist (1961), this condition is common in most Compositae. Bundle number in the groups is two to 10 in the ovary. *Gutierrezia taltalensis*, *Greenella ramulosa*, and *Gymnosperma glutinosum*, with ten outer vascular bundles in the achene wall, are regarded as representing a more primitive condition. *Xanthocephalum gymnospermoides*, with two to three achene bundles, represents the advanced condition. *Greenella arizonica* is particularly interesting in terms of the secretory canal distribution on the wall of the achene. There are five bundles but 10 secretory canals. A secretory canal is adaxial to each bundle and one is between each two bundles. *Amphipappus* exhibits five to seven achene bundles with no secretory canals on the achene wall. In the other species the number of secretory canals correlates well with the number of bundles in the achene wall. In *Gutierrezia microcephala* (Fig. 6) and all species of *Amphiachyris* (Figs. 9, 10, 11) the disc florets are aborted, but five bundles are present in the outer wall of the ray achene. *Thurovia triflora* shows about the same degree of specialization as the majority of *Gutierrezia* and *Xanthocephalum* species although commonly nine bundles were seen in the achene wall with a secretory canal adaxial to each bundle.

Trichomes in all of the genera, when present on disc or ray achenes, are of the "Zwillingshaar" type, a biseriate non-glandular trichome. In all species studied the tips of the two apical cells usually do not terminate at the same point. The length of these trichomes is generally 70–550 μm. The shortest of these occur in *Gymnosperma*, and the longest, in *Thurovia*. The only other variation noted was the papillate hairs of *Thurovia* and *X. gymnospermoides*; the trichomes appear to arise from little mounds on the achene wall (Fig. 14a).

Disc and ray corollas. The ray corollas show significant differences in average number, width, and length among genera as well as within a single genus. The five-lobed disc corollas show minor differences in length and width but vary tremendously in terms of number per head.

In all of the species studied the tendency is toward more disc florets than ray florets. Tables 2 and 3 show the counts and measurements of these.

TABLE 3. Averages (in mm) for floral features and leaves of *Amphiachyris*, *Amphipappus*, *Greenella*, *Gutierrezia*, *Gymnosperma*, *Thurovia*, and *Xanthocephalum*

Species	Voucher	length of ray	width of ray	length of style appendage (disc)	length of style branch (disc)	length of style branch (ray)	length of pappus (disc)	length of pappus (ray)	leaf width	leaf length
Amphiachyris amoenum var. *amoenum*	*Ruffin 7033*	6.5	1.9	—	0.7	0.9	2.3	0.1*	1.7	22
	Ruffin 7034	6.9	1.9	—	0.7	0.9	2.5	0.1*	1.6	29
	Ruffin 7035	6.6	1.8	—	0.6	0.9	2.2	0.1*	1.8	26
A. amoenum var. *intermedium*	*Ruffin 7030*	4.2	1.7	—	0.6	1.0	2.4	0.1*	1.8	22
	Ruffin 7031	4.3	1.8	—	0.6	1.0	2.5	0.1*	1.8	22
	Ruffin 7032	4.2	1.9	—	0.7	1.0	2.4	0.1*	1.5	14
A. dracunculoides	*Ruffin 7036*	3.2	1.9	—	0.8	0.8	2.3	0.1*	2.0	20
	Ruffin 7037	3.3	1.8	—	0.8	0.9	2.4	0.1*	1.7	20
	Ruffin 7038	3.0	1.9	—	0.7	0.9	2.3	0.1*	1.9	27
	Ruffin 7039	3.7	1.9	—	0.7	0.9	2.3	0.1*	1.7	22
Amphipappus fremontii	*Clokey 5962*	2.5	1.4	0.3	0.5	1.2	3.7	2.9	6	11
Greenella arizonica	*Peebles et al. 3842*	10.3	1.7	1.0	1.9	0.9	0.3	0.1*	0.9	12
Gutierrezia californica	*Krikorian s.n.*	3.5	0.9	1.4	1.5	1.0	1.4	0.6	1.5	21
G. microcephala	*Ruffin 7005*	3.2	0.6	—	1.5	1.0	0.8	0.5	1.9	2.4
	Ruffin 7006	3.4	0.6	—	1.6	1.0	0.7	0.5	2.1	25
G. sarothrae	*Ruffin 7001*	4.2	1.0	1.4	1.6	0.6	1.0	0.3	1.2	17
	Ruffin 7002	4.1	1.1	1.5	1.6	0.6	1.0	0.2	1.4	19
	Ruffin 7003	4.1	1.0	1.5	1.7	0.6	0.9	0.3	1.5	19
	Ruffin 7004	4.0	1.0	1.4	1.6	0.6	1.0	0.3	1.4	18
G. texana	*Ruffin 7007*	3.3	1.3	0.2	1.0	0.5	0.7	0.1*	2.4	25
	Ruffin 7008	3.3	1.6	0.3	1.0	0.5	0.8	0.1*	2.2	24
	Ruffin 7009	3.6	1.3	0.2	0.9	0.7	0.8	0.1*	2	22
Gymnosperma glutinosum	*Ruffin 7010*	2.3	0.3	0.6	1.0	0.7	0.1*	0.1*	5.7	60
	Ruffin 7011	2.2	0.2	0.6	1.0	0.6	0.1*	0.1*	5.1	59
	Ruffin 7012	2.5	0.3	0.6	1.0	0.8	0.1*	0.1*	5.3	58
	Ruffin 7013	2.5	0.3	0.6	1.0	0.7	0.1*	0.1*	7	63

Thurovia triflora	*Tharp 280*	0.0	0.0	0.8	1.4	0.0	1.6	0.0	1.0	2.5
Xanthocephalum centauroides	*Palmer 501*	6.2	1.9	0.3	1.0	0.9	0.1	0.1	2.4	46
X. gymnospermoides	*Ruffin 7024*	7.4	1.5	0.2	1.0	0.9	0.5	0.1*	19.3	82
	Ruffin 7025	7.5	1.4	0.3	1.0	0.9	0.4	0.1*	14.7	72
	Ruffin 7026	7.4	1.7	0.2	1.0	0.9	0.5	0.1*	17.8	80
X. linearifolium	*Leavenworth 950*	7.9	2.1	1.3	1.5	0.7	0.4	0.1*	3.1	44
X. sericocarpum	*Palmer 143*	7.4	1.4	0.6	1.0	0.8	1.2	0.1*	2.1	34
X. wrightii	*Ruffin 7020*	7.8	2.8	1.2	1.5	0.7	0.1*	0.1*	3.1	42
	Ruffin 7021	7.9	2.8	1.2	1.5	0.7	0.1*	0.1*	2.4	30
	Ruffin 7022	8.1	3.1	1.2	1.5	0.7	0.1*	0.1*	2.2	36
	Ruffin 7023	8.0	3.0	1.2	1.5	0.6	0.1*	0.1*	2.1	29

* slightly less than 0.1.

Xanthocephalum shows the greatest degree of variation. In terms of number of ray florets present, it ranges from nine to 13 in *X. wrightii* to as many as 45 in *X. gymnospermoides*. *Gutierrezia* ranges from one to two ray florets in *G. microcephala* to as many as 14 in *G. texana*. *Greenella* commonly shows 13 ray florets, thus corresponding to the Fibonacci sequence.

The number of ray florets in *Gymnosperma glutinosum* ranges from six to eight. The length and width of the ray corolla exceeds that of the disc corolla in all of the species studied except in *Gymnosperma*, where the average length of the ray corollas is shorter than that of the disc corolla. *Gymnosperma* also shows a reduction in the number of teeth on the corolla tip. Most of the species commonly show three lobes at the apex of the ray corolla; *Gymnosperma*, commonly two lobes.

Amphipappus also shows a reduction in number of ray florets. Commonly one or two are present. The number of ray florets in *Amphiachyris* also corresponds to a Fibonacci sequence. All species of *Amphiachyris* studied had eight fertile ray florets. Ray florets are absent in *Thurovia*.

Histologically, the ray corolla of most species varies little. The tissues are composed mostly of parenchyma. At their broadest point the rays are five to eight cells thick in transection. The cells of the lower epidermis in all species are papillate (Fig. 15c), some more pronouncedly so than others. Secretory canals in the ray florets are found only in *X. wrightii*, where they appear adaxial (Fig. 15c) to each vascular bundle.

Uniseriate trichomes, usually of one to three cells, occur on the outer surface of the lobes of the ray and disc corollas. These trichomes are very infrequent but usually more abundant on the lobes of the disc corolla. *Xanthocephalum gymnospermoides* has both uniseriate and biseriate trichomes present on the lobes of its disc and ray corollas.

As in the ray florets, the inner surface of the lobes of the disc corolla is characterized by an abundance of papillate cells. The outer epidermal cells of the disc floret in all species are highly cutinized. The disc lobes are from two to four cells thick. In each of the five lobes of the disc corolla in all the genera are two lateral vascular bundles. Very large secretory canals are associated laterally with each bundle. However they are less frequent and less conspicuous in the disc corollas of *X. wrightii* and *X. sericocarpum* and are absent in *Amphipappus*.

The vascular anatomy of the disc floret in all the genera appears to be fairly advanced. Carlquist (1961) has given a summation of vascular evolution in Compositae. Generally five vascular bundles occur in the base of the disc corolla. These bundles usually extend to the base of each lobe where the individual bundles fork, with a vein entering each adjacent lobe along the margin. The two veins in each of the lobes then meet and fuse at the very top of the lobe.

