9-2001

Stem Morphology and Anatomy in *Amaranthus* L. (*Amaranthaceae*)—Taxonomic Significance

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Journal of the Torrey Botanical Society 128(3), 2001, pp. 254–281

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COSTEA, MIHAI (Department of Botany, University of Agronomical Sciences, Bucharest, Romania) and DARLEEN DEMASON (Botany and Plant Sciences, University of California, Riverside, CA 92521). Stem morphology and anatomy in Amaranthus L. (Amaranthaceae) taxonomic—significance. J. Torrey Bot. Soc. 128: 254–281. 2001.—The range of variation within the genus *Amaranthus* L. (Amaranthaceae) is described for a number of stem characters including: morphology, epidermis, primary stem vasculature and mechanism of secondary growth. The results provide new characters (phyllotaxy, complexity of leaf vascular supply and relative amount of secondary growth) that support (1) a new infrageneric classification (subgenus *Amaranthus* vs subgenus *Albersia* (Kunth)Gren. & Dodr.), and (2) the separation within the "*hybridus*" complex of cultivated amaranths (*A. caudatus* L., *A. cruentus* L. and *A. hypochondriacus* L.) from their presumed wild ancestors (*A. hybridus* L. subsp. *quitensis* (Kunth) Costea & Carretero, *A. hybridus* L. subsp. *hybridus* and *A. powellii* S. Wats. subsp. *powellii* respectively).

Key words: *Amaranthus,* stem, morphology, anatomy, trichomes, primary vascular system, secondary growth, taxonomy.

In spite of the fact that the genus *Amaranthus* has been the subject of many taxonomic studies, it is still poorly understood and is widely considered to be a "difficult" genus. It consists of about 70 species, of which about 40 are native to the Americas and the rest to Australia, Africa, Asia and Europe. The infrageneric classification of the genus is still an unresolved problem. The classification most frequently used was suggested by Sauer (1955) in which he designates 2 subgenera: *Acnida* (L.) Aellen ex K. R. Robertson, which includes the dioecious species; and *Amaranthus,* which includes the monoecious species. Traditionally, the subgenus *Amaranthus* has been divided in two sections: *Amaranthus* (= *Amaranthotypus*); and *Blitopsis* Dumort *sensu lato* (Thellung 1914; Covas 1940; Morariu 1940; Aellen 1959; Brenan 1961, 1981; Gusev 1972; Frey 1974; Carretero 1979; Robertson 1981; Hugin 1986, 1987; etc.). Carretero (1985, 1991) divided the section *Blitopsis sensu lato* in two sections: *Blitopsis,* which includes those species having indehiscent fruits and x = 17; and *Pyxidium,* which includes those with dehiscent fruits and x = 16. Another section, *Puncticulatae,* was proposed by Kowal (1954) for *A. viridis* and *A. acutilobus,* but it was not validated by later studies (Klopper and Robel 1989a; Costea 1997c). Recently, Mosyakian and Robertson (1996) proposed the subgeneric rank [subgenus *Albersia* (Kunth) Gren. & Godr.] for the section *Blitopsis sensu lato.* This infrageneric classification with 3 subgenera (*Acnida, Amaranthus* and *Albersia*) is based on classical characters, such as those of inflorescence and floral characteristics, and it would be interesting to see if other characters support it too.

At the species level, most of the taxonomic problems involve the most studied group of species, the *A. hybridus* aggregate. The actual taxonomic treatments in this group of species, assuming that the nomenclatural problems are solved, range between two extremes. At one extreme is that of Sauer (1950, 1967) in which he recognizes the cultivated taxa (*Amaranthus caudatus, A. cruentus* and *A. hypochondriacus*) as species. And at the other is that of Greuter (1981, 1984) who lumps the cultivated species with their putative wild progenitors (*A. quitensis, A. hybridus* and *A. powellii* respectively). All possible intermediate possibilities between these

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two opposing treatments, many of them published since the beginning of the century by Thellung (1907, 1914, 1919), have also been used (Aellen 1959, 1964, 1972; Dostal 1950; Morariu 1952; Brenan 1961, 1981; Gusev 1972; Ehrendorfer 1973; Townsend 1974, 1985, 1988; Carretero 1979, 1985, 1990; Stace 1991, 1997; Lambinon 1992; Cserepanov 1995; etc.). Detailed studies of the relationship among the amaranth species using cytological or molecular methods are often contradictory. However, the combined results support separating the cultivated and wild taxa, over combining them (Pal and Khoshoo 1972, 1974; Hauptli and Jain 1984; Wilkin 1992; Sammour et al. 1993; Greizerstein and Poggio 1994, 1997; Transue et al. 1994; Lanoue et al. 1996; Chan and Sun, 1997).

Some common, unusual features characterize the stem anatomy of many families in the Caryophyllales (including *Amaranthaceae*). Among these are anomalous secondary thickening, occurrence of two or more rings of primary vascular bundles and complex organization of leaf traces associated with leaf gaps (Gibson 1994). Some of these features have been used to characterize relationships between families within this order (Eckardt 1976; Cronquist 1981; Thorne 1983; Gibson and Nobel 1986).

Although there are some detailed morphological studies of seeds (Kowal 1954, Klopper and Robel 1989a; Costea 1997b), fruits (Klopper and Robel 1989a; Costea 1997a), and pollen (Costea 1998), anatomical characteristics of vegetative and reproductive organs have not previously been seriously used for the resolving taxonomic relationships of the genus. Viana (1993) described some general aspects of anatomy in *A. viridis*. The influence of herbicides on the stem structure was studied in *A. retroflexus* and *A. powellii* (Rugina et al. 1984; Nita 1997), and ecological factors in *A. blitoides* (Toma et al. 1994). The primary vascular system has been analyzed only in *A. caudatus* (Gravis and Constantinesco 1907), *A. hybridus* and *A. graecizans* (? = *A. albus*) (Wilson 1924).

The objectives of this study were to evaluate the taxonomic value of stem characters in the amaranths to see if they provide additional perspectives on the taxonomic problems elaborated upon above. We analyzed general stem morphology, epidermal characteristics, the primary vascular system and the mechanism of secondary growth in the stems of amaranths.

Materials and Methods. MATERIALS. Taxa were collected between 1991 and 1996. Seeds collected from wild populations or received from various Botanical Gardens were cultivated in the Botanical Garden of the University of Agronomy, Bucharest, Romania (Table 1). All *Amaranthus retroflexus* plants were collected from the ruderal flora of Bucharest. Seedlings were transplanted into 17 x 29 x 18 cm plastic pots filled with clay soil (57.2% clay, 31.9% silt, 3.9% fine sand, 2.8% medium sand and 1.2% coarse sand). Organic matter content and pH were 10% and 7.2 respectively. Voucher specimens were placed in the Herbarium of the University of Agronomic Sciences, Bucharest (BUAG in the next edition of the Index Herbariorum) and in BUCA herbarium.

MICROSCOPY. Seedlings, young shoots, and stems of different ages, were fixed in a 50 or 70% ethanol mixture with 2% formalin, and 5% acetic acid (FAA) and embedded in Paraplast or paraffin. Typically, 25 plants of all ages, for each population were serially sectioned at 10μm, stained with safranin and fast green, mounted in Canada balsam, and examined with standard brightfield optics and with polarized light. The courses of primary vascular bundles were traced downward from each node through serial transverse sections. The courses of these bundles were presented both in transverse sections chosen at characteristic points (where changes in phyllotaxy and bifurcation of leaf trace bundles occurred) and in longitudinal diagrams. The thickness of the secondary tissue produced by the first cambium was measured immediately above the area of anomalous growth. Stem epidermal peels were obtained from the middle region of stems of mature plants. These peels were cleared with chloral hydrate, stained with carmine-alaunate (carmin "Nacarat", 0.1% in 0.7% $AlK(SO_4)_2$) and mounted in gelatinized glycerine (Serbanescu-Jitariu et al. 1983). Trichomes from the upper part of the stem, both in sections and from epidermal peels stained with Delafield's haematoxylin were also examined with standard brightfield optics. All drawings were made using a Reichart camera lucida.

VASCULAR TISSUE TERMINOLOGY. In this work, we have combined the older terminology specific to the *Amaranthaceae* of Gravis and Constantinesco (1907) with the more modern and general eustele terminolgy used by Beck et al. (1982). A *leaf trace* is a bundle that diverges from an axial bundle, or another leaf trace, and extends into a leaf. *Leaf vascular supply* is used for the sum total of traces passing to one leaf.

Table 1. Provenance of *Amaranthus* species examined for stem features.

Taxa	Voucher no.	Provenance	Collection date
Subgenus *Acnida* (L.) Aellen ex K. R. Robertson			
A. palmeri S. Wats.	23150 (a-j)	Romania-Constantza, ruderal	20 Sep 1994
A. rudis Sauer	23033 (a-j)	Romania-Constantza, ruderal	20 Sep 1994
Subgenus *Amaranthus* (= section *Amaranthus*)			
A. caudatus L.	23050 (a-s)	Romania, Bucharest	18 Nov 1994
		Mexico*	29 Sep 1995
A. cruentus L.	23037 (a-s)	Romania, Bucharest	18 Nov 1994
		India*	29 Sep 1995
A. hypochondriacus L.	22769 (a-s)	Romania, Bucharest	18 Nov 1994
		India*	29 Sep 1995
A. powellii S. Wats. subsp. *powellii*	22770 (a-s)	Romania, Constantza, ruderal	10 Oct 1993
		Spain, Valencia, ruderal	30 July 1996
A. powellii S. Wats. subsp. *bouchonii* (Thell.) Costea et Carretero	23041 (a-s)	Romania, Bucharest, ruderal	26 Aug 1996
		Spain, Valencia, ruderal	24 July 1996
A. hybridus L. subsp. *hybridus*	22721 (a-s)	Romania, Constantza, ruderal	15 Oct 1994
		Spain, Valencia, ruderal	25 July 1996
A. hybridus L. subsp. *quitensis* (Kunth) Costea et Carretero	22840 (a-s)	Romania, Ploiesti, ruderal	12 Nov 1995
A. spinosus L.	23160	Gatersleben, Germany	16 Oct 1996
A. retroflexus L.	21822 (a-s)	Romania, Bucharest, ruderal	10 Aug 1993
		Spain, Valencia, ruderal	28 July 1996
Subgenus *Albersia* (Kunth) Gren. & Godr. (= Section *Blitopsis* Dumort.)			
A. albus	21800 (a-s)	Romania, Bucharest, ruderal	3 Aug 1993
		Spain, Valencia, ruderal	28 July 1996
A. blitum L. subsp. *blitum*	23049 (a-j)	Romania, Danube Delta, ruderal	16 Sep 1994
A. blitum subsp. *oleraceus* (L.) Costea	23051 (a-s)	Germany*	9 Oct 1994
A. blitum L. subsp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Munoz Garmendia & Pedrol var. *emarginatus*	22996 (a-s)	Romania, Tulcea, ruderal	16 Sep 1994
		Spain, Valencia, ruderal	24 July 1996
A. blitum L. subsp. *emarginatus* var. *pseudogracilis* (Thell.) Costea	23046 (a-s)	Romania, Tulcea, ruderal	16 Sep 1994
		Spain, Valencia, ruderal	16 July 1996
A. viridis L. = *A. gracilis* Poiret	23034 (a-s)	Romania, Constantza, ruderal	20 Sep 1994
		Spain, Valencia, ruderal	7 July 1996
A. blitoides S. Wats. var. *blitoides*	23045 (a-s)	Romania, Constantza, ruderal	20 Sep 1994
		Spain, Valencia, ruderal	6 July 1996
A. blitoides S. Wats. var. *reverchonii* Uline & Bray	23046 (a-s)	Romania, Constantza, ruderal	20 Sep 1994
A. graecizans L. subsp. *graecizans*	23042 (a-s)	Romania, Bucharest, ruderal	25 Aug 1996
A. graecizans subsp. *sylvestris* (Vill.) Brenan	2632 (a-j)	Romania, Ghimpati, ruderal	8 Aug 1994
A. crispus (Lesp. & Thev.) N. Terracciano	22225 (a-j)	Romania, Bucharest, ruderal	3 Sep 1993
A. deflexus L.	22228 (a-s)	Romania, Bucharest, ruderal	9 Nov 1993
		Spain, Valencia, ruderal	18 July 1996

Branch traces are comparable to leaf traces, except that the former is associated with lateral shoots. An *interfascicular region* is a region of interfascicular parenchyma in the vascular cylinder between two axial bundles and opposite a diverging leaf trace or several associated traces of a leaf. An *axial bundle* is a major longitudinal vascular bundle that runs continuously along the length of a stem and produces leaf and branch traces. In *Amaranthus* there are two types of axial bundles: larger, inner bundles, which we call *major axial anastomotic bundles* and smaller, outer bundles derived from them, which we call *minor axial bundles.* A *sympodium* is generally defined as an axial bundle and its associated leaf and branch traces. However, it is not a very useful term in *Amaranthus* due to the closed nature of the stele and the fact that the vascular supply to each leaf is derived from two adjacent major axial anastomotic bundles.

