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STRUCTURE OF THE PERICARP IN SOME *AMARANTHUS* L. (AMARANTHACEAE) SPECIES AND ITS TAXONOMIC SIGNIFICANCE

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ABSTRACT

In order to determine their taxonomic significance, 10 pericarp structure characters were scored for 21 *Amaranthus* L. taxa. In many, pericarp patterns permit recognition of the taxa as species. Differences between cultivated taxa and their wild relatives offer new arguments against their taxonomic union. The relationships between other closely related taxa are also analyzed (*A. quitensis* and *A. hybridus*; *A. bouchonii* and *A. powellii*; *A. hybridus* and *A. powellii*; *A. blitum* and *A. emarginatus*). Mechanisms of dehiscence and terminology for the fruit of *Amaranthus* are considered.

Key words: *Amaranthus,* carpology, fruit anatomy, pericarp, taxonomy.

INTRODUCTION

The genus *Amaranthus* includes mostly wild and weedy, but also some domesticated vegetable, grain-crop and ornamental species. Although the taxonomy of this genus has been the subject of many previous studies, the problems in the "*hybridus*" and "*blitum*" groups have not been resolved. The relationship between the cultivated taxa and their presumed wild progenitors needs resolution in the grain amaranths. The taxonomic treatment of the *A. hybridus* group of species ranges between two different extremes with many intermediates. At one extreme is Sauer's treatment (1967), which recognizes the cultivated taxa (*Amaranthus caudatus, A. cruentus* and *A. hypochondriacus*) as species, while at the other extreme is Greuter's treatment (1981) which unites the cultivated species with their supposed wild progenitors (*A. quitensis, A. hy-*

bridus and *A. powellii,* respectively) without any further infraspecific classification. We studied anatomical aspects of the pericarp in order to re-evaluate these taxonomic relationships.

According to Judd (1985) and Spjut (1994), the genus *Amaranthus* has two types of fruit: "pyxidium" (or "pyxis") and "utricle". The question is, has *Amaranthus* two different types of fruit? Another question is the mechanism of fruit dehiscence and the taxonomic significance of fruit dehiscence. The case of closely related *A. bouchonii* and *A. powellii* is well known in Europe (Costea et al. 2001a). The main morphological difference between the two is that *A. powellii* has dehiscent fruits, whereas *A. bouchonii* has indehiscent fruits. Presumably, the latter originated from the former by a relatively simple mutation. *Amaranthus bouchonii,* which is very widespread in Europe, was regarded as conspecific with *A. powellii* by Sauer (1967), Carretero (1990) and Akeroyd (1993), but maintained

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at the species level by Hügin (1987), Stace (1991) and Wilkin (1992). The objectives of this study were to evaluate the taxonomic value of pericarp characters in the amaranths and to see if they provide additional perspectives on the taxonomic problems briefly discussed above. Also we analyzed the mechanism of dehiscence and the carpologic nomenclature for the fruit of amaranths.

MATERIALS AND METHODS

Twenty-one taxa representing 17 species and six infraspecific taxa (Table 1) were scored for 10 anatomical characters pertaining to the fruits. Fruits were collected by Costea, either from the wild flora (mainly from Romania and Spain), or from cultivated accessions provided by the USDA and Gatersleben germplasm collections (the latter marked in the table with "*") (Table 1). Voucher specimens are preserved in the BUAG herbarium collection, except for the USDA accessions, which are preserved in US. Twenty fruits were collected from each plant, and 15–20 different plants for each species were taken into account. Fruits were fixed in formalin-acetic acid-alcohol (5:5:90) (FAA) and embedded in paraffin. Transverse and longitudinal sections were made at 5–7 μm in thickness and stained with Toluidine Blue. Drawings were made with a Reichert camera lucida. The structure of the pericarp is constant immediately above the dehiscence line for the circumscissile fruits, and in the middle zone of the fruit for the indehiscent ones, descriptions referring to these regions.