In all species studied, the tube of the disc corolla is five to eight cells thick just above the nectaries, and no secretory canals are present. Occasional biseriate and/or uniseriate glandular trichomes may be present on the corolla tube. However, in *X. gymnospermoides*, *X. humile*, and *X. centauroides*, the entire lower half of the corolla tube is covered with conspicuous glandular trichomes (Fig. 15a). This occurrence is of particular interest since these three species were the only members of the *Xanthocephalum* group studied that lacked the receptacular glands.

Pappus. Pappus development shows degrees of variation among as well as within genera and thus is a somewhat questionable taxonomic character as far as absolutely delimiting the groups. Generally speaking, all of the genera except *Amphiachyris* and *Amphipappus* can be characterized as having a scaly or reduced pappus in the disc as well as the ray florets. The reduced condition appears slightly more pronounced in *Gymnosperma* (Fig. 8a, b). The pappus of both ray and disc florets in *Amphipappus* is composed of long well-developed setae that are slightly shorter in the ray florets (Fig. 7a, b). The latter condition also characterizes the florets of *Amphiachyris*, except the pappus of the ray floret commonly possesses a low scaly crown (Figs. 9, 10, 11).

Anatomically the pappus of the various species shows very little cellular differentiation. In no instances were vascular traces seen in the pappus. The pappus in cross section appears variously shaped and is usually two to four cells thick at the widest.

Style. As described by Solbrig (1960), the styles of the ray florets are distinctly different from those of the disc ones in all of the species considered. These styles are characterized by two elongated branches with a border of papillae along both sides of the stigmatic branches. On the style branches of the disc florets the papillae are confined to the lower quarter on both sides or are absent, with collecting hairs covering the greater outside portion of the branches. Solbrig, in his assessment of this group, also pointed out that the style branches of the disc florets are shorter than those of the ray ones. However, actual measurements of the branches (Table 2) show that the style branches are shorter in disc florets only in *Amphipappus* and *Amphiachyris* with the difference being slightly greater in *Amphipappus*.

Thurovia triflora shows the greatest degree of stylar variation (Fig. 12b). All the other taxa differ in minor respects. Style branches of *Thurovia* are characterized by short collecting hairs on the upper half of the branches. Just beneath the collecting hairs and some distance from the base of the branches are peculiar brush-like hairs. According to Rose (1895), this peculiarity led Hoffman in 1895 to conclude that perhaps *Thurovia* belonged with Heliantheae instead of Astereae.

In *Xanthocephalum*, *Gutierrezia*, and *Greenella* the styles of the disc florets possess triangular or elongate tips with collecting hairs occupying various degrees of the outer surface of the branches.

Node and leaf. Nodal anatomy proved to be a very conservative feature. In all species it is trilacunar with one trace per leaf gap (Fig. 15b).

Leaves of *Xanthocephalum* are alternate, linear-lanceolate to lanceolate, simple, and entire or shallowly toothed. Leaves of *X. gymnospermoides* and *X. centauroides* show the greatest amount of serration or toothing, but entire leaves may occur as well. *Xanthocephalum gymnospermoides* has the broadest leaves of all *Xanthocephalum* studied.

Leaves of *Gutierrezia*, *Greenella*, *Amphiachyris*, *Thurovia*, and *Gymnosperma* are also alternate and linear-lanceolate. Those of *Gymnosperma* are much longer than those of most species studied.

Leaves of *Amphipappus* are alternate, entire, and, in contrast to those of the other species, oval to elliptic or obovate. Table 3 gives averages for both length and width of leaves of certain species. Figure 13 shows some of the shape and venation patterns noted.

Leaf anatomy of the genera shows striking similarities. A pronounced cuticle covers the upper and lower leaf epidermis of all species studied. At regular intervals on both surfaces of the epidermis are narrow cavities. Within each of these cavities is one to two multiseriate glands (Fig. 16a, b). This condition was found in all the species except *Amphipappus*. Solbrig (1966) found this condition to be uniform in the South American *Gutierrezia*. In addition to the multiseriate glands within the cavities, *X. gymnospermoides*, *Gutierrezia texana*, *G. sarothrae*, *G. microcephala*, and *Thurovia* show infrequent uniseriate trichomes on the surface of the upper epidermis as well. In *Amphipappus*, uniseriate trichomes two to three cells high are frequent on the upper and lower surfaces.

In all species studied the mesophyll contains abundant chloroplasts throughout the tissue except for the parenchymatous sheath surrounding the collateral vascular bundles. The leaves have prominent secretory canals associated adaxially with the vascular bundles.

DISCUSSION AND CONCLUSIONS

Features of the pappus were used chiefly by earlier botanists in delimiting these genera with less emphasis being placed on other morphological features. The character of the pappus, when coupled with features from other parts of the plant, is still a very important diagnostic feature. Solbrig (1960) points out that to use pappus characters successfully one must consider the pappus of both ray and disc florets. In addition one must comprehend the variation present in different species as well as the magnitude of variation within a given genus. *Gymnosperma* and *Greenella* are described by Solbrig (1960) as being similar in possessing, in both ray and disc florets, a reduced crown of minute scales instead of a well developed pappus. Yet in *Greenella ramulosa* both ray and disc florets have a well-developed pappus formed by lanceolate palae that resembles the characteristic pappus of *Gutierrezia*. The pappus of *Xanthocephalum* has been described as having only a low rim or crown in both ray and disc florets. Yet in *X. sericocarpum*, *X. linearifolium*, and *X. gymnospermoides* it is not uncommon to find well-developed pappi resembling to a great extent that in *Gutierrezia*. Certainly the nature of the pappus in *Amphiachyris* and *Amphipappus* is distinct enough to characterize these genera. Differences in structure and the fact that the ray floret in *Amphiachyris* does not show a well-developed pappus may serve as evidence for not including these two in the same genus.

The style of *Thurovia* definitely distinguishes it from the other genera. Even though these show some degree of coherence in style structure, it is worth noting that the style branch of the ray florets is longer than that of the disc florets in *Amphiachyris* and *Amphipappus* and no stigmatic papillae are present on the lower surface of the style branch. These characters can also be used to segregate the latter two genera from the others.

Amphipappus appears to demonstrate the greatest degree of differences in characters. In addition to those characters already mentioned, the structure of the leaves in *Amphipappus* is distinct from that of the other genera. In addition, secretory canals, except in the phyllaries, appear to be lacking. Sectioned leaves of all the other genera are almost indistinguishable, and secretory canals are frequent in various plant parts.

Certainly the occurrence of the hook-tipped receptacular glands in all species of *Gutierrezia* studied, in *Greenella*, and in *Xanthocephalum* adds unifying evidence to these previously distinct genera. In addition to the habit of *Thurovia* and other features already mentioned, the presence of these hook glands in *Thurovia* perhaps suggests the close relationship of *Thurovia* to the latter genera. A more thorough survey of the presence or absence of these glands in Astereae may prove valuable in determining the extent and usefulness of this character.

Because such few chromosome numbers were known in certain of the genera, a clear cytological concept of the groups was not perceived by Solbrig. At the time of Solbrig's study, the base chromosome number was considered to be four or a multiple of four in all *Gutierrezia* counted, five in *Amphiachyris*, seven in *Gymnosperma*, and nine in *Amphipappus*. Only one species of *Xanthocephalum* (*X. gymnospermoides*, $n=6$) and none of *Green-*

ella had been counted. In addition, Tomb (personal communication) has found $n=5$ for *Thurovia triflora*. Table 13 shows that counts now available for *Greenella arizonica* and for four more of the eight species of *Xanthocephalum* indicate a base of $n=4$. These findings certainly eliminate the generic differences suggested by Solbrig (1960) among *Xanthocephalum*, *Gutierrezia*, and *Greenella*.

TABLE 4. Previous meiotic chromosome counts in *Amphiachyris*, *Amphipappus*, *Greenella*, *Gutierrezia*, *Gymnosperma*, *Thurovia*, and *Xanthocephalum*

Species	Counts	Reference	Habit
Amphiachyris dracunculoides	$n=5$	Solbrig et al. (1964), Solbrig (1960).	annual
Amphipappus fremontii	$n=9$	Raven et al. (1960), Solbrig (1960).	perennial
Greenella arizonica	$n=4$	Solbrig et al. (1964).	annual
Gutierrezia californica	$n=8$, 12, 16 24	Rudenberg & Solbrig (1963).	perennial
G. mandonii ssp. *mandonii*	$n=12$	Solbrig (1966).	perennial
G. microcephala	$n=8$, 16	Solbrig (1960), Rudenberg & Solbrig (1963).	perennial
G. sarothrae	$n=4$, 8	Solbrig (1960), Rudenberg & Solbrig (1963).	perennial
	$n=8$	Solbrig et al. (1964), Solbrig (1965).	
G. texana	$n=4$	Solbrig (1960), Turner & Ellison (1960), Rudenberg & Solbrig (1963), Solbrig et al. 1964).	annual
Gymnosperma glutinosum	$n=7$, 8	Solbrig (1960), Solbrig et al. (1964), Solbrig et al. (1969).	perennial
Thurovia triflora	$n=5$	Spencer Tomb (Unpublished count).	annual
Xanthocephalum gymnospermoides	$n=6$	Raven et al. (1960), Solbrig (1960), Turner et al. (1962), Dejong & Longpre (1963).	annual
X. humile	$n=4$	Turner et al. (1962).	annual

X. linearifolium	$n=4$	Turner (Solbrig, 1961), Beaman & Turner (1962).	perennial
X. sericocarpum	$n=4$	Dejong & Longpre (1963).	annual
X. wrightii	$n=4$	Solbrig (1961).	annual

Based on morphological and anatomical data and also recent cytological findings, I believe that the most reasonable concept for this complex would be to merge *Xanthocephalum*, *Gutierrezia*, and *Greenella* into one genus and to maintain *Gymnosperma*, *Amphiachyris*, *Amphipappus*, and *Thurovia* as distinct genera. Since *Xanthocephalum* is the earliest name in the group to be merged, it is the correct name for it.