Results. MORPHOLOGY OF THE STEM. Depending on environmental conditions, the stem of amaranths is remarkably variable in terms of length, diameter, orientation, branching pattern and color. For example, in unfavorable condi-

tions the shoot of *A. retroflexus*, *A. powellii* and *A. hybridus* may not exceed several centimeters long, whereas in favorable conditions it can exceed 2 meters long, or even more. In this respect, Prof. A. J. Sharp sent Sauer a photograph taken in a Florida swamp showing a man climbing on a tree-like (7–9 meters tall) *Amaranthus australis* (Sauer 1955). Although normally erect, this species can also adopt a prostrate habit as a result of mechanical (cutting, trampling) or chemical (herbicides) perturbations. Axillary bud initiation and branching patterns depend on the species as well as environmental conditions. In *Amaranthus blitoides* and *A. crispus* the main shoot usually begins to branch during seedling development from axillary buds associated with the cotyledons. *A. albus* normally has a divaricate pattern of branching, but in the absence of light it tends to remain unbranched (f. *simplex* Morariu). This commonly occurs when seeds germinate in a field that is already covered by the plants of other species. In all species of this genus, mechanical factors such as clipping or trampling trigger the development of secondary shoots. Stem color may vary even in the same vegetation cycle, and in temperate climates stems typically turn red in the autumn. Based on such "characters", an impressive number of varieties, forms and subforms have been described (Thellung 1912; Priszter 1952; Morariu 1950). To test the stability of stem morphology, we cultivated several such "forms" of *A. retroflexus* in the same conditions.

1. f. *pusillus* Opiz.—stems 2–5 cm height.
2. f. *humistratus* Thell.—prostrate stems.
3. f. *simplex* Priszter –unbranched stems.
4. f. *nivrensis* Zapal.—stems very branched, branches divaricate.
5. f. *semidecumbens* Dum.—main axis erect, branches decumbent.
6. f. *major* (Moq.) Thell.—stems up to 2 m height.

During the flowering and fruiting phases of development, the plants grown from these seeds were impossible to tell apart because they were not genetically distinct. Although such ecophenes do not deserve taxonomic status, they are ecologically important and should be listed in a future monograph of the genus. They could be indicated with a name that is not governed by the code of nomenclature and subject to priority, as Buch (1922–1928) did for the liverworts, for example. Stace (1989) referred to such names as "modifications" (abbreviated mod.). In many cases the previous Latin names are appropriate because they are suggestive.

Although the potential (and real) morphological variability of stems in this genus is tremendous, we have to emphasize that each species has a tendency toward a characteristic morphological type (Table 2).

THE STEM EPIDERMIS. The stem epidermis in this genus does not have a uniform arrangement of cells. It possesses narrow longitudinal zones with stomata and wide longitudinal zones lacking stomata. In the areas with stomata, which we call *stomatiferous zones*, the epidermal cells are more or less isodiametric, contain chloroplasts and have thin, primary cell walls (Fig. 1). Only in *A. powellii* subsp. *bouchonii* (Fig. 1i) and *A. deflexus* (Fig. 1d) are there elongated cells in the stomatiferous zones. In most species, the guard cells are surrounded by 2 to 8 neighboring general epidermal cells, so the stomatal apparatus is *anomocytic*. Only in *A. spinosus* (Fig. 1k) are distinct subsidiary cells present around some guard cells and the arrangement is the *actinocytic* along with the *anomocytic* types. The stomatiferous zones are typically 3–20 cells wide and may be sunken or not in comparison with the areas without stomata. If plants are grown in the same environmental conditions, the width, level of the stomatiferous zones and number of neighboring cells around the guard cells, can be considered reliable characters. The species of the "*hybridus*" complex have relatively uniform epidermal features compared to the variability exhibited by the species of the subgenus *Albersia* (except for those of the A. *blitum* agg.) (Table 3).

In zones that lack stomata, epidermis cells are heterodiametric and very narrow. In addition, they have thickened primary cell walls and lack chloroplasts. Trichomes occur only in the non-stomatiferous zones. They are identical to those present on the leaves, in that they are multicellular and uniseriate or mixed multiseriate and uniseriate, and rarely papillate (Table 3). The uniseriate trichomes frequently have a multicellular base and the terminal cell is swollen and is larger than the other cells (Fig. 2). An indumentum was noted in the inflorescence region or in the upper part of the stem. It is glabrescent, puberulent, pubescent or lanate.

PRIMARY VASCULAR SYSTEM IN THE STEM OF AMARANTHUS. The main stem of amaranths possesses a great number of primary and secondary vascular bundles (up to several hundred). This

Table 2. Simple characteristics of the stem in *Amaranthus* species.

Taxa	Position of the stem	Color of the stem
Subgenus *Acnida*		
A. palmeri	erect	green
A. rudis	erect	green
Subgenus *Amaranthus*		
A. caudatus	erect	red
A. cruentus	*erect*	*red*
A. hypochondriacus	*erect*	*red*
A. powellii subsp. *powellii*	*erect*	*green with reddish stripes*
A. powellii subsp. *bouchonii*	*erect*	*green or green with reddish stripes*
A. hybridus subsp. *hybridus*	*erect*	*green*
A. hybridus subsp. *quitensis*	erect	green
A. retroflexus	erect	green, sometimes whitish
Subgenus Albersia		
A. albus	erect	bone-whitish
A. blitum subsp. *blitum*	plagiotrophic to ascendant	green (rarely reddish)
A. blitum subsp. *oleraceus*	erect	green or reddish
A. blitum subsp. *emarginatus* var. *emarginatus*	prostrate	green
A. blitum subsp. *emarginatus* var. *pseudogracilis*	ascendant	green
A. viridis	erect/ascendant	green
A. blitoides	prostrate	green
A. graecizans subsp. *graecizans*	erect/ascendant	green
A. graecizans subsp. *sylvestris*	erect/ascendant	green
A. crispus	prostrate	brownish
A. deflexus	prostrate/decumbent	green/brownish

number varies along the stem at different levels. As seen in transverse section, the primary bundles are organized in 2 or 3 concentric rings (secondary bundles are treated in the next section). The outer ring consists of minor axial and branch trace bundles. The innermost ring(s) is (are) formed by the major axial anastomotic and leaf trace bundles. Each set of leaf traces (leaf vascular supply) is flanked on either side by two major axial anastomotic bundles.

The eustele of seed plants is made up of primary vascular tissue that is organized as individual strands of continuous axial bundles, which sequentially and periodically produce leaf trace complexes (Esau 1965; Beck et al. 1982; Romberger 1993; Fahn 1995). Each leaf trace is ultimately derived from an axial bundle or bundles. The same principle applies to all branch traces (bud traces in the early stages of development). Shoot vascular systems in dicotyledons are either open, when sympodia (axial bundles and their associated leaf traces) are separate and do not anatomose or are closed when regular connections occur between sympodia (Dormer 1945; Beck et al. 1982). Although sympodia in closed systems can be interconnected, either by regular anastomoses between adjacent sympodia or by interconnections of leaf traces, they are arranged more or less parallel to the stem axis, following the phyllotactic spirals of the shoot. According to Gibson (1994) the primary vascular system in amaranths is of the closed type because it consists of a network of bundles that anastomose along their path through the stem.

The number of primary bundles at a given level of the stem is determined by phyllotaxy, the organization of the leaf vascular supply, the number of axial bundles, the presence of branch traces and the number of internodes that both leaf and branch traces traverse before exiting the stem.

Phyllotaxy and Sympodium Arrangement. There is a direct relationship between phyllotaxy and the arrangement of the primary vascular

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FIG. 1. Stem epidermis and stomatal complexes of *Amaranthus*. a. *A. rudis*, b. *A. blitoides*, c. *A. cripsus*, d. *A. deflexus*, e. *A. albus*, f. *A. viridis*, g. *A. blitum* agg., h. *A. graecizans*, i. *A. powellii* subsp. *bouchonii*, j. *A. hypochondriacus*, *A. cruentus*, *A. caudatus*, *A. powellii* subsp. *powellii*, k. *A. spinosus*, l. *A. hybridus*, *A. retroflexus*.