Even though *Thurovia* shares many morphological and anatomical features with members of the *Xanthocephalum* complex, its absence of ray flowers, its style, and its base chromosome number suggest that further biosystematic studies are needed to assess its relationship with *Xanthocephalum*. However, morphological, anatomical, and cytological evidence clearly indicates that *Greenella* and *Gutierrezia* should not be maintained as distinct and show enough unifying characters to be transferred into *Xanthocephalum*.

KEY TO THE GENERA

A. Pappus of disc florets composed of well-developed setae basally united, almost equaling corolla.
  B. Involucre elongate-turbinate; ray florets 1–2; disc florets fewer than 10; pappus of both ray and disc florets composed of well-developed setae; perennial shrubs . . . . *Amphipappus*
  BB. Involucre broadly campanulate; ray florets more than 5; disc florets more than 10; pappus of ray florets reduced to a low crown; annuals herbs (or possibly short-lived perennials) . . . . *Amphiachyris*
AA. Pappus scaly or reduced to low crown in disc as well as in ray florets.
  C. Ray florets absent . . . . *Thurovia*
  CC. Ray florets present
    D. Ray corollas shorter than or equal to the disc corollas *Gymnosperma*
    DD. Ray corollas longer than disc corollas . . . . *Xanthocephalum*

GENERIC SYNONOMY

AMPHIACHYRIS Nutt., Trans. Amer. Philos. Soc. 7:313. 1840.
AMPHIPAPPUS Torr. & Gray, Boston J. Nat. Hist. 5:107. 1845.
GYMNOSPERMA Less., Syn. Gen. Comp. 194. 1832. (nom. conserv.)
  Selloa Spreng., Nov. Prov. Hal. 36. 1819.
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XANTHOCEPHALUM Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 1:132. 1807.
  Brachyris Nutt., Gen. 2:163. 1818.

Brachyachyris Spreng., Syst. 3:574. 1825.
Greenella Gray, Syn. Fl. N. Amer. 1:480. 1884.
Gutierrezia Lag., Nov. Gen. et Spec. 30. 1816.
Hemiachyris DC., Prodr. 5:313. 1836.
Odontocarpha DC., Prodr. 5:71. 1836.

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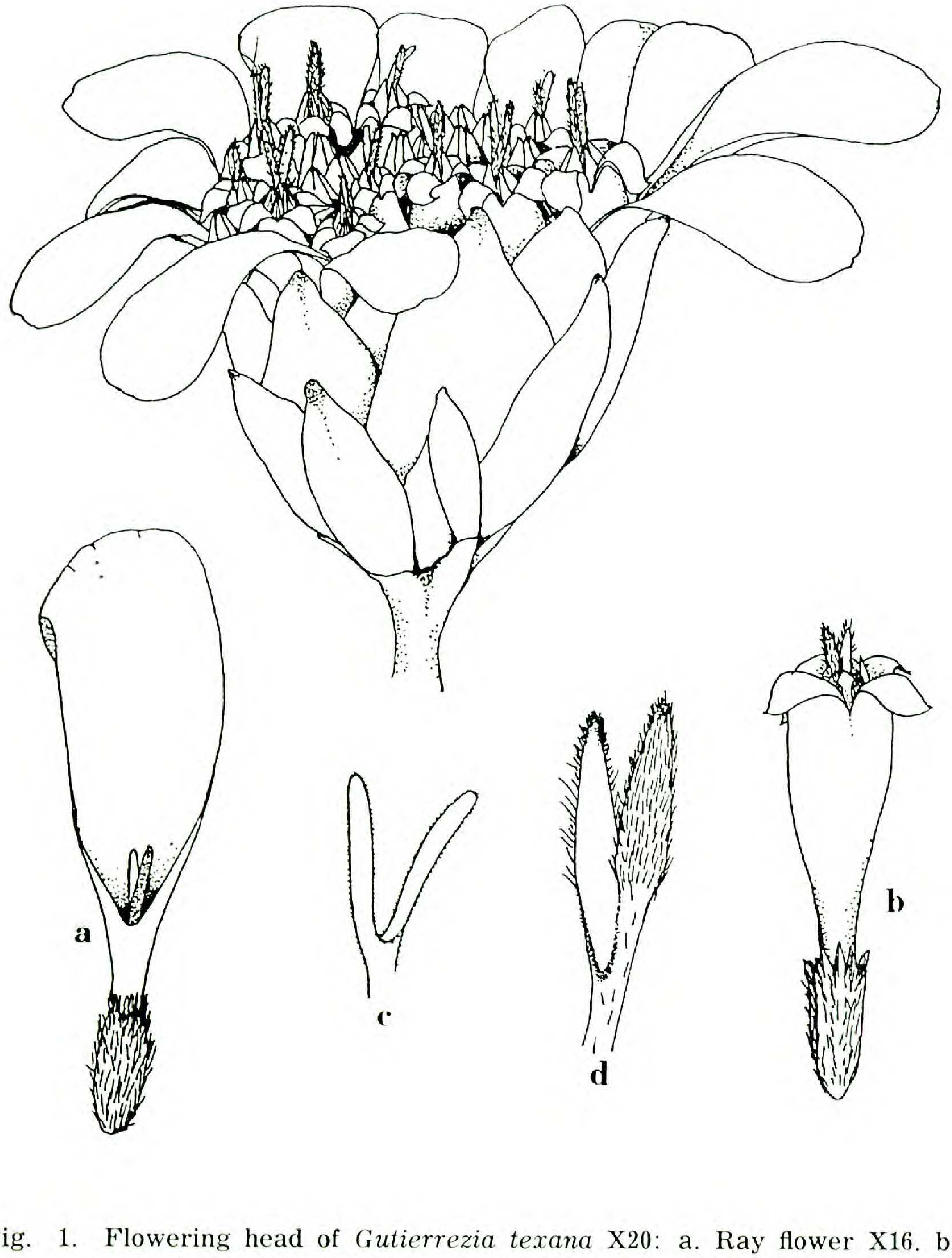

Fig. 1. Flowering head of *Gutierrezia texana* X20: a. Ray flower X16. b. Disc flower X20. c. Style branch of ray flower X30. d. Style branch of disc flower X25.

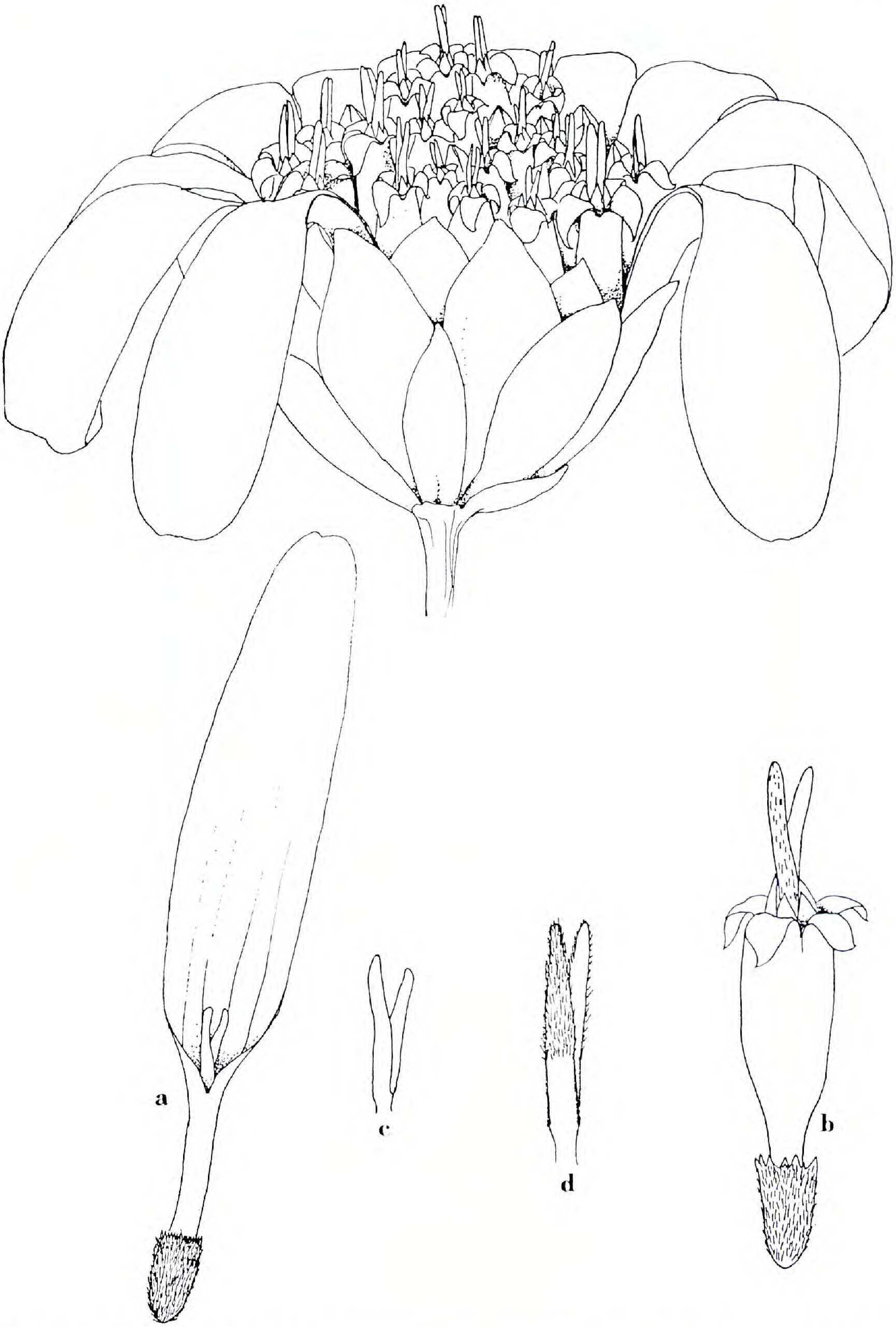

Fig. 2. Flowering head of *Greenella arizonica* X16: a. Ray flower X10. b. Disc flower X10. c. Style branch of ray flower X16. d. Style branch of disc flower X10.