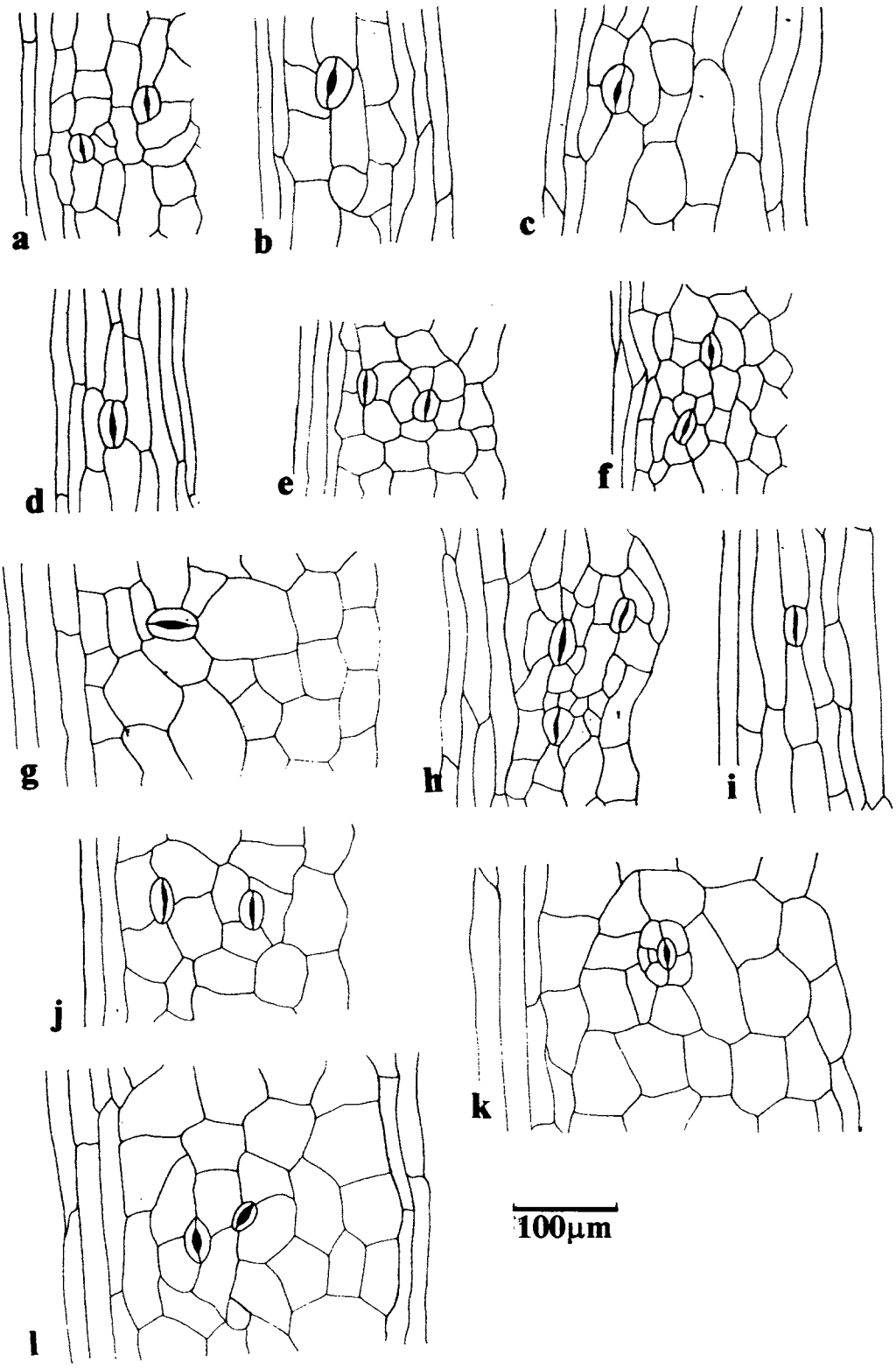
a
b
c
d
e
f
g
h
i
j
k
l
100µm

Table 3. Characteristics of the epidermis in *Amaranthus* species

Taxa	Width of the stomatiferous zones µm	Level of the stomatiferous zones: sunken = + unsunken = −	Number of cells surrounding stomata	Richomes and indumentum*
A. caudatus	45–90	+	2–5	m_u, 3–15 cells; pu to l
A. cruentus	45–90	+	2–5	m_u or $m_u + m_m$, 3–15 cells; pu = l
A. hypochondriacus	45–90	+	2–5	m_u, 3–10 cells; pu to pub
A. powellii subsp. *powellii*	45–90	+	2–5	m_u, 3–10 cells; pub
A. powellii subsp. *bouchonii*	−60	+/−	3–4	m_u, 3–10 cells; pub
A. hybridus subsp. *hybridus*	45–90	+	3–4	$m_u + m_m$, 4–25 cells; l
A. hybridus subsp. *quitensis*	45–90	+	3–4	$m_u + m_m$, 4–25 cells; l
A. retroflexus	45–90	+	3–4	$m_u + m_m$, 4–27 cells; l
A. albus	40–90	+	4–8	m_u or $m_u + m_m$, 4–18 cells pu to l
A. blitum subsp. *blitum*	200–260	−	3–5	m_u, 3–6 cells; g to pub
A. blitum subsp. *oleraceus*	200–260	−	3–5	m_u, 3–6 cells; g to pub
A. blitum subsp. *emarginatus*	200–230	−	2–5	m_u, 3–8 cells; g to pub
A. viridis	150–200	−	3–5	m_u, 3–8 cells; pu to pub
A. blitoides	40–90	−	3–4	unicellular, bicellular, m_u, 3-cells, sometimes with multiseriate base; pub
A. graecizans	40–90	−	4–8	bicellular, m_u, 3–9 cells; pub
A. crispus	85–130	+	3–4	p, $m_u + m_m$, 7–15 cells; pu
A. deflexus	40–75	+	3–4	m_u, 3–14 cells; pub to pu
A. rudis	100–120	+	2–6	m_u, 3–14 cells; pub to pu

* m_u = multicellular, uniseriate; m_m = multicellular, multiseriate; p = papillae; pu = pubescent; l = lanate, pub = puberulent; g = glabrescent.

system because the number of sympodia present at a given level in the stem axis corresponds to the number of leaf orthostichies (vertical ranks of superimposed leaves) at that particular position (Beck et al. 1982; Romberger et al. 1993). In *Amaranthus* this number may be 3, 4, 5 or 8. The sympodia are arranged more or less parallel to the stem axis and follow the phyllotactic spirals of the leaves.

The phyllotaxis varies at different stages of shoot ontogeny of an individual plant and within the genus. The phyllotaxis of the seedling and therefore of the basal, juvenile leaves (at the first 4 nodes) is approximately 1/2 (distichous). During shoot ontogeny the apical meristem becomes larger and the phyllotaxy is transformed into more complex patterns. However, the phyllotaxis of leaves from nodes 5 to 21 (23) is relatively constant for each species. It varies within the genus, being predominantly 2/5 for species of subgenus *Amaranthus* and 1/3 for species of the subgenus *Albersia.* Later in shoot ontogeny the phyllotaxis can increase to 3/8 in the species of the subgenus *Amaranthus* (especially in *Amaranthus caudatus, A. cruentus* and *A. hypochondriacus*) and to 2/5 in some species of the subgenus *Albersia* (*A. albus, A. blitoides* and *A. graecizans*).

Axial Anastomotic Bundles. Illustrated diagrammatically the axial bundles describe a more or less regular reticulum (Fig. 3a-b; Fig. 4a-b). This pattern is produced by the major axial bundles from the inner ring(s) that we call *anastomotic* (A), following the terminology of Gravis and Constantinesco (1907). Nodal anatomy in the amaranths is unilacunar. A parenchymatous *interfascicular region* (i.e. leaf gap or lacuna) is associated with the leaf traces between a pair of major axial anastomotic bundles giving rise to and flanking them along their course through the stem. Finally, this pair of major axial bundles fuses above the node at which the leaf vascular supply diverges into the leaf closing the interfascicular region. The minor axial bundles in the outer ring are branches of the major axial anastomotic bundles and they are positioned between the external branch bundles. Each major axial bundle is associated with 2 to 4 minor axial bundles (not represented in the longitudinal diagrams but illustrated in the transverse sections.) After they ascend one or 2 internodes they rejoin the major axial anastomotic bundles at the nodes. All the axial bundles in the stem join at more or less regular points along their course through the stem axis as is typical of a closed system.

Leaf Traces. The organization of leaf traces in amaranths is very peculiar. The leaf vascular

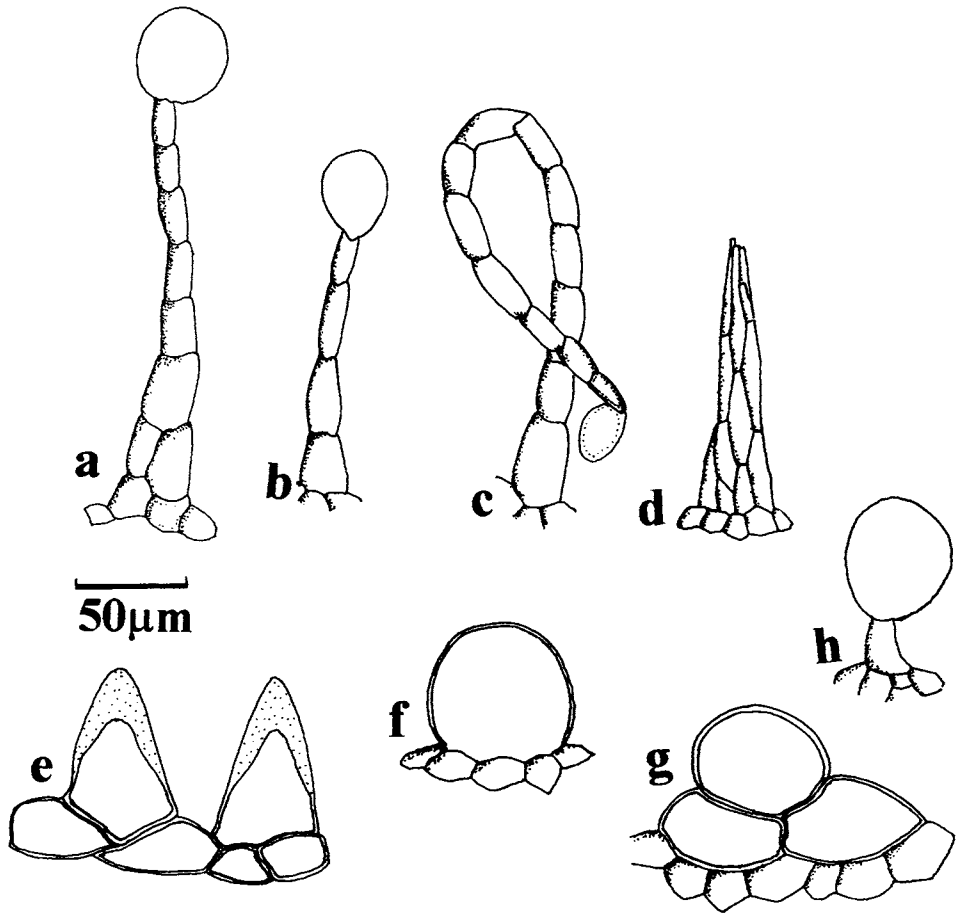

FIG. 2. Stem trichomes of *Amaranthus*. a. *A. caudatus*, b. *A. powellii*, c. *A. deflexus*, d. *A. retroflexus*, *A. hybridus*, e. *A. crispus*, f.-g. *A. blitoides*, h. *A. graecizans*.

supply (examined along its entire course) consists of a central bundle—the *median bundle* (M), which is flanked laterally and symmetrically by 2 *intermediate* (i), 2 *lateral* (L) and a number (1–3) of *marginal* bundles *of various orders* (m, m' and m"). The number of bundles within the leaf vascular supply varies both during shoot ontogeny and also between the species (or groups of species). During shoot ontogeny, the number of bundles associated with juvenile leaves (base of the stem) is lower, it increases gradually reaching a maximum, and finally, decreases again toward the end of the plant's life span. An exception to this rule among the species examined is *A. crispus*, which displays a constant 3-bundle leaf vascular supply throughout shoot ontogeny. The range of variation in leaf trace bundle arrangements is stable during the life of the plant if the plants are grown in the same ecological conditions.

Each species or group of species is characterized by a maximum number of bundles that can be found in the leaf vascular supply at a certain level in the stem. This number can be: 3 bundles (LML), 5 bundles (LiMiL), 7 bundles (mLiMiLm), 9 bundles (m'mLiMiLmm') or 11 bundles (m"m'mLiMiLmm'm"). In transverse section, the traces composed of 7, 9, and 11 bundles display a characteristic zigzag pattern (Fig. 8–10). In the species with leaf traces that posses 3 or 5 bundles, this zigzag pattern is lacking (Fig. 5–7). The vascular supply to each cotyledon has a different organization, although uniform for all the amaranths examined. It consists of only 2 bundles (Fig 4a, 5a-c).

Leaf traces are produced by adjacent pairs of major axial anastomotic bundles and the number of bundles in the leaf vascular supply increases progressively and gradually up the stem. The median bundles (M) have the longest course up

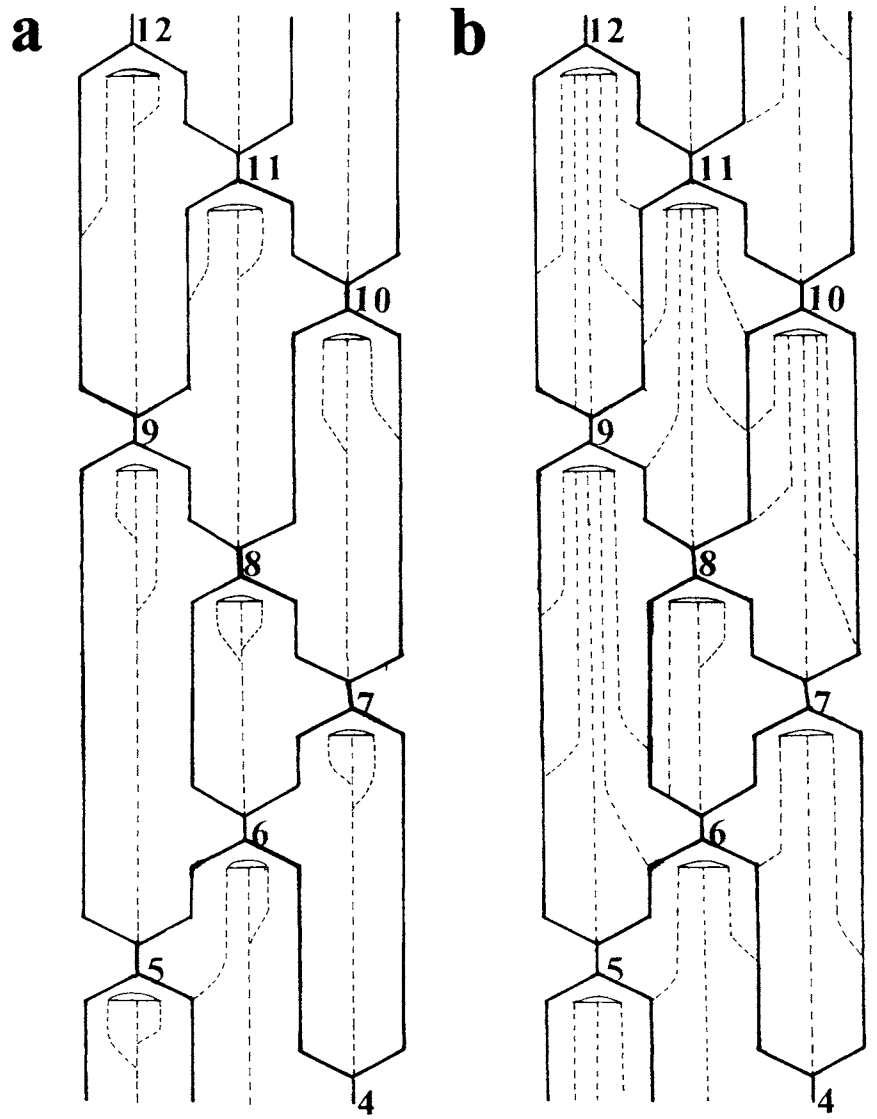

FIG. 3. Longitudinal courses of major axial anastomotic bundles in the stem of *Amaranthus*. a. *A. crispus*, b. *A. blitum*.

the axis and diverge first from major axial anastomotic bundles. Gradually, the intermediate (i) and the lateral (L) bundles diverge in pairs from the major axial bundles, and eventually the marginal bundles (m, m', m") do the same. These leaf trace bundles traverse the number of internodes equal to the number of orthostichies of the phyllotactic fraction (i.e. 5 internodes in the species with 2/5 phyllotaxy and 3 internodes in the species with 1/3 phyllotaxy, etc). The number of vascular bundles at the base of the petiole is not always equal to the number of bundles that diverge into it because the vascular bundles fuse and separate repeatedly within the petiole.

Branch Traces. All species of the genus *Amaranthus* possess lateral branches and the vascular system of these branches is connected to the vascular system of the main axis. These branches have a similar arrangement of vascular bundles as the main axis (although they lack anomalous secondary growth at their bases). Bundle arrangement in the main axis of the branches is as described by Gravis and Constantinesco (1907) in *A. caudatus* and is the same

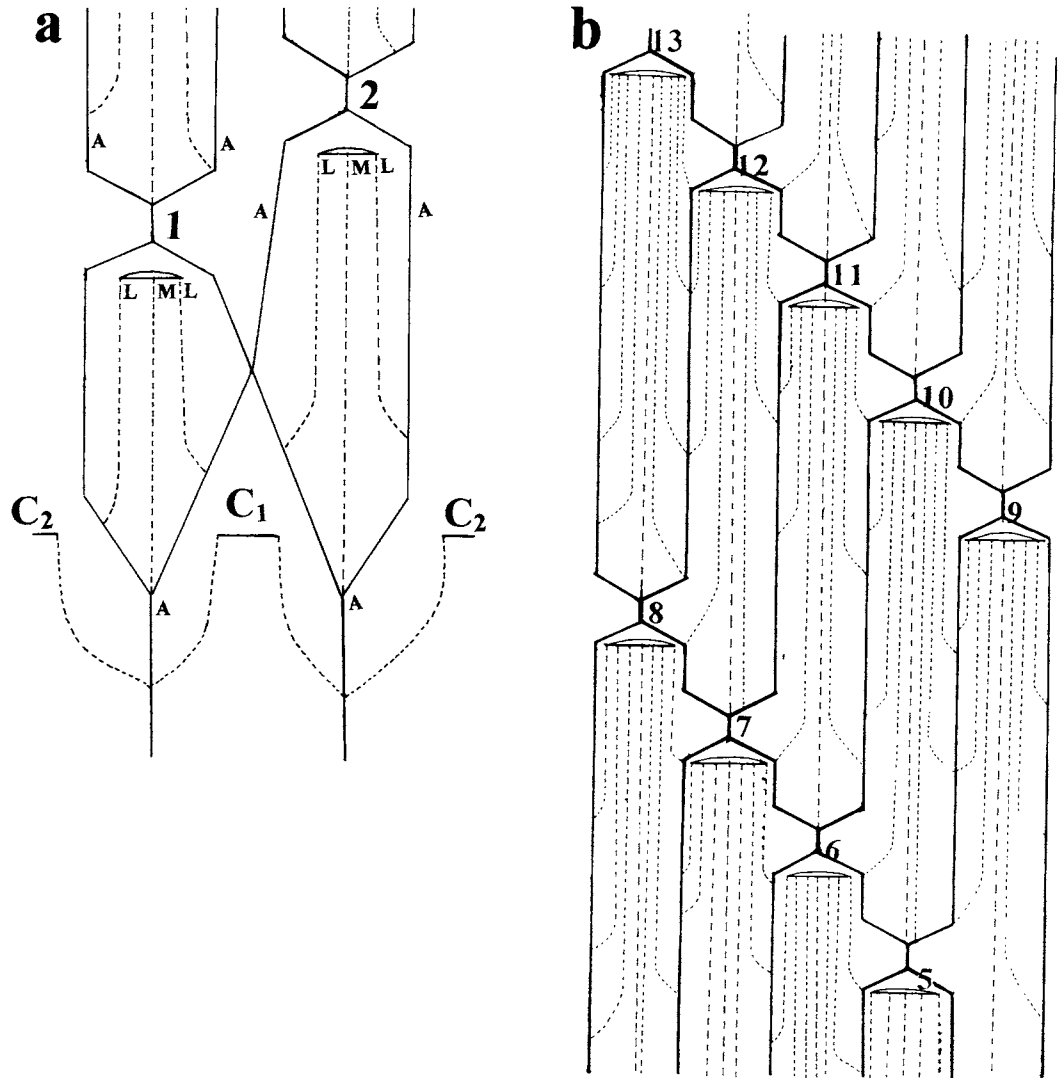

FIG. 4. Longitudinal courses of major axial, anastomotic bundles in the stem of *Amaranthus retroflexus*. a. seedling, b. adult plant. A, major axial, anastomotic bundles; C1, C2, cotyledon traces; L, lateral leaf traces; M, median leaf traces bundles.

for all amaranth species. The only differences noticed between the species are in the number of the branch bundles. Since the lateral axes have more or less the same pattern of arrangement of sympodia as the main axis, the number of branch bundles is related to the number of bundles within the leaf vascular supply characteristic for that species.

In a transverse section through a node at the insertion point of a branch, there are *branch bundles,* which are connected to the vascular supply of the main axis. Depending on their position they are either *external branch bundles* (Be) or *internal branch bundles* (Bi) (Fig. 6a). External branch bundles are derived from the outer, minor axial bundles of the main stem and internal branch bundles are derived from the inner, major axial anastomotic bundles of the main stem. Approximately 1 mm below the node in question, the external branch bundles (Be) are parallel to one another and the internal branch bundles (Bi) are positioned centrally and are closer to the stem axis (Fig. 6b). In the region where the leaf traces diverge from the major axial bundles, the external branch bundles (Be) are positioned between the bundles of the leaf trace

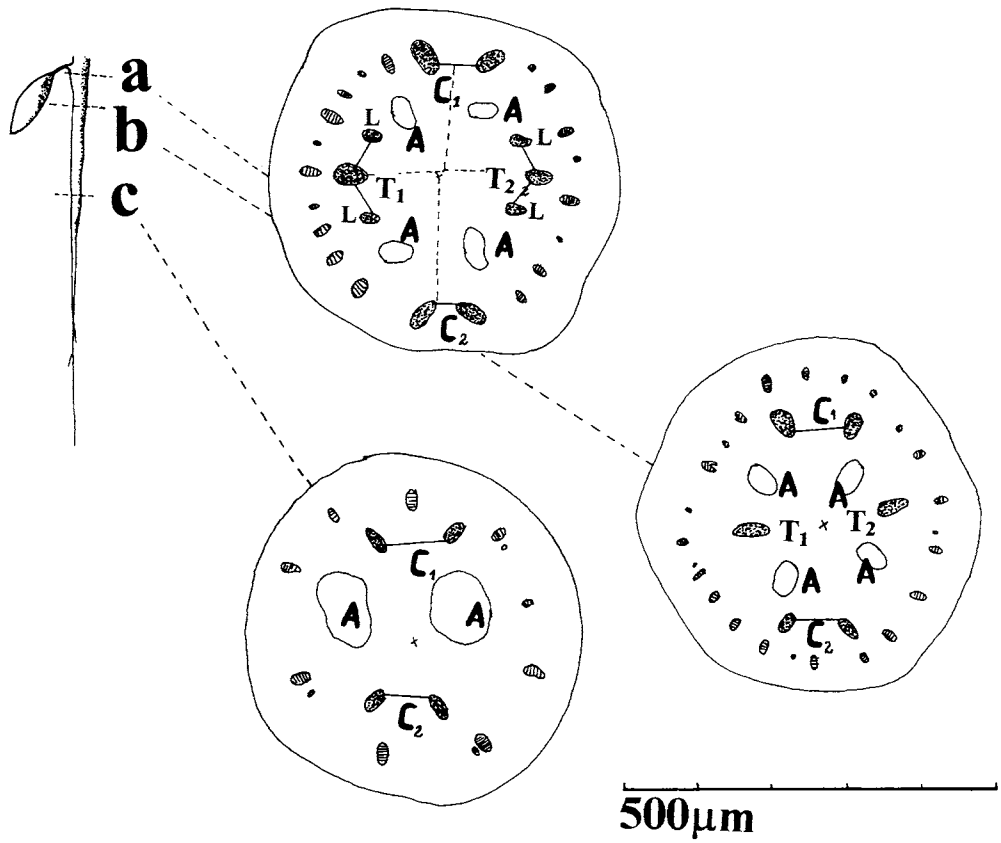

FIG. 5. Transverse sections through the hypocotyle of *Amaranthus*. A, major axial, anastomotic bundles; C1, C2, cotyledon traces; T1, T2, leaf trace bundles.

(F_9) and the inner branch bundles (Bi), which are diverging from the major axial anastomotic bundles (A) (Fig. 6c). At the middle of the internode below the branch, the external branch bundles (Be) are positioned in a distinct ring of peripheral bundles along with small axial bundles and the internal branch bundles (Bi) have not yet diverged from the major axial anastomotic bundles (Fig 6d). Therefore the course of the external branch bundles (Be) is longer than that of the internal branch bundles. Typically, they traverse the same number of internodes between the position at which they diverge from the minor axial bundles until they enter the branch base (A) as the number of leaf orthostichies on the shoot. However, this is not a general rule since many external branch bundles traverse only 1–2 internodes.

VARIATIONS DURING SHOOT ONTOGENY. *Seedlings.* The primary vascular system of the hypocotyl is similar for all the species of the genus *Amaranthus* examined. In a transverse section made through the hypocotyl below the cotyledonary node, there are 4 major axial anastomotic bundles (A), 2 cotyledon traces (C), each consisting of 2 bundles, the leaf traces of the first 2 leaves (F_1 and F_2), and a ring of minor axial bundles (Fig. 5a). In serial transverse sections through the hypocotyl, we observed the cotyledonary traces (C) and the origin of the leaf trace bundles from 2 large, original major axial anastomotic bundles (Fig 4a, 5b-c).

Mature plants. Group 1. *Amaranthus crispus* (Figs.3a, 7e).

All leaf vascular supplies consist of 3 bundles (LML) and these generally originate within the previous internode. The number of leaf traces present in transverse sections is 4 or 3.

Group 2. *Amaranthus deflexus, A. blitoides, A graecizans, A. blitum* and *A. viridis* (Table 4; Figs. 3b, 7a-d).

Nodes 1–8(11)..... L M L
Nodes 9(12)–13(15).....**L i M i L**
Nodes 14(16)..... L M L