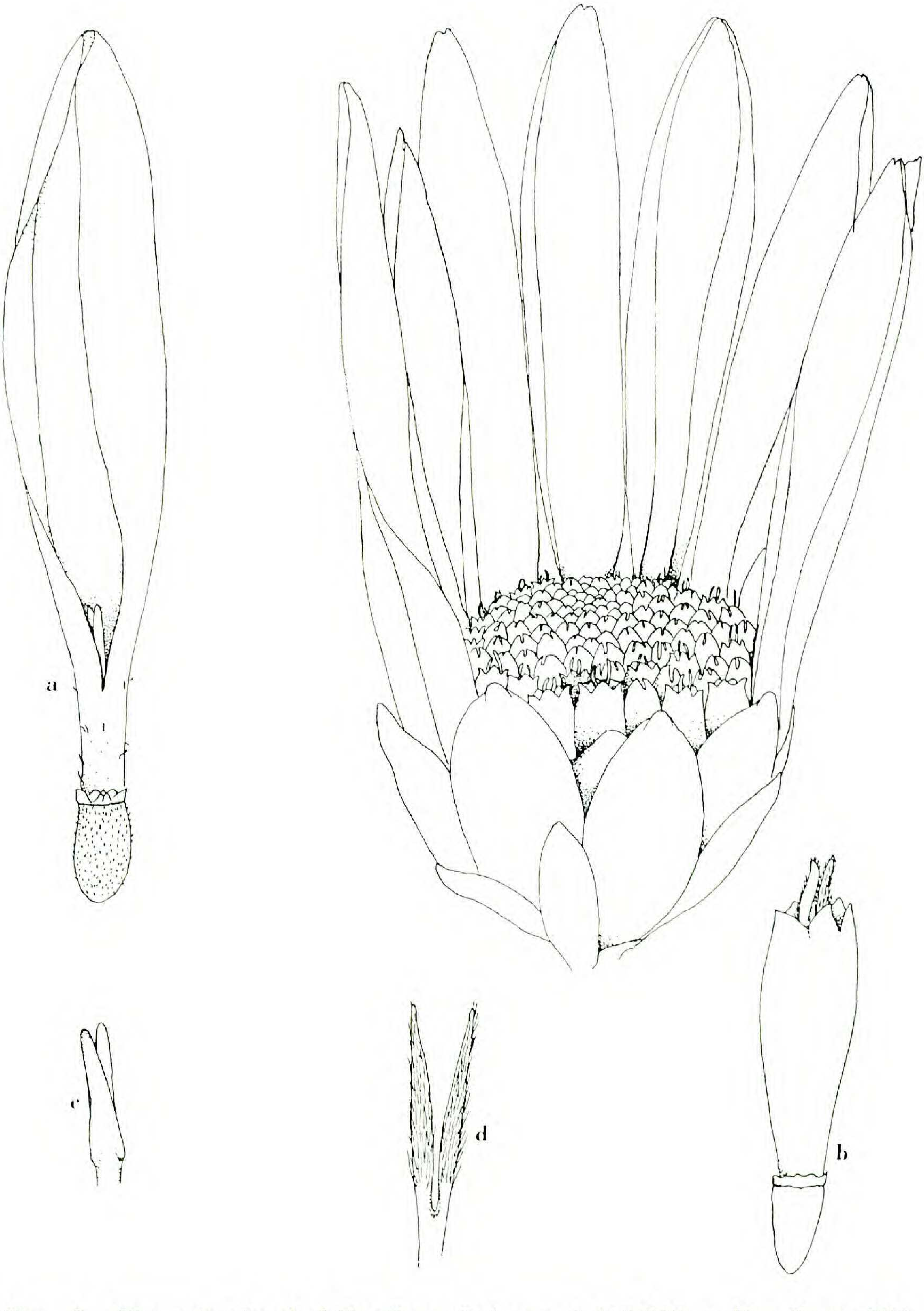

Fig. 3. Flowering head of *Xanthocephalum wrightii* X25: a. Ray flower X10. b. Disc flower. Note the presence of glabrous achene, X10. c. Style branch of ray flower X20. d. Style branch of disc flower X16.

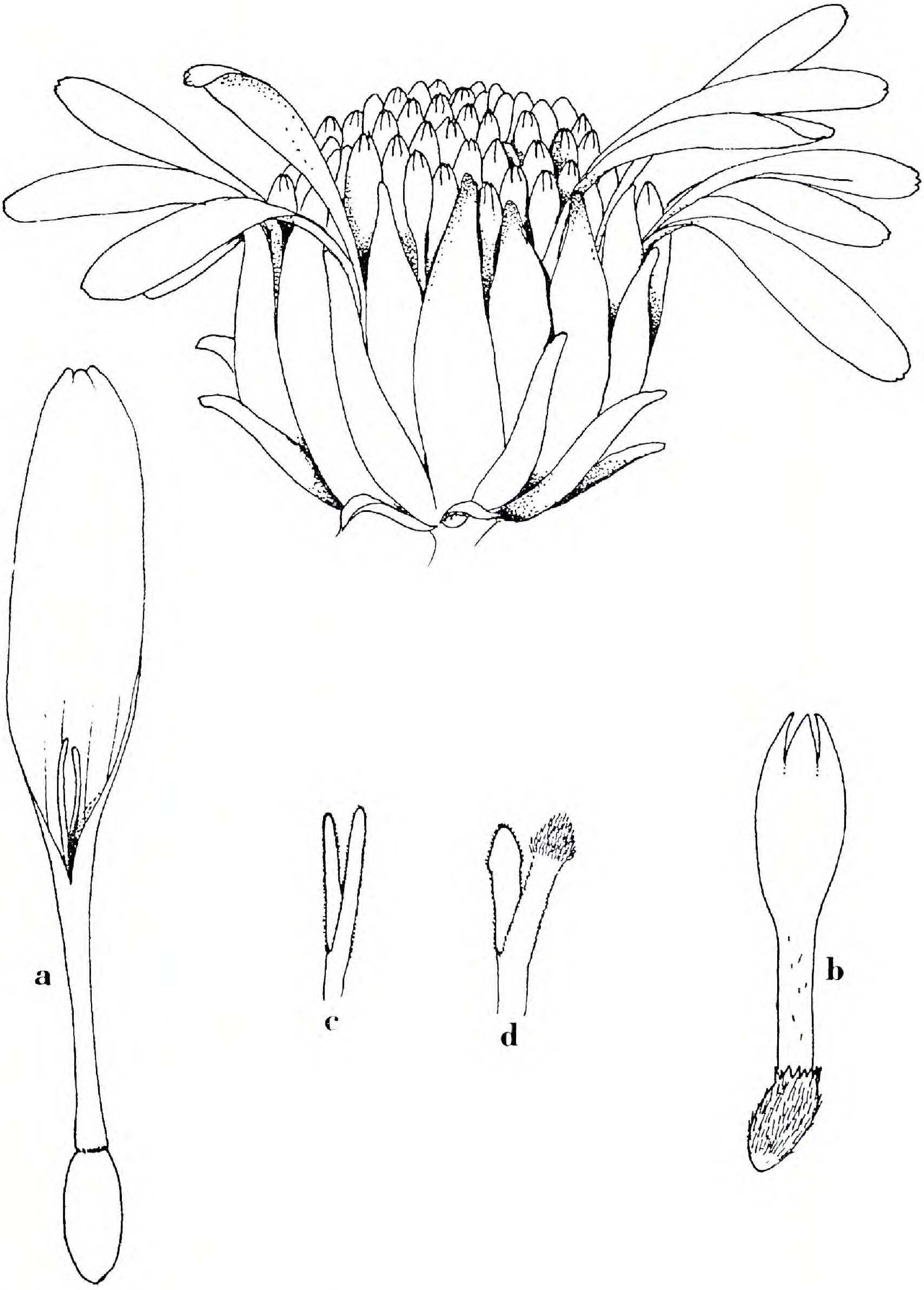

Fig. 4. Flowering head of *Xanthocephalum gymnospermoides* X12: a. Ray flower X12. b. Disc flower X10. c. Style branch of ray flower X16. d. Style branch of disc flower X16.