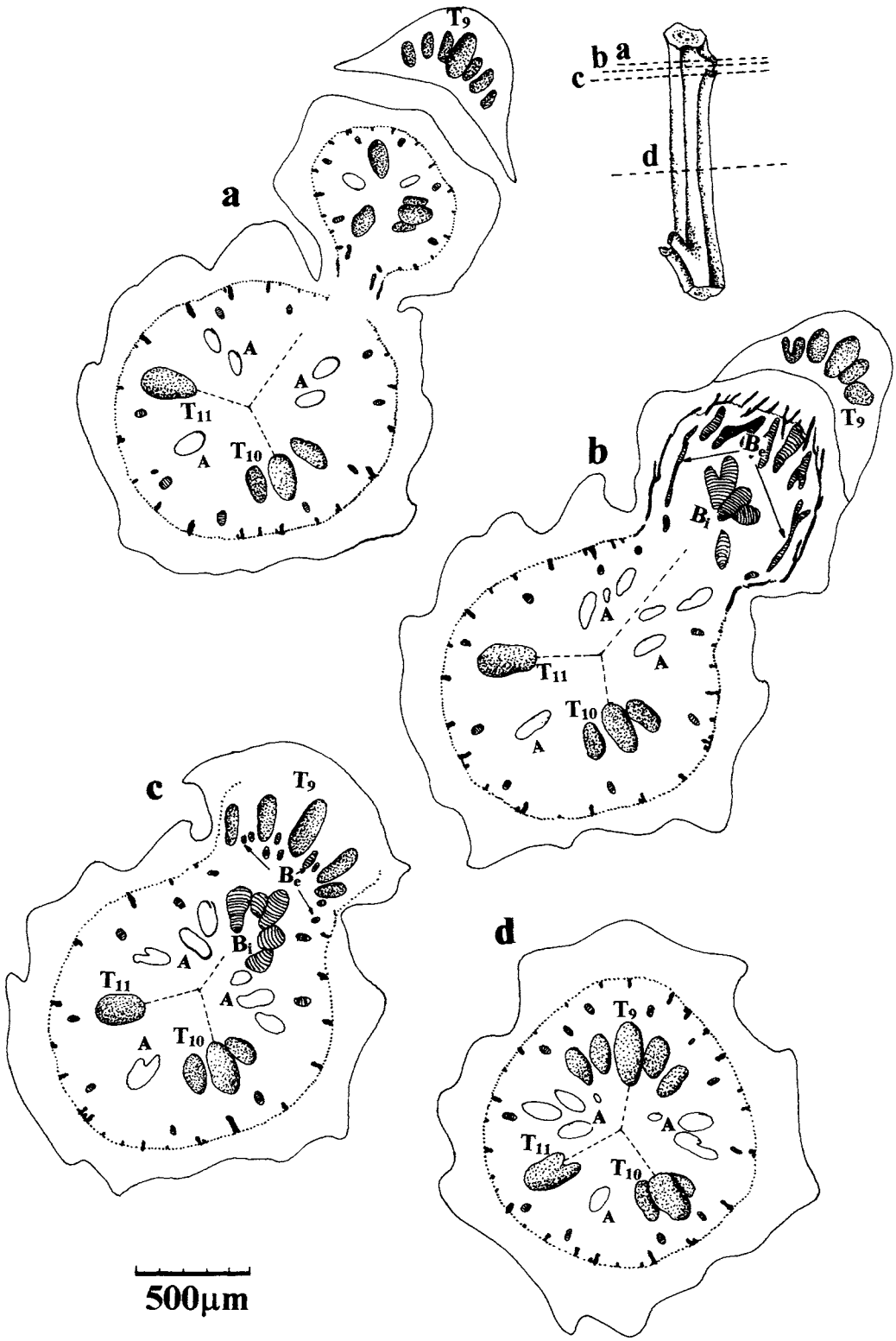

FIG. 6. Origins of branch traces within the internodes of *Amaranthus blitoides*. A, major axial, anastomotic bundles; Be, outer branch traces; Bi, inner branch traces; T, leaf traces bundles.

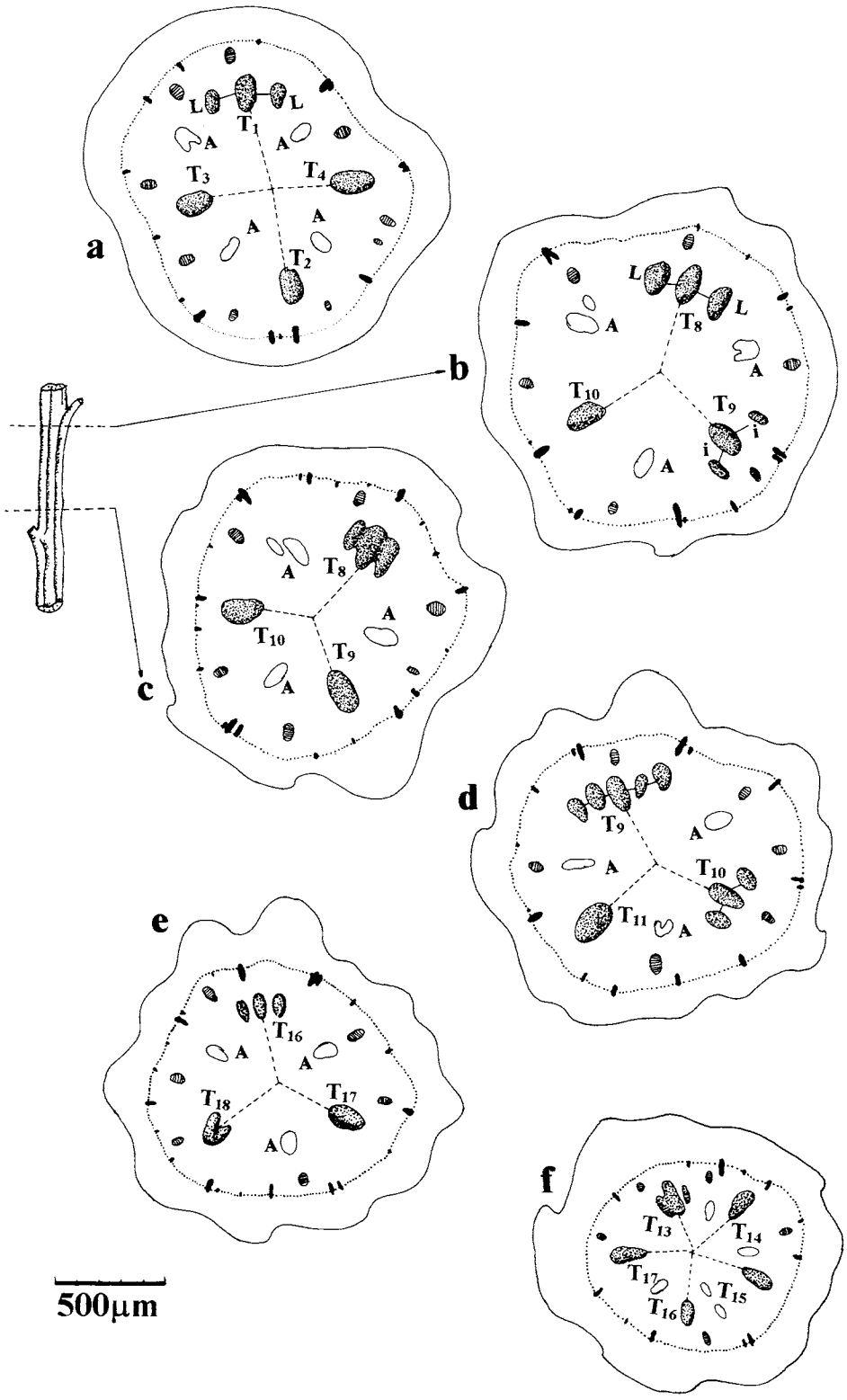
a
L
T1
L
A
A
T3
T4
A
A
T2
b
L
T8
L
A
A
T10
T9
i
i
A
c
A
T8
A
T10
T9
A
d
T9
A
A
T10
T11
A
e
T16
A
A
T18
T17
A
f
T13
T14
T17
T15
T16
500μm

Table 4. Variations in leaf vascular supply along the stem in group 2 species—*Amaranthus deflexus, A. blitoides, A. graecizans, A. blitum* and *A. viridis.*

Internode and phyllotaxis	1 1/2	8 1/3	9 1/3	13 1/3	13 2/5 (only in *A. blitoides A. graecizans*)
Leaf vascular supply	T1-LML T2-M T3-M T4-M	T8-LML T9-M or LML T10-M	T9-LiMiL T10-iMi or M T11-M	T13-LiMiL T14-iMi T15-iMi	T13-LML T14-M T15-M T16-M T17-M

—The number of bundles within the leaf vascular supply varies along the stem axis.
—The most complex leaf vascular supply has 5 bundles.
—The number of leaf traces present in transverse sections is 4, 3 or 5.

Group 3. *Amaranthus albus* (Table 5; Fig. 8a-d).

Nodes 1–2 ..... L M L
Nodes 3–8(9)..... L i M i L
Nodes (9)10–13(14)..... **m L i M i Lm**
Nodes 14(15)–18..... L i M i L
Nodes 19–20(21) .....i M i
—The most complex leaf vascular supply has 7 bundles.
—The number of leaf traces present in transverse sections is 3, 4 or 5.

Group 4. *Amaranthus retroflexus, A. powellii* and *A. hybridus* (Table 6; Figs. 4b, 9a-d).

Nodes 1–2 ..... L M L
Nodes 3–5 ..... L i M i L
Nodes 6–10(11) ..... m L i M i Lm
Nodes (11)12–16..... **m' m L i M i L m m'**
Nodes 17–19(20)..... m L i M i L m
Nodes 20(21)–24..... L i M i L
—The most complex leaf vascular supply has 9 bundles.
—The number of leaf traces present in transverse sections is 4, 5, 6 or 8.

Group 5. *Amaranthus caudatus, A. hypochondriacus* and *A. cruentus* (Table 7; Fig. 10).

Nodes 1..... L M L
Nodes 2..... L i M i L
Nodes 3–4 ..... m L i M i Lm
Nodes 5–11(12) ..... m' m L i M i L m m'
Nodes (12)13–15... **m" m' m L i M i L m m' m"**
Nodes 16–20(22)..... m' m L i M i L m m'
Nodes 21(23)– 24..... m L i M i L m
—The most complex leaf vascular supply has 11 bundles.
—The number of leaf traces present in transverse sections is 4, 5, 6 or 8.

SECONDARY GROWTH OF THE STEM. *Mechanism of secondary growth* The mechanism of secondary growth in *Amaranthaceae, Chenopodiaceae* and *Nyctaginaceae* has attracted the attention of many anatomists since the earliest times (de Bary 1877; Van Tieghem 1884; Morot 1885; Fron 1899; Solereder 1899; Pax 1904; Artschwager 1926; Pfeiffer 1926; Iljin 1950; Studholme and Philipson 1966; Balfour 1965; Philipson and Ward 1965; Fahn and Shchori 1967; Esau and Cheadle 1969; Mennega 1969; Philipson et al. 1971; Stevenson and Popham 1973; Wheat 1977; Zamski 1979; Mikesell 1979; Bailey 1980; Zamski and Azenkot 1981; Stieber and Beringer 1984; Fahn 1985; Kirchoff and Fahn 1984; Viana 1993; Toma et al. 1994; Nita 1997). All authors refer to the mechanism of secondary growth of these plants as "anomalous" or "atypical". Sometimes the process of secondary growth is divided into two phases. Differentiation and activity of the first cambial zone (the first phase) is often regarded as "nor-

←

FIG. 7. Internode anatomy of *Amaranthus.* a.-d. *A. blitum* (group 2). a. Internode 1, b. Upper region of internode 8, c. Middle region of internode 8, d. Internode 9, e. *A. crispus* (group 1), internode 16, f. *A. blitoides* and *A. graecizans* (group 2), internode 13. A, major axial, anastomotic bundles; L, lateral leaf trace bundles; T, leaf trace bundles.

Table 5. Variations in leaf vascular supply along the stem of *A. albus* (group 3).

Internode and phyllotaxis	1 1/2	6 1/3	10 1/3	14 2/5	19 2/5
Leaf vascular supply	T1-LML T2-LiMiL T3-iMi T4-M	T6-LiMiL T7-iMi T8-iMi	T10-mLiMiLm T11-LiMiL T12-iMi	T14-LiMiL T15-iMi T16-iMi T17-M T18-M	T19-iMi T20-iMi T21-M T22-M T23-M

mal" and the second phase, which consists of the initiation and development of supernumerary cambia is regarded as "anomalous" (Viana 1993). We interpret the term "anomalous" as Esau (1965) did, "growth patterns that appear less common". For plants of these families, the process is quite normal and a separation of the process of secondary growth into "normal" and "abnormal" phases is arbitrary. Again, the differences observed between amaranths are quantitative and are comparable only if the plants are grown in the same ecological conditions.

In serial transverse sections made through the epicotyl of the embryo, near the apex, there is a ring of provascular strands (Fig. 11a). Each strand develops acropetally and produces nascent leaf traces. In each strand, the protophloem differentiates earlier than the protoxylem (Fig. 11b). Later when the plants have 3–4 leaves, there are 8–13 large, collateral major axial bundles and a ring of peripheral, minor axial bundles within the internodes (Fig. 11c,d). Still later, the fascicular cambia of these peripheral bundles connects with interfascicular arcs of cambium (Fig. 11d,e). Some authors report that the interfascicular cambium is generated by the pericycle. In the stem of amaranths, the pericycle can not be identified and the first periclinal divisions occur within the cortex, several layers internal to the endodermis, which can be identified by the characteristic presence of betalain pigments. The first cambial zone is circular and continuous around the main and secondary axes, producing a distinct secondary vascular cylinder. In species of the subgenus *Amaranthus,* the first cambium functions for the entire life of the plant and the amount of secondary tissues produced is appreciable (Table 8). The fascicular cambium produces secondary xylem and phloem bidirectionally, while the interfascicular cambium generates only parenchyma that lignfies later. During the summer and autumn months in temperate climates, this cambium produces mostly parenchyma that soon lignifies and the stems become very hard. In the subgenus *Albersia,* the growth activity of this first cambium is more limited (excepting *A. albus*) (Table 8), because from the time the first flowers appear, the rate of cell divisions decreases. This quantitative variation explains a difference we noticed between the plants of the subgenera *Amaranthus* and *Albersia* in the temperate climate conditions of Central and Eastern Europe. After the plants of the subgenus *Amaranthus* die, their dry, lignified stems are still evident through the winter. In contrast, most of the species of the subgenus *Albersia* (except for *A. albus*) have stems that disappear completely in late autumn after the first frost, because they are less lignified.