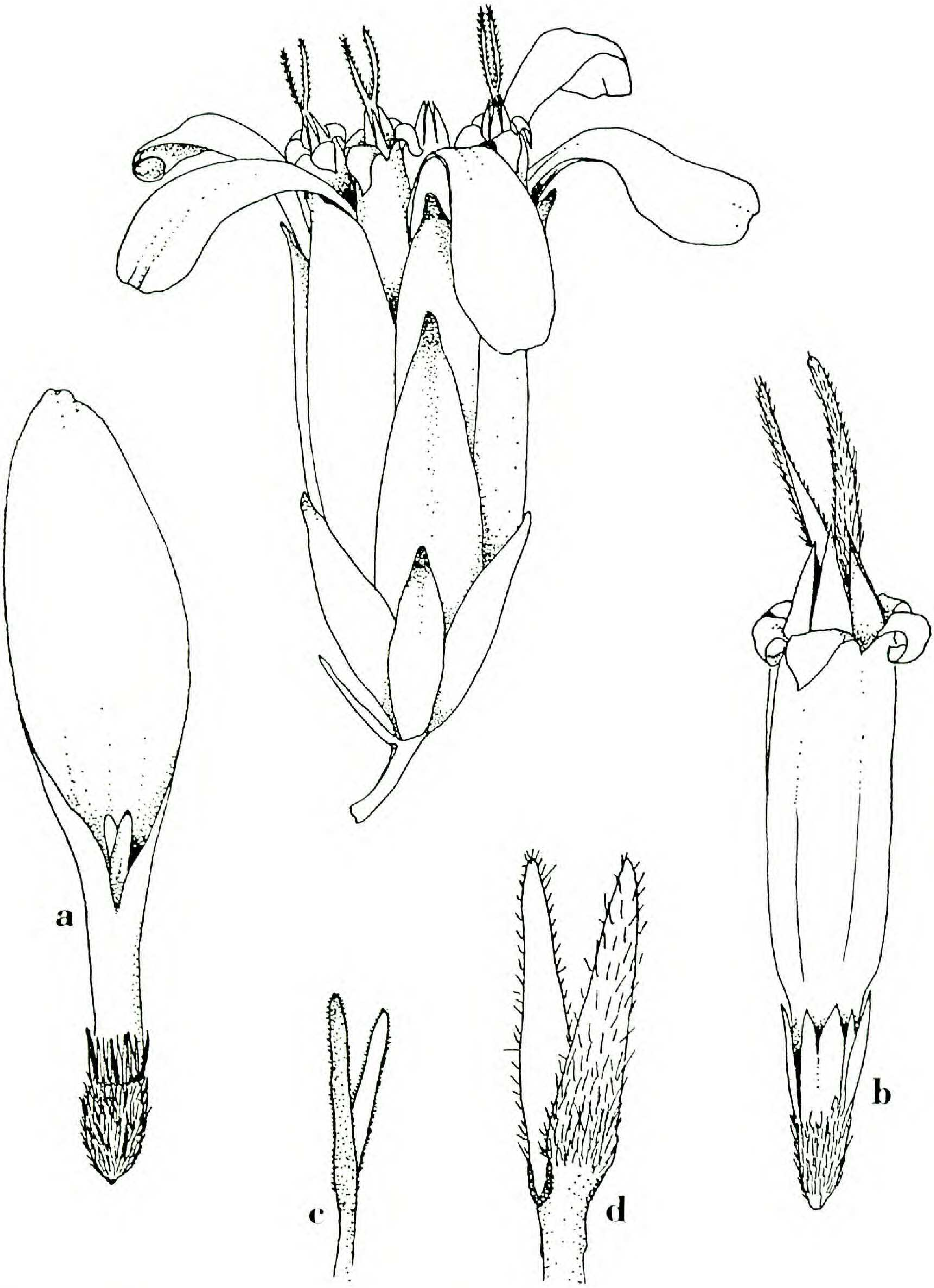

Fig. 5. Flowering head of *Gutierrezia sarothrae* X20: a. Ray flower X20. b. Disc flower X20. c. Style branch of ray flower X25. d. Style branch of disc flower X25.

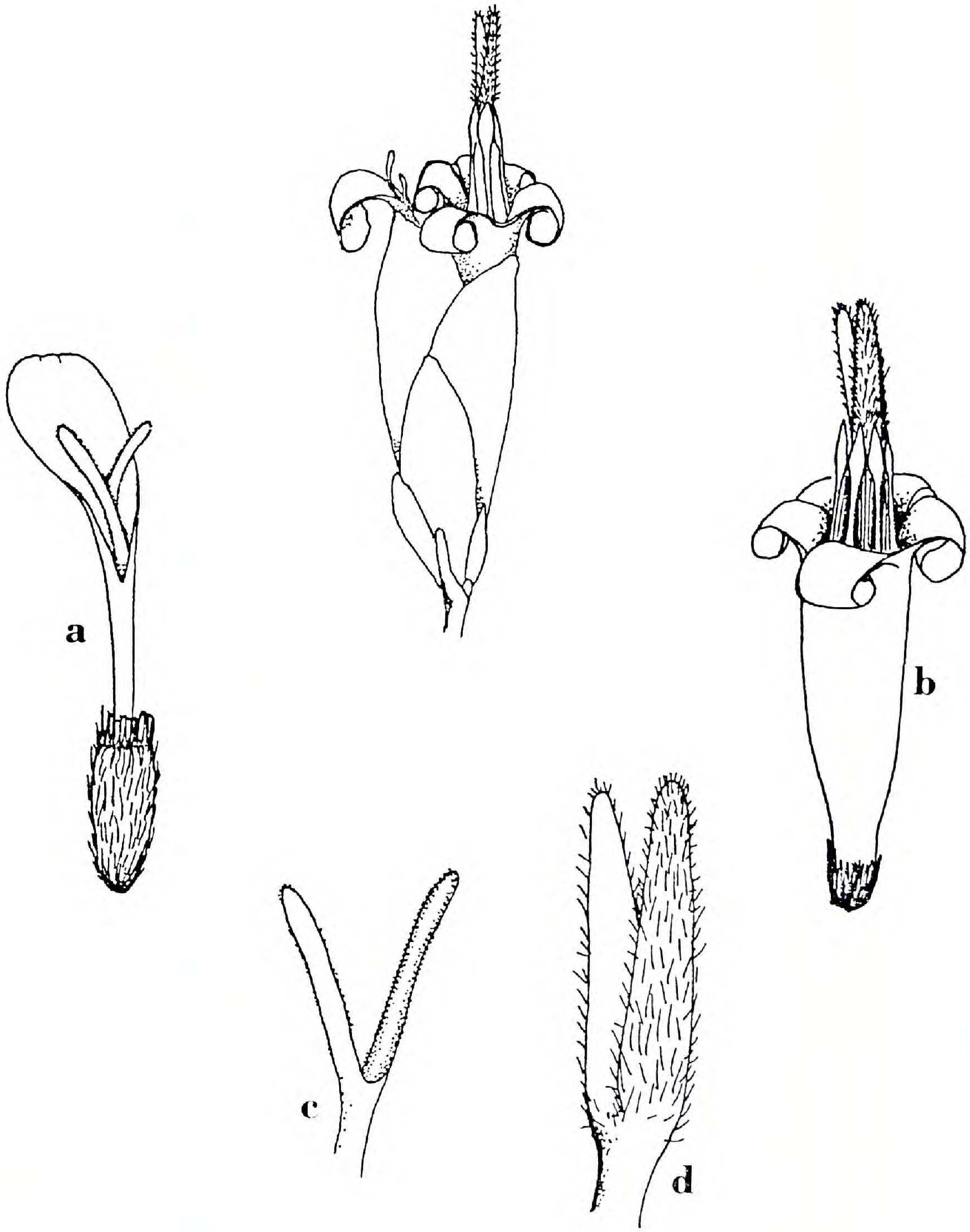

Fig. 6. Flowering head of *Gutierrezia microcephala* X20: a. Ray flower X16. b. Disc flower X20. c. Style branch of ray flower X25. d. Style branch of disc flower X25.

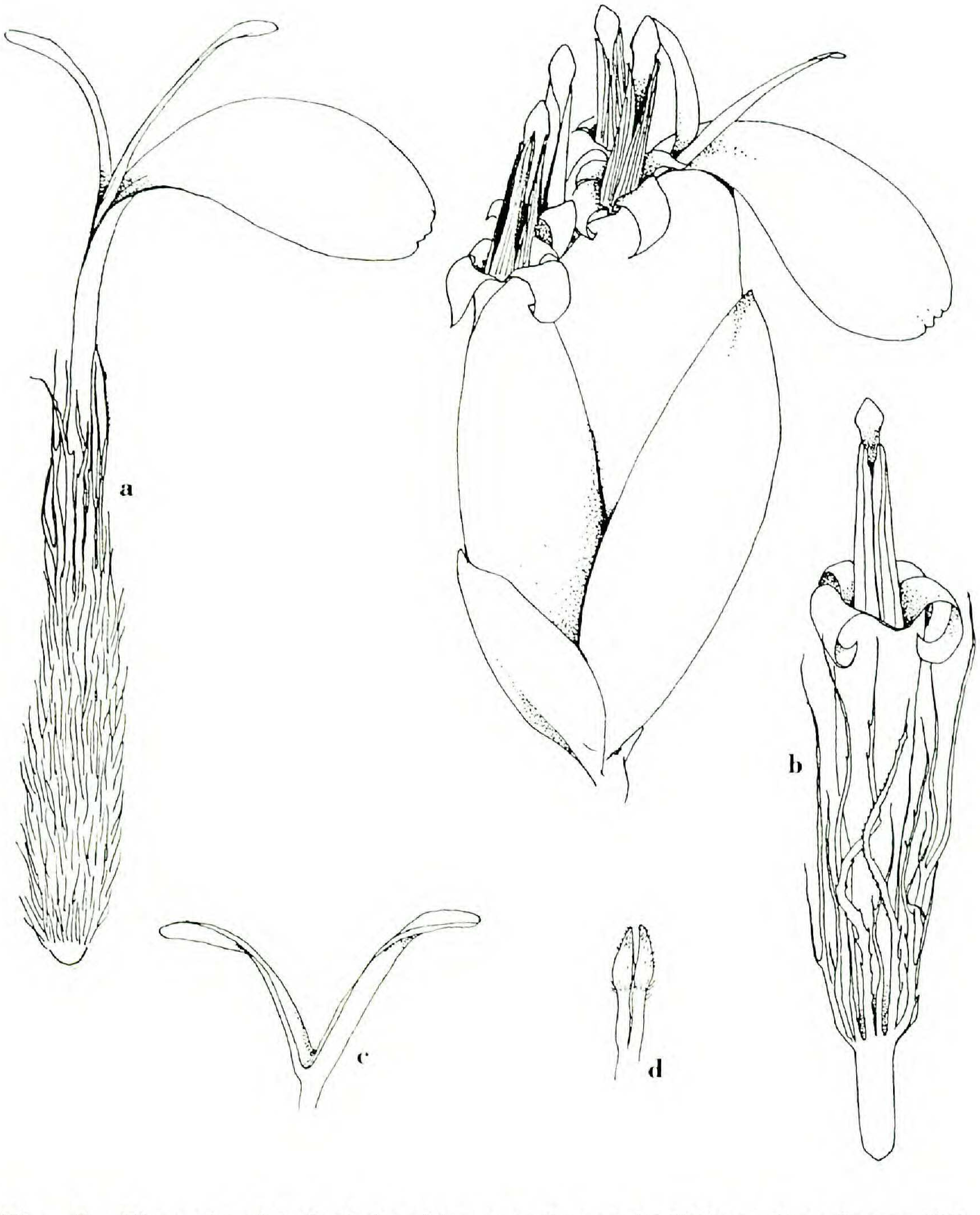

Fig. 7. Flowering head of *Amphipappus fremontii* X20: a. Ray flower X25. b. Disc flower X16. c. Style branch of ray flower X16. d. Style branch of disc flower X25.

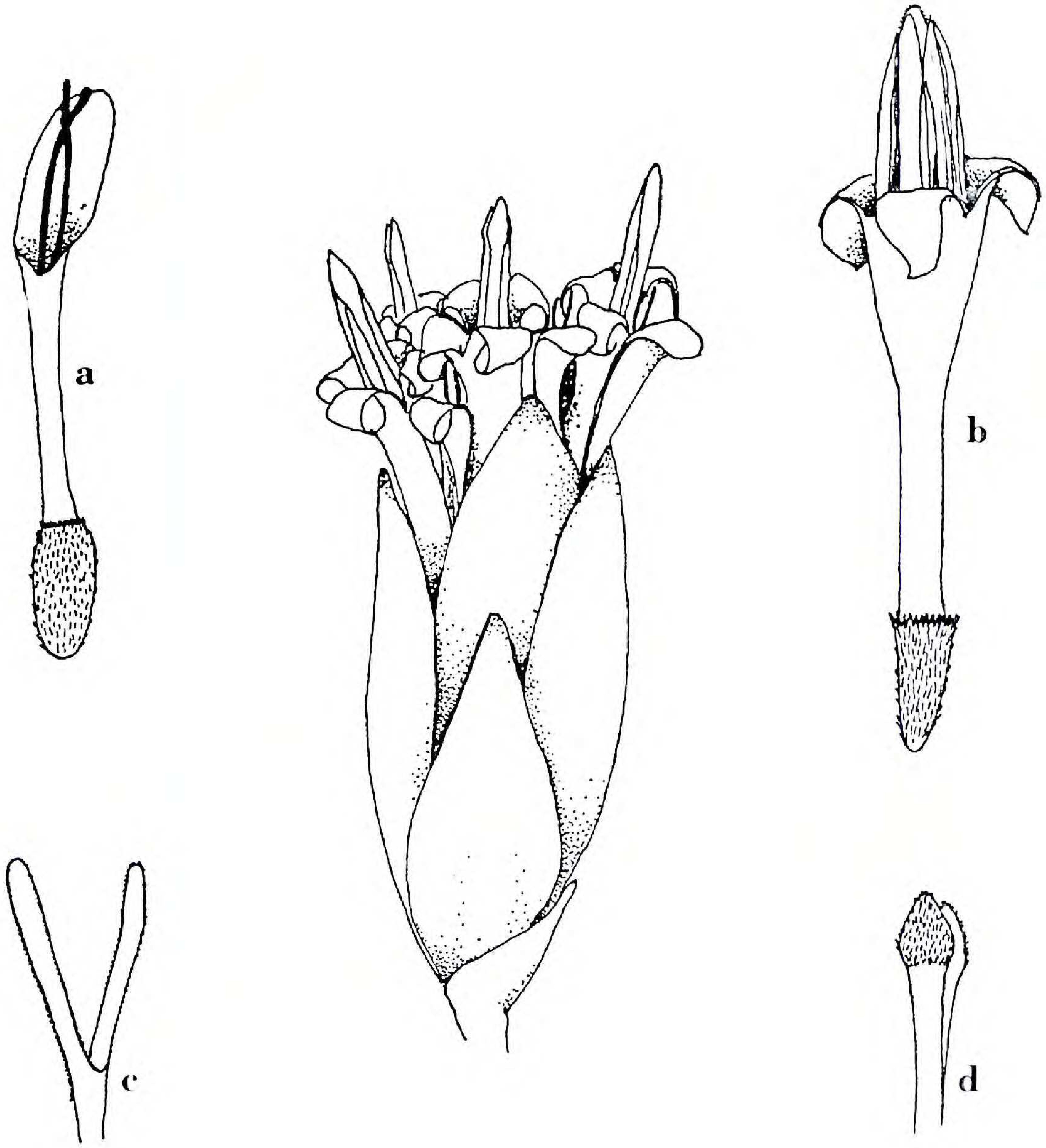

Fig. 8. Flowering head of *Gymnosperma glutinosum* X16: Note ray flowers which do not surpass the tubular ones giving the head a discoid appearance: a. Ray flower X20. b. Disc flower X20. c. Style branch of ray flower X25. d. Style branch of disc flower X20.

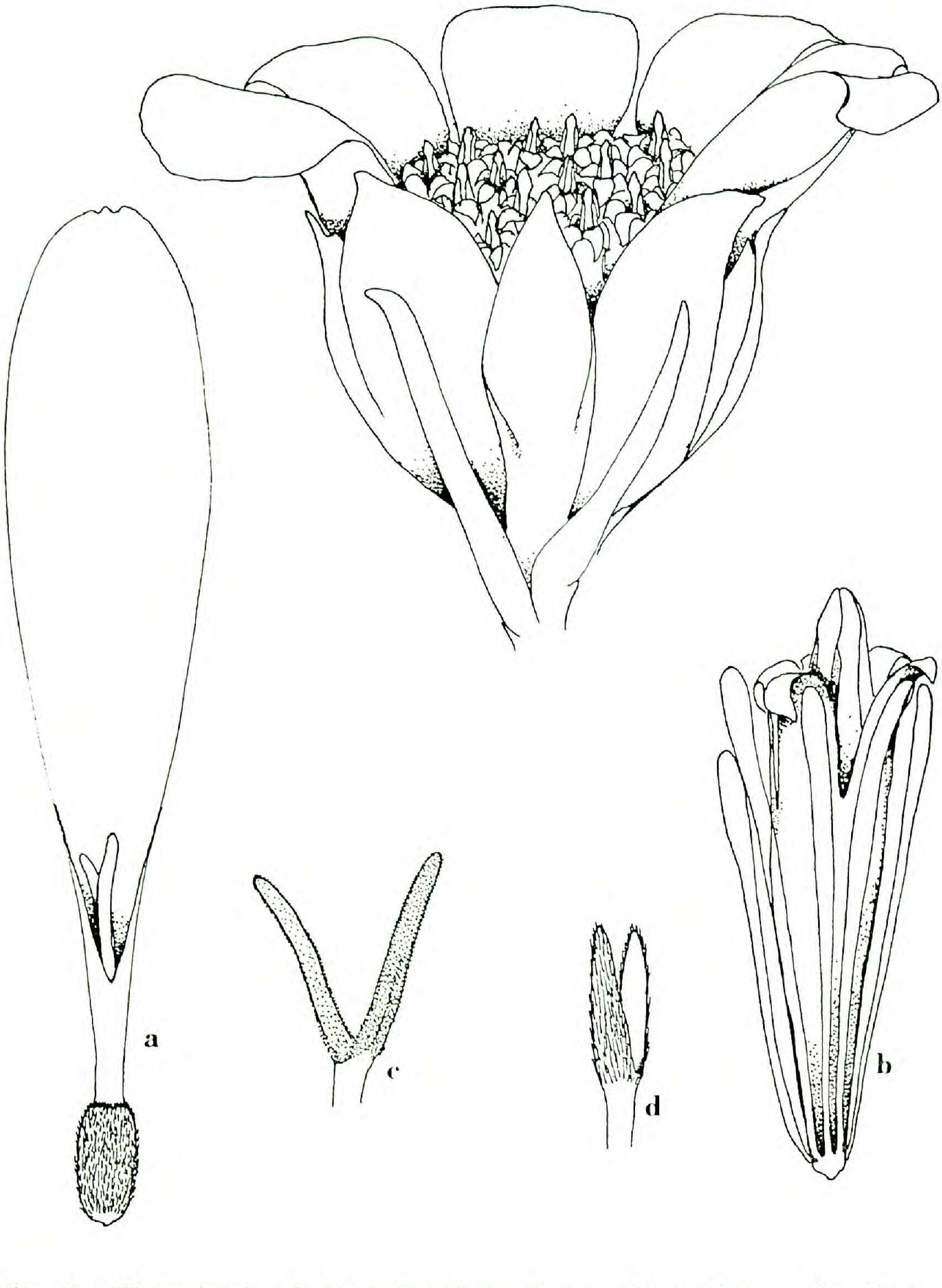

Fig. 9. Flowering head of *Amphiachyris dracunculoides* X20: a. Ray flower X30. b. Disc flower X25. c. Style branch of ray flower X30. d. Style branch of disc flower X25.