The first supernumerary cambia develop from parenchyma of the outer phloem. These additional cambia act as fascicular cambia producing secondary phloem towards the outside and secondary xylem toward the inside. Later, interfascicular cambia connect the fascicular cambia of these arising secondary bundles with the fascicular cambium of the primary bundles. The new growing zones, as seen in cross-section, are not circular, but take the shape of large arcs. Within the bundles, the cambium produces vascular tissues, while between the bundles it produces parenchyma that soon lignifies. While a supernumerary cambium is still functional, new supernumerary cambia begin to develop in a similar way. All cambia in the stem (first and subsequent) are functionally interconnected and form a continuous system, and therefore a single secondary growth region. Secondary growth, as seen in transverse section, advances centrifugally, the first formed secondary bundles being the inner-most ones. Because there is a decrease in cell division activity of the old cambial zones and because development of the new ones does not occur simultaneously, they are difficult to separate from one another (Fig. 12). However, if we estimate the outline of these successive cambial zones, we notice that the species of the subgenus *Amaranthus* typically produce 3 to 6 such zones while the species of the subgenus *Albersia* produce only 1–3 zones. An exception to this

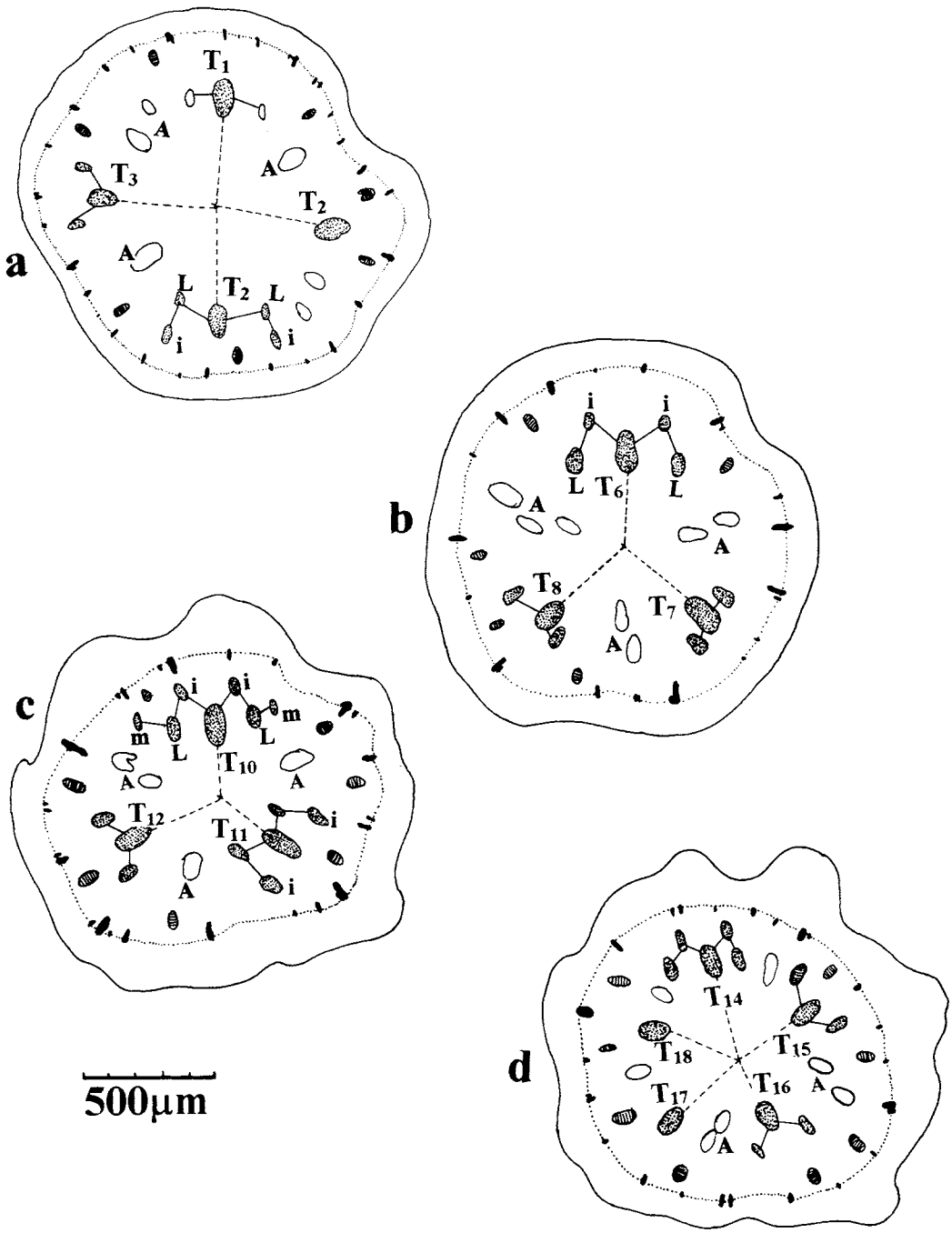

FIG. 8. Internode anatomy of *Amaranthus albus* (group 3). a. Internode 1, b. Internode 6, c. Internode 10, d. Internode 14. A, major axial, anastomotic bundles; i, intermediate leaf trace bundles; L, lateral leaf trace bundles; m, marginal leaf trace bundles; T, leaf trace bundles.

rule is *A. albus,* which may produce 2–4 supernumerary cambia.

Due to this method of secondary tissue formation, the base of the amaranth stem resembles a foraminate structure with interxyllary (included) phloem ("corpus lignosum foraminulatum" of Pfeiffer 1926). This type of secondary growth occurs only in the root and at the base of the

Table 6. Variations in leaf vascular supply along the stem in group 4 species—*Amaranthus retroflexus*, *A. powellii* and *A. hybridus*.

Internode and phyllotaxis	1 1/2	3 1/2	6 2/5	13 2/5	17 2/5	21 2/5
Leaf vascular supply	T1-LML	T3-LiMiL	T6-mLiMiLm	T13-m'mLiMiLmm'	T17-mLiMiLm	T21-LiMiL
	T2-iMi	T4-LiMiL	T7-LiMiL	T14-mLiMiLm	T18-LiMiL	T22-LiMiL
	T3-iMi	T5-iMi	T8-LiMiL	T15-LiMiL	T19-LiMiL	T23-iMi
	T4-iMi	T6-iMi	T9-iMi	T16-iMi	T20-iMi	T24-iMi
		T7-M	T10-iMi	T17-iMi	T21-iMi	T25-iMi
			T11-M			

stem. While the successive cambia in the root form complete and concentric rings ("corpus lignosum circumvallatum" of Pfeifer 1926), the supernumerary cambia in the stems are limited to interconnected arcs.

Amaranthus deflexus is one of the few, short perennial species in the genus. The short rhizomes possess a concentric pattern of secondary growth similar to that present in the roots. The secondary parenchyma produced by the successive cambia is not lignified and serves as a starch storage tissue. The only difference between the anatomy of the rhizomes and the roots in this species is the presence of the primary collateral bundles in the rhizomes.

Wood Anatomy. Wood anatomy in the amaranths is similar. Cell types present in the axial system of the secondary xylem include: tracheids, vessel members, fibers and axial parenchyma. Vessels range in diameter from 40–140μm and are solitary or in small groups of 2 or 3. Perforations are simple. Axial parenchyma is paratracheal and limited to a few cells round the vessels. Fibers have simple pits.

Discussion. The goals of this study were to look at the range of variation of stem structural characters including: the epidermis, primary stem vascular system and mechanism of secondary growth within the genus *Amaranthus* and to use this information to determine whether they provide additional perspectives on the taxonomic problems within the genus. Also, we evaluate our findings with respect to the extensive, confusing and contradictory observations of previous authors on the unique features of stem anatomy characteristic of the *Caryophyllales.*

EPIDERMIS. Characteristics of the stomata and trichomes of the stem epidermis provide the same amount of information as those of the leaves (Solereder 1899; Metcalfe and Chalk 1950; Fischer and Evert 1982; Viana 1993; Esparza-Sandoval et al. 1996; Costea 1998b). The species of the "hybridus" complex are impossible to separate with this approach. An exception is *A. powellii* subsp. *bouchonii* that had elongated cells in the stomatiferous zones, but this characteristic still needs to be confirmed by examining plants from other populations too. Another exception is *A. hybridus-A. powellii,* considered by some to be conspecific (Stace 1991, 1997; Townsend 1974, 1985, 1988). However, the two species are easily distinguished by their indumentum and trichomes:

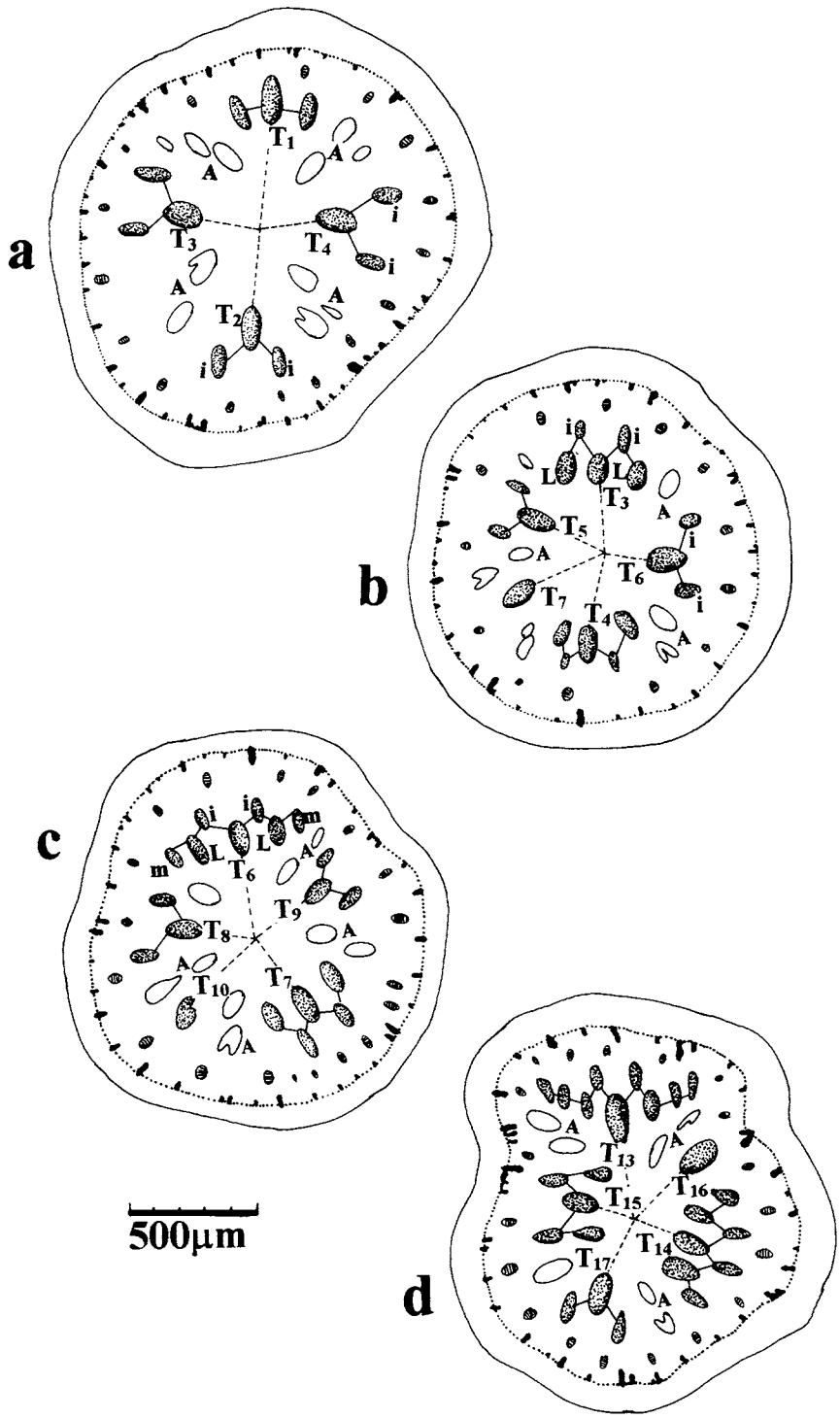

FIG. 9. Internode anatomy of *Amaranthus hybridus* and *A. powellii* (group 4). a. Internode 1, b. Internode 3, c. Internode 6, d. Internode 13. A, major axial, anastomotic bundles; i, intermediate leaf trace bundles; L, lateral leaf trace bundles; m, marginal leaf trace bundles; T, leaf trace bundles.