Fig. 10. Flowering head of *Amphiachyris amoenum* var. *intermedium* X16: a. Ray flower X16. b. Disc flower X20. c. Style branch of ray flower X20. d. Style branch of disc flower X25.

Fig. 11. Flowering head of *Amphiachyris amoenum* var. *amoenum* X16: a. Ray flower X16. b. Disc flower X20. c. Style branch of ray flower X20. d. Style branch of disc flower X20.

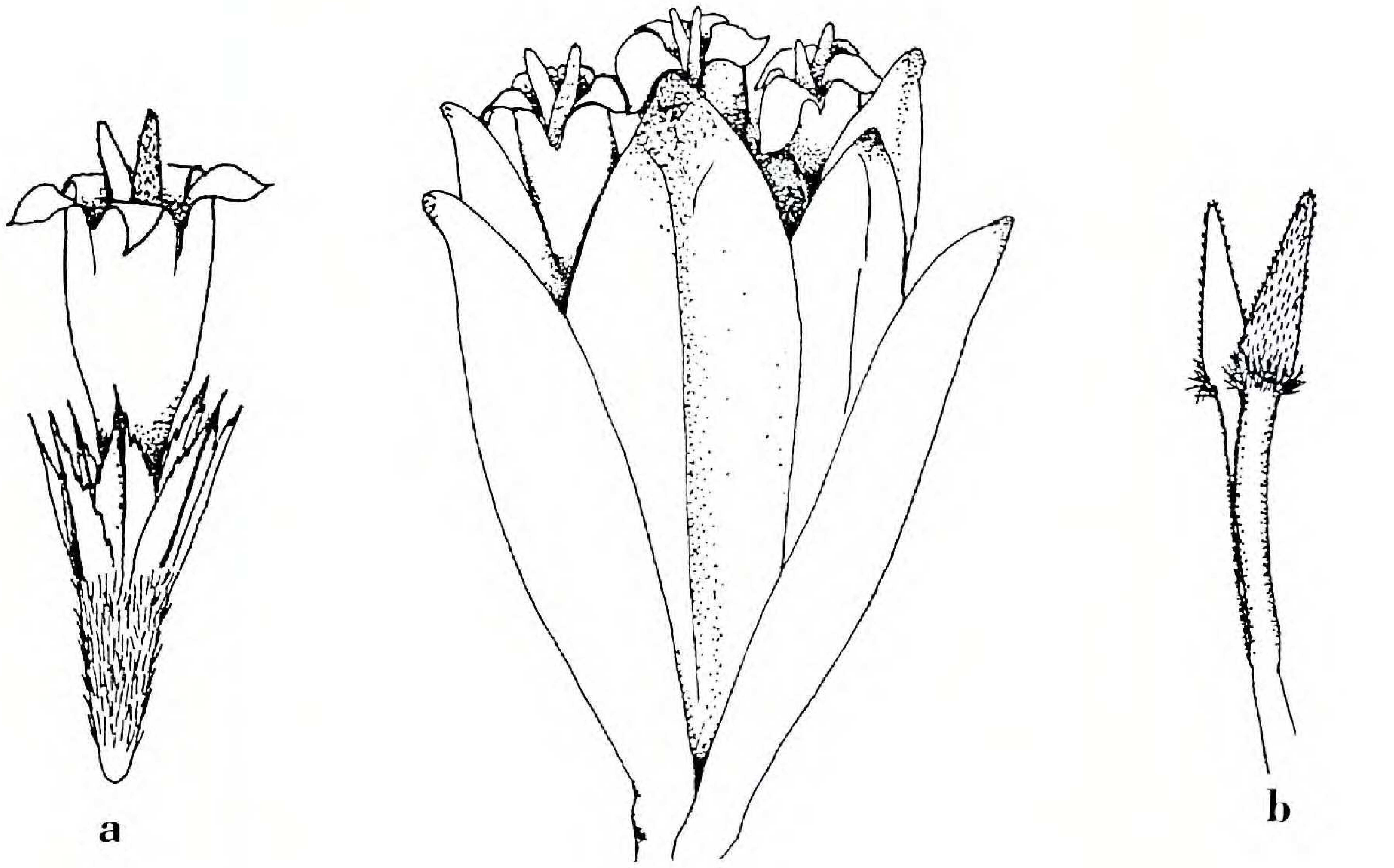

Fig. 12. Flowering head of *Thurovia triflora* X20: a. Disc flower X16. b. Style branch of disc flower X16.

Fig. 13. Leaf shape and venation. Only major veins are drawn: a. *Xanthocephalum linearifolium*. b. *X. gymnospermoides*. c. *X. wrightii*. d. *X. centauroides*. e. *X. sericocarpum*. f. *Gymnosperma glutinosum*. g. *Greenella arizonica*. h. *Thurovia triflora*. i. *Amphipappus fremontii*. j. *Gutierrezia sarothrae*. k. *G. taltalensis*. l. *Amphiachyris dracunculoides*. m. *A. amoenum* var. *intermedium*.

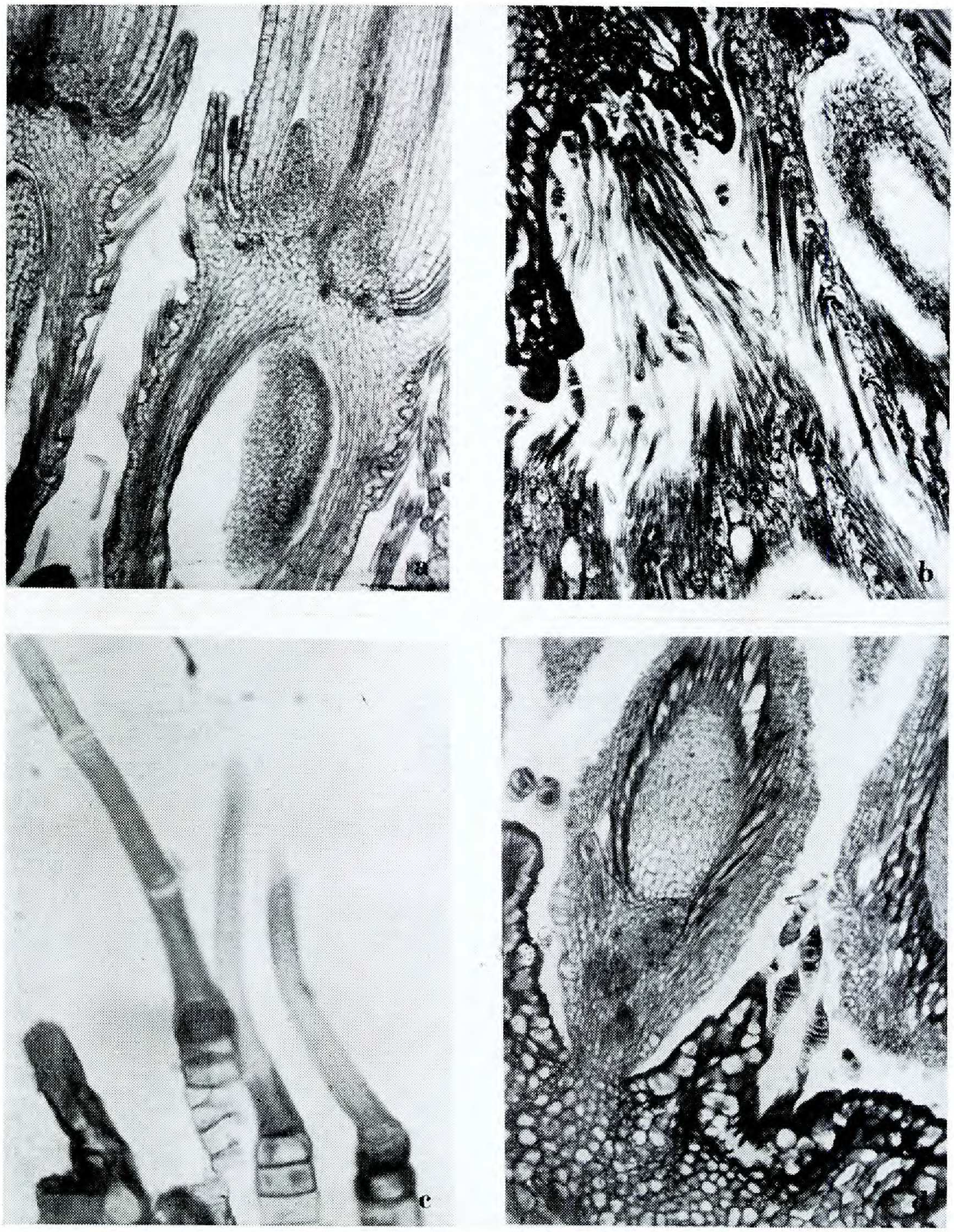

Fig. 14. Longitudinal sections: a. *Xanthocephalum gymnospermoides* flower showing biseriate non-glandular "zwillingshaar" trichomes. Note trichomes are situated on "mounts" originating on the wall of the achene. Also note nectary glands surrounding the style base, X89. b-d. Hook-like receptacular glands: b. *Gutierrezia texana*, X89. c, *Greenella arizonica*, X351. d. *Xanthocephalum wrightii*, X89.

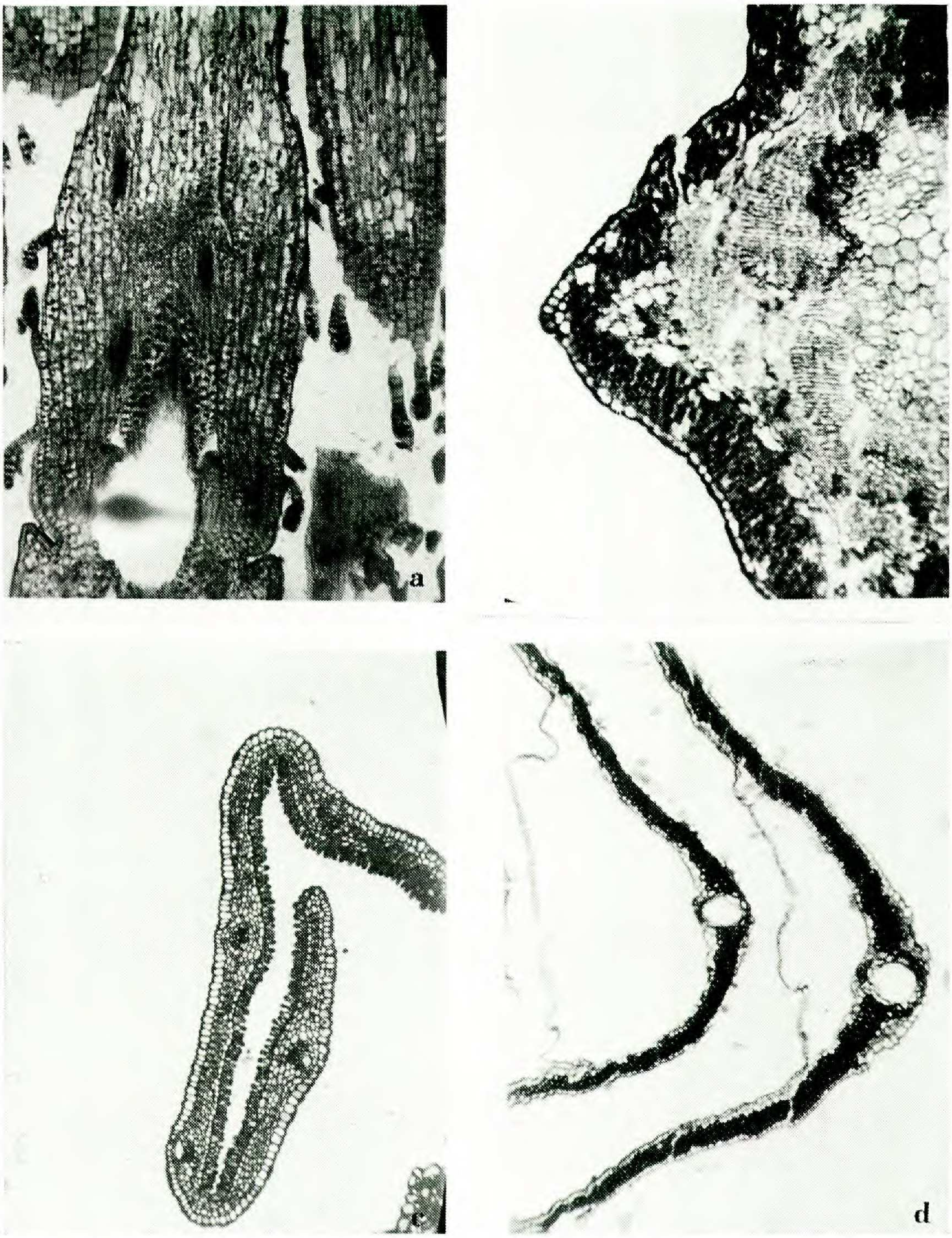

Fig. 15. a. Longitudinal section of *Xanthocephalum humile* flower showing abundant occurrence of glandular trichomes along lower half of corolla tube, X89. b. Cross-section of *Gutierrezia texana* stem showing trilacunar nodal structure, X89. c. *Xanthocephalum wrightii* ray cross-section showing papillate epidermal ray cells and secretory canals adaxial to each vascular bundle, X89. d. *Greenella ramulosa* showing vascular bundle with conspicuous secretory canal. Note strong alignment of involucral bracts, X89.

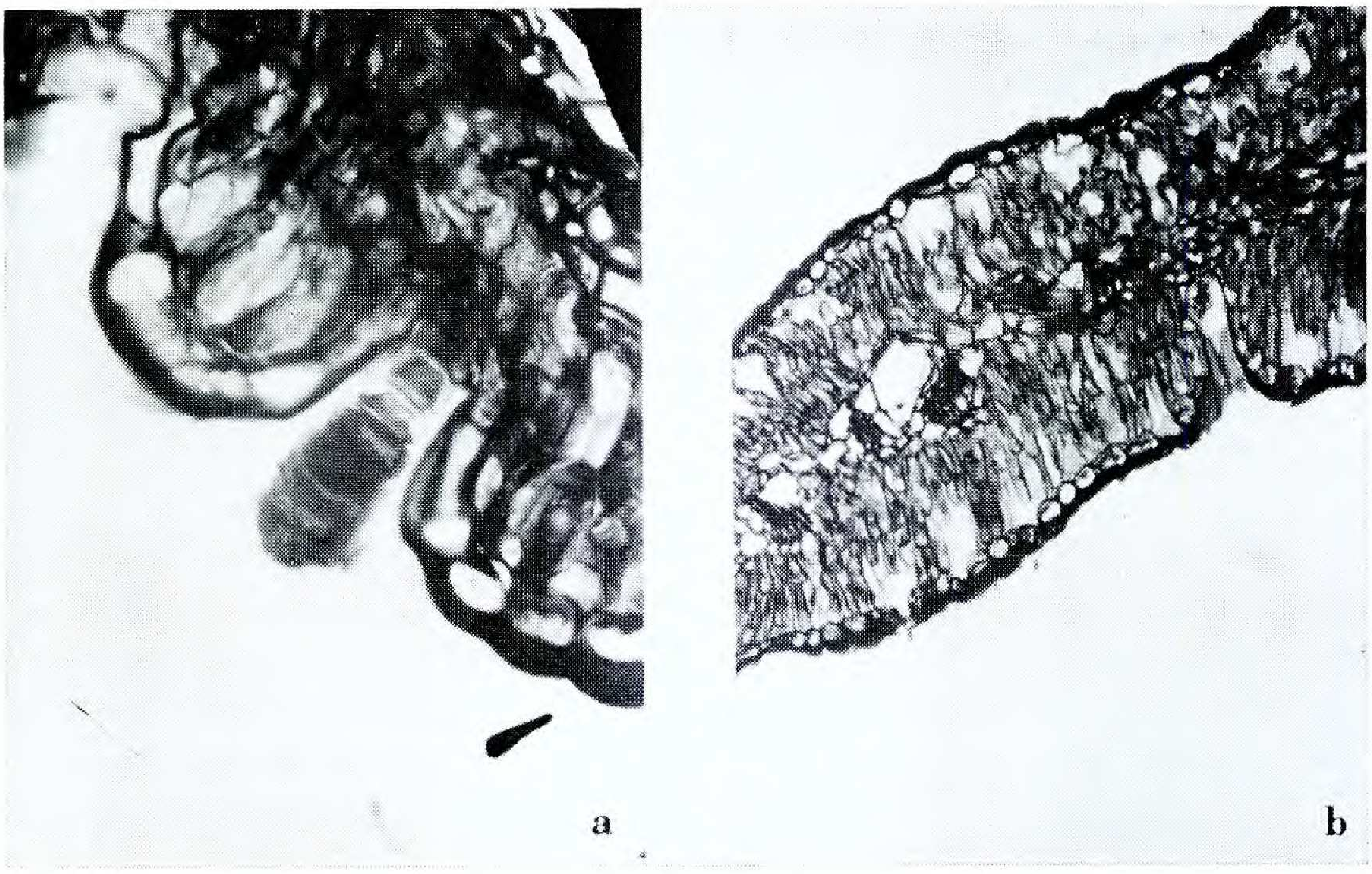

Fig. 16. Leaf transections showing the presence of glands within cavities: a. *Gutierrezia texana*, X351. b. *Gymnosperma glutinosum*, X89.