Table 7. Variations in leaf vascular supply along the stem in group 5 species—*Amaranthus caudatus*, *A. hypochondriacus* and *A. cruentus*.

Internode and phyllotaxis	1 1/2	2 1/2	3 1/2	5 2/5	13 2/5	23 3/8
Leaf vascular supply	T1-LML	T2-LiMiL	T3-mLiMiLm	T5-m′mLiMiLmm′	T13-m″m′mLiMiLmm′m″	T23-m′mLiMiLmm′
	T2-LiMiL	T3-LiMiL	T4-mLiMiLm	T6-mLiMiLm	T14-mLiMiLm	T24-mLiMiLm
	T3-iMi	T4-iMi	T5-LiMiL	T7-LiMiL	T15-LiMiL	T25-LiMiL
	T4-iMi	T5-iMi	T6-iMi	T8-iMi	T16-iMi	T26-iMi
			T7-iMi	T9-iMi	T17-iMi	T27-iMi
						T28-M
						T29-M
						T30-M

1. Indumentum lantate; trichomes uniseriate and multiseriate ..... *A. hybridus*
1. Indumentum puberulent, trichomes uniseriate only ..... *A. powellii*

Excluding the species of the *A. blitum* aggregate, which are very similar, the other species of the subgenus *Albersia* are more variable:

1. Stomatiferous zones 200–260μm in width *A. blitum* agg.
1. Stomatiferous zones narrower, 40–130μm in width 2
2. Trichomes multiseriate and uniseriate ... *A. albus*
2. Trichomes uniseriate only 3
3. Stomatiferous zones sunken 4
4. Guard cells surrounded by 4–8 neighboring cells ..... *A. graecizans*
4. Guard cells surrounded by 3–4 neighboring cells ..... *A. blitoides*
3. Stomatiferous zones not sunken 5
5. Stomatiferous zones 85–130μm in width; papillae present ..... *A. crispus*
5. Stomatiferous zones 40–75μm in width; papillae absent ..... *A. deflexus*

Unquestionably, these species can be more easily identified using classical characters. The above key is presented only to show that differences between some species exist and that these characters are reliable enough for identification.

PRIMARY VASCULAR SYSTEM. The presence of "medullary bundles", which we have called major axial anastomotic bundles, is regarded as a striking and anomalous feature that has been reported in more than 30 angiospermous families (Weiss) 1883; Lignier 1887; Col 1904; Wilson 1924; Dastur 1925; Maheshwari 1929, 1930; Joshi 1931a,b, 1933; Metcalfe and Chalk 1950, 1983; Pant and Mehra 1961; Davis 1961; Kirchoff and Fahn 1984; Raj and Nagar 1980, 1989). In *Amaranthus* there are two types of primary vascular bundles, the inner ring of major bundles, which gives rise to leaf traces and the inner branch trace bundles and the outer ring of minor bundles, which gives rise to the outer branch traces. The inner, so called medullary bundles of previous authors is actually comparable to the axial bundles of all seed plants. The existence of the outer, minor bundles, which are produced by and eventually fuse again with the major bundles, are "anomalous" compared to other seed plants. The number and arrangement of continuing bundles and leaf trace bundles in the stem are variable even along the same plant. In addition, Joshi (1931b) noted differences in the arrangement of the medullary bundles in

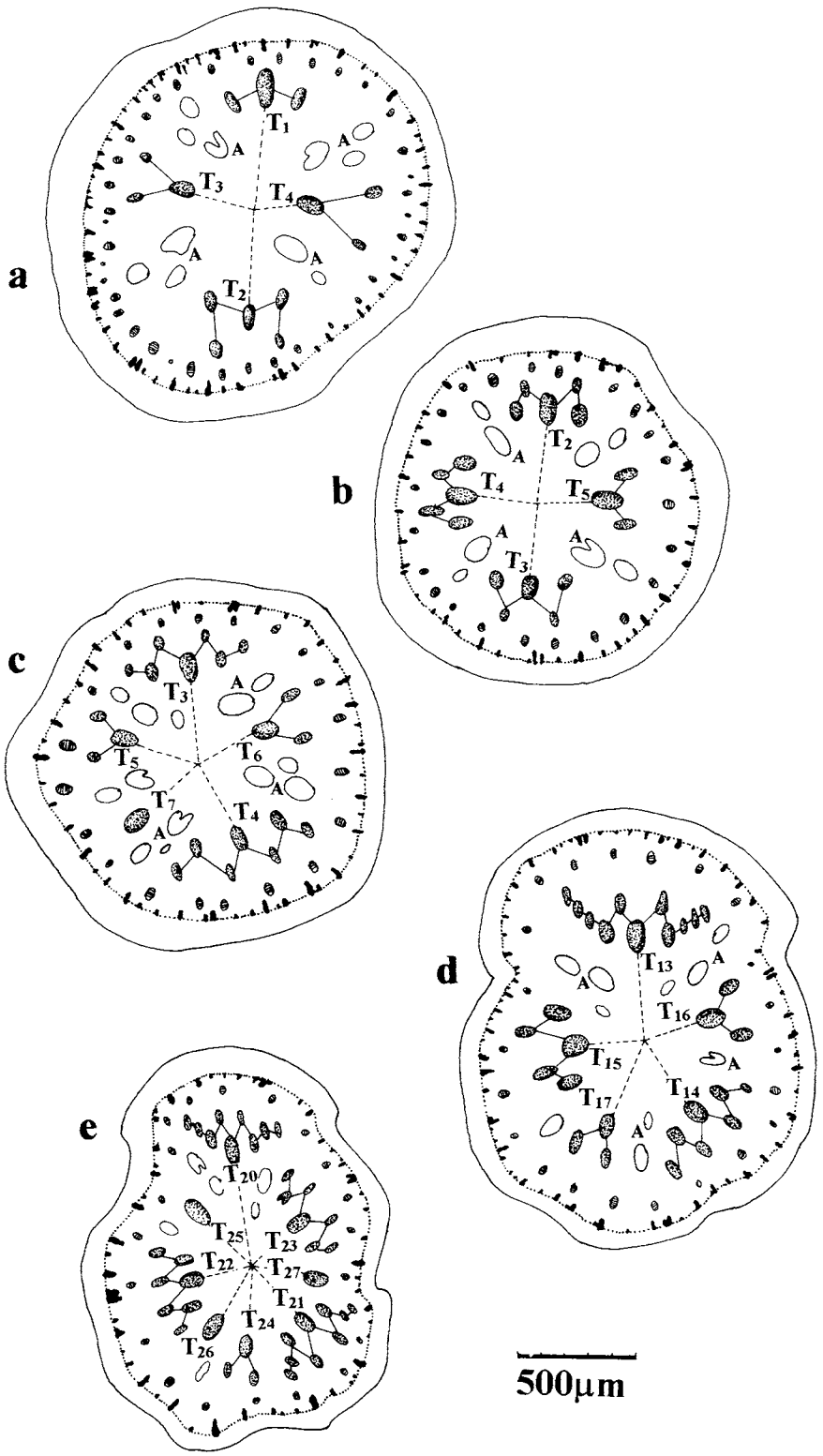

FIG. 10. Internode anatomy of *Amaranthus hypochondriacus, A. cruentus,* and *A. caudatus* (group 5). a. Internode 1. b. Internode 2; c. Internode 3; d. Internode 13, e. Internode 20. A, major axial, anastomotic bundles; i, intermediate leaf trace bundles; T, leaf trace bundles.

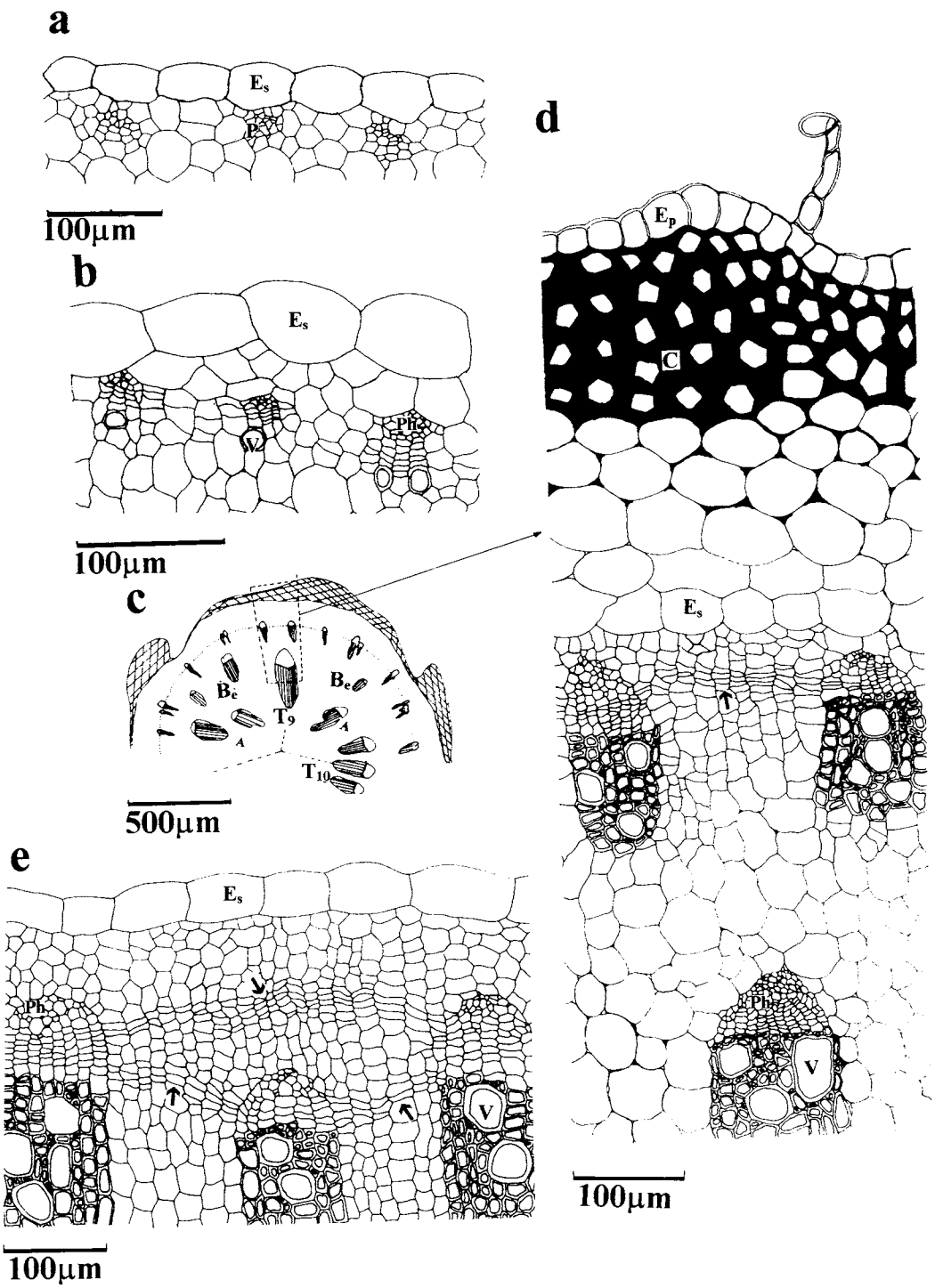

FIG. 11. Stages of secondary growth at the stem base of *Amaranthus blitum*. a. embryo, b. seedling, c. and d. Initiation of first cambium, e. Initiation of accessory cambium. Be, external branch bundles; C, collenchyma; Es, endodermis; P, procambial strands, Ph, phloem; T, leaf trace bundles; V, vessel members.

Table 8. Quantitative variation of the secondary tissue produced by the first cambium.

Taxa	Thickness of the secondary growth zone produced by the first cambium −μm; (approximate number of cells)
Subgenus *Amaranthus*	
Amaranthus powellii subsp. *powellii*	780–1050 (1500)
A. powellii subsp. *bouchonii*	700–1200
A. hybridus	750–1100 (1500)
A. hybridus subsp. *quitensis*	750–1100 (1500)
A. retroflexus	780–1050 (1500)
A. caudatus	875–1500 (1600)
A. cruentus	875–1500 (1600)
A. hypochondriacus	875–1500 (1600)
Subgenus *Albersia*	
A. blitum	
subsp. *blitum*	300–370
subsp. *oleraceus*	350–390
subsp. *emarginatus*	300–350
A. viridis	300–380
A. deflexus	245–280
A. blitoides	235–260
A. graecizans	
subsp. *graecizans*	240–275
subsp. sylvestris	
A. crispus	250–270
A. albus	600–900

plants of the same species from different localities. After comparing several *Amaranthaceae* and *Chenopodiaceae,* Wilson (1924) stated that *Amaranthus* "represents the highest point of development of the medullary condition in these two families" because all the major axial bundles in amaranths are "medullary." This pattern and arrangement of bundles is thought to have originated independently in the various groups of plants in which they are found. In amaranths, this particular disposition of bundles is purely functional being the most logic way to distribute—in a topological sense—the many primary bundles.

Information on the vascular system in the *Caryophyllales* is still uneven. Some families, such as the *Chenopodiaceae* (Wilson 1924; Joshi 1934; Fahn and Arzee 1959; Bisalputra 1961, 1962; Fahn and Broido 1963; Zamski and Azenkot 1981; Fahn and Zimmerman 1982) and Cactaceae (Gibson 1976; Gibson and Nobel 1986) have received a lot of attention. But information about the other families is much spottier (Gravis and Constantinesco 1907; Wilson 1924; Dastur 1925; Maheshwari 1929, 1930; Joshi 1931a, b, 1934; Inouye 1956; Balfour and Philipson 1962; Philipson and Balfour 1963; Stevenson and Popham 1973; Kirchoff and Fahn 1984; Gibson 1994). In view of this it is difficult to clarify the phylogenetic relationships and evolutionary trends in primary vascular tissue characteristics in the order. According to Gibson (1994), the primitive condition in the betalaine-containing families is an open primary vascular system in which the leaf vascular supply consists of 3 or more leaf trace bundles arising from two axial bundles and unilacular nodal anatomy. Closed systems, those with more leaf traces or systems in which the leaf vascular supply originates from a single bundle are considered potential synapomorphies. Therefore, the characteristics of *Amaranthus,* closed system, complex anastomotic axial bundles, leaf vascular system with more than 3 bundles arising from 2 axial bundles, is rather derived. Within the genus *Amaranthus,* the condition of having a leaf vascular supply of 3 bundles can be considered to be plesiomorphic (as in *A. crispus*), while having more bundles can be considered to be derived.

The number of leaf trace bundles within the leaf vascular supply in *Amaranthus* varies both along the same plant and between species. The range between different species is great—from 3 to 11 bundles. Our results confirm previous observations on the number of bundles reported by Gravis and Constantinesco (1907) and Viana (1993) and only partially those of Wilson (1924). The differences observed in phyllotaxy, combined with the organization of the leaf vascular supply, support the classification of Mosyakin and Robertson (1996) with the former

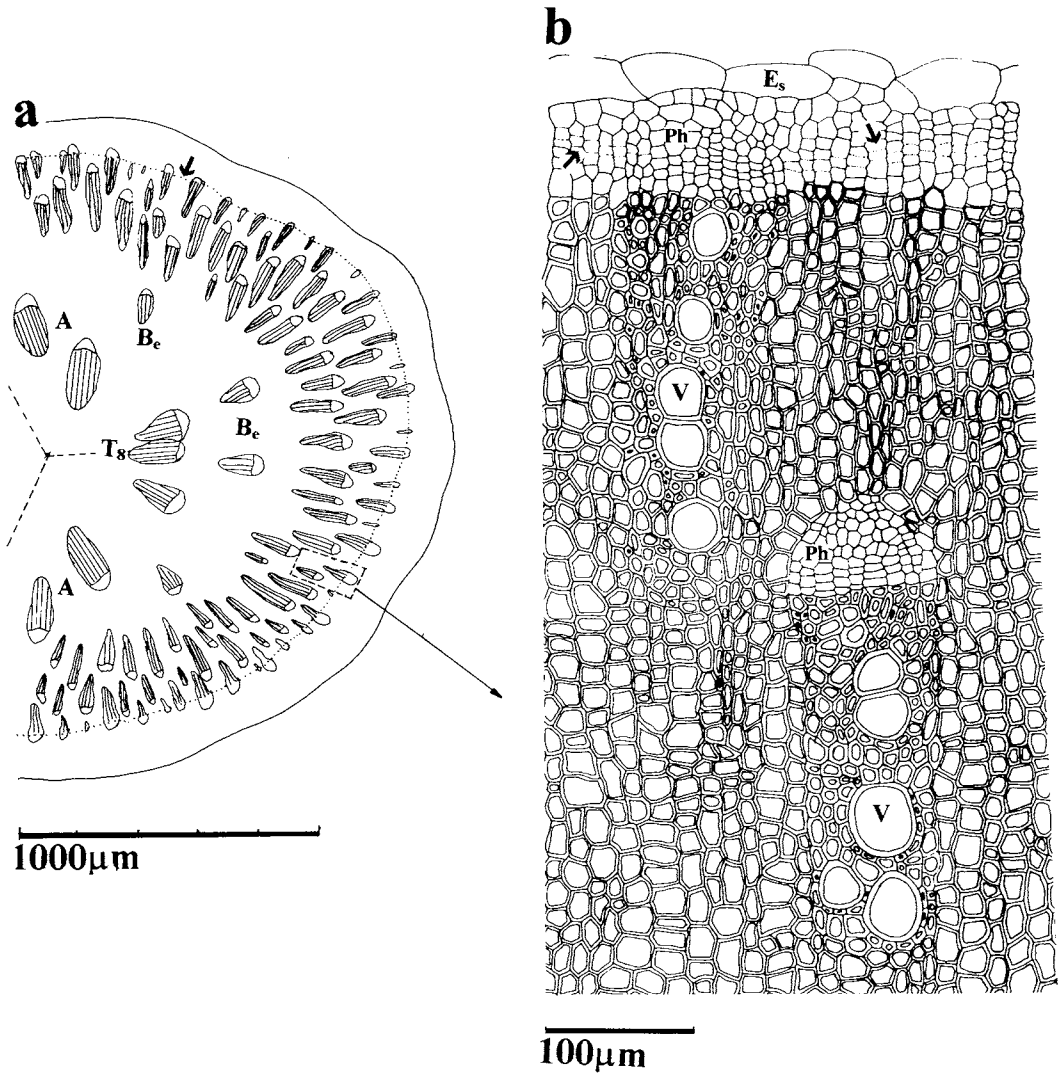

FIG. 12. Secondary growth in older stem of *Amaranthus blitum*. a. Lower magnification of stem, b. Higher magnification of outer cambial layer. Be, external branch bundles; Es endodermis; Ph, phloem; T8 leaf vascular supply of leaf 8; V, vessel member.

section *Amaranthus* and *Blitopsis* raised as subgenera (*Amaranthus* and *Albersia,* respectively).

1. Plants dioecious . . . . . Subgenus *Acnida*
1. Plants monoecious 2
   2. Phyllotaxy predominantly 2/5; the most complex vascular supply of leaves in stems with 9–11 bundles . . Subgenus *Amaranthus* (≡ *section Amaranthus*)
   2. Phyllotaxy predominantly 1/3; the most complex vascular supply of leaves in stems with 3, 5, or 7 bundles; seeds with hilum beneath tip of the radicle . . Subgenus *Albersia* (≡ Subgenus *Amaranthus* section *Blitopsis* Dumort.)

In addition, the fact that hybrids between the subgenus *Amaranthus* and the subgenus *Albersia* are unknown (Priszter 1958) confirms the separation of *Albersia* as a subgenus.

We compared the phyllotaxy and characteristics of the vascular system for two of the dioecious species (subgenus *Acnida*). We found that they are actually more similar to species in the other subgenera, *Amaranthus* and *Albersia* than they are to one another. *A. palmeri* fits in the group of *A. retroflexus* and *A. rudis* in the group of *A. deflexus*. It is known that some dioecious species are related to and hybridize with species

of the "hybridus" complex (Murray 1940; Sauer 1955; Brenner 1980; Brenner et al. 2000). Wilson (1924) described the primary vascular system in the dioecious species, *A. torreyi* (? *A. watsoni*) and it is also similar to *A. hybridus* and *A. retroflexus*. Our data suggest that at least one dioecious species, *A. rudis*, might be related to species in the subgenus *Albersia* (group 2). Further information is necessary to test whether the dioecious species of *Amaranthus* are actually not a natural group and whether dioecy evolved more than once in the genus.

An important difference in the subgenus *Amaranthus* is that between the cultivated species (*A. caudatus*, *A. cruentus* and *A. hypochondriacus*) and their presumed wild progenitors (*A. hybridus* subsp. *quitensis*, *A. hybridus* subsp. *hybridus* and *A. powellii* respectively). The grain amaranths belong to the group 5 species, which have the most complex leaf vascular supply (with 11 bundles) and a tendency toward higher phyllotaxy (3/8) in the adult stem. In contrast, their wild relatives belong to group 4, which possesses 9 leaf traces in the most complex leaf vascular supply and only rarely have higher phyllotaxies. The difference is subtle but important because it is universal.

Based on its complex leaf vascular supply (7 bundles), *A. albus*, in the subgenus *Albersia*, holds a position that is intermediate between the other members of its subgenus and species of the subgenus *Amaranthus*. The species in our group 2 come close to delimiting the section *Blitopsis* sensu Mosyakin and Robertson (1996). Within our group, *A. blitoides* and *A. graecizans* are indeed somehow different by their tendency to have more complex phyllotaxy (2/5) in the adult stem. It remains to seen if *Amaranthus crispus* shares the same affinities with *A. standleyanus* Parodi ex Covas, *A. vulgatissimus* Spegaz, *A. crassipes* Schlecht and *A. muricatus* (Moquin) Hieron circumscribed by Mosyakin and Robertson (1996) in the section *Pentamoryon*.

SECONDARY GROWTH. The mechanisms of secondary growth are similar in the *Amaranthaceae, Chenopodiaceae, Nyctaginaceae* and *Phytolaccaceae*. There have been contrasting interpretations of the secondary growth processes in the plants of these families. In the multilingual Glossary of Descriptive Terms (International Assoc. Wood Anat. 1964) it is stated that the foraminate type is produced by a single cambium which is "normal" except for the fact that it sporadically produces strands of phloem that become embedded in xylem. Balfour (1965), Studholme and Philipson (1966), Philipson and Ward (1965) also describe a single cambium, unidirectional in action, that alternatively produces secondary xylem and phloem. Our interpretation is that the cambia in this group produce secondary xylem and secondary phloem bidirectionally and since secondary xylem and parenchyma are produced more actively than secondary phloem, the cambial zone moves outward leaving behind strands of phloem engulfed in secondary xylem and parenchyma. However, both concepts of the anomalous cambia are present in the older literature. de Bary (1877), Van Tieghem (1884), Solereder (1899), and Pax (1904), Schinz (1933) all described the mechanism of secondary growth as involving a single unidirectional cambium. Morot (1885) was the first to describe this cambium as bidirectional, and Fron (1899) confirmed his results in *Chenopodium album*. At that time, only Haberlandt (1904) and Strasburger (1933) used this interpretation of the secondary growth in their anatomy treatises.

Gibson (1994) has concluded that normal cambial growth is the primitive state for the betalain-containing families and that anomalous secondary thickening may have evolved multiple times in the group. According to Joshi (1937), the formation of a succession of cambia is an ancestral character in the mentioned families. The most primitive condition is the presence of several consecutive rings of growth that produce collateral bundles embedded in a parenchymatous ground tissue. Evolution has led either to the loss of anomalous thickening from the stem alone or from both the stem and the root, or to the reduction of the secondary cambia to smaller and smaller segments. If we accept this hypothesis, many members of the *Amaranthaceae* seem more evolved than those of the *Chenopodiaceae*. Frequently in the latter family, the additional cambia generate more or less concentric regions of secondary growth, while in many *Amaranthaceae* secondary growth in the stem is foraminate. However, these 2 families are so closely related that in some recent taxonomic treatments (APG 1998; Judd et al. 1999) they are combined into a single monophyletic family—*Amaranthaceae*. Further, the subgenera *Amaranthus* and *Albersia* differ in the relative amount of secondary growth produced since both the first cambium is more active and more

accessory cambia are produced in the species of the subgenus *Amaranthus*.

GENERAL CONCLUSIONS. The results of this study fill gaps in the general knowledge on the morphology and anatomy of stems in the *Amaranthaceae* and in doing so have provided new characters (phyllotaxy, complexity of the leaf vascular supply and relative amounts of secondary growth) that support (1) a new infrageneric classification (subgenus *Amaranthus* vs subgenus *Albersia*), and (2) the separation of the "*hybridus*" group (group 5) from their presumed wild progenitors (group 4).

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