List of Pericarp Characters Examined:

1. General appearance of pericarp structure
   2, two-layered pericarp
   3, three-layered pericarp
   4, four-layered pericarp
2. Uniformity of epidermal cell size
   UNI, cells with ± uniform size
   VAR, cells with very variable size
3. Shape of epidermal cells, as seen in transverse section
   ROU, round
   RAEL, radially elongated
   TAEL, tangentially elongated
   SQU, square
4. Number of layers in the mesocarp
   0, mesocarp crushed, usually no longer distinguishable
   1, mesocarp 1-layered
   2, mesocarp 2-layered
5. Orientation of cells in the 1-layered mesocarp
   LONG, cells are preponderantly longitudinally stretched

VARS, cells are variously stretched: transversely, longitudinally and obliquely
6. Orientation of the inner layer of cells in the 2-layered mesocarp
   TRANS, cells are preponderantly transversely extended
   TLO, cells are variably stretched: transversely, longitudinally and obliquely
7. Presence in the mesocarp of additional, loosely arranged cells with a sustaining role
   0, absent
   +, present
8. Adherence between epidermis + mesocarp and endocarp
   STI, the epidermis + mesocarp and the endocarp are mostly fused
   DET, the epidermis + mesocarp are mostly detached from the endocarp, resulting in large intercellular spaces:
   l, the epidermis + mesocarp form intercellular spaces in form of loops
   p, the epidermis + mesocarp lie parallel to the endocarp, loops not being formed
9. Thickening of walls in endocarp cells
   1, endocarp cells with the inner and to a less extent radial walls thickened, while the tangential walls are thin.
   2, endocarp cells with either uniformly thickened or thin walls
   2a, walls uniformly thickened
   2b, walls thin
10. Adherence between endocarp cells and the seed coat
    +, a slight adhesion before the fruit dries
    0, no adhesion observed

RESULTS

The data matrix for the 10 pericarp characters is presented in Table 2. Quantitative characteristics of the pericarp are listed in Table 3. The structure of pericarp is congruent at the species level and all the accessions, populations and infraspecific taxa examined shared the characteristics of their species. Therefore, to avoid redundancy, the infraspecific taxa are not indicated in the tables (with the exception of A. blitum subsp. blitum and subsp. oleraceus which exhibited minute quantitative differences—Table 3). As seen in transection, the mature pericarp has a very simple, 2–4 layered structure, consisting of epicarp, mesocarp and endocarp. The epicarp is the epidermis and has thickened cell walls. The size and shape of epidermal cells as seen in transverse section are quite variable in species belonging to subgenus Amaranthus (= section Amaranthus), but fairly uniform in subgenus Albersia (= section Blitopsis Dumort). The thickness of radial cells

Table 1. Provenance of *Amaranthus* taxa (Amaranthaceae) examined for pericarp features. Accessions provided by the Gatersleben germplasm collection are marked with an asterisk.

Taxa	Voucher No. or accession	Provenance
Subgenus *Acnida* (L.) Aellen ex K. R. Robertson		
A. *rudis* Sauer	23033 (a–j)	Romania
Subgenus *Amaranthus* (= section *Amaranthus*)		
A. *caudatus* L.	23050 (a–j)	Romania
	(k–s)	Mexico*
	Ames 2026	Nepal
	PI 16604	India
	PI 490440	Peru
A. *cruentus* L.	23037 (a–j)	Romania
	(k–s)	India*
	PI 566896	Arizona, USA
	PI 566897	India
	PI 511919	Guatemala
A. *hypochondriacus* L.	22769 (a–j)	Romania
	(k–s)	India*
	PI 511 721	Mexico
A. *powellii* S. Wats.	22770 (a–j)	Romania
	(k–s)	Spain
A. *bouchonii* Thell.	23041 (a–j)	Romania
	(k–s)	Spain
A. *hybridus* L.	22721 (a–j)	Romania
	(k–s)	Spain
A. *quitensis* Kunth	22840 (a–j)	Romania
	(k–s)	Ecuador*
A. *retroflexus* L.	21822 (a–j)	Romania
	(k–s)	Spain
Subgenus *Albersia* (Kunth) Gren. & Godr. (= Section *Blitopsis* Dumort.)		
A. *albus* L.	21800 (a–j)	Romania
	(k–s)	Spain
	Ames 13788	Canada
A. *blitum* L. subsp. *blitum*	23049 (a–j)	Romania
	(k–s)	Germany*
A. *blitum* subsp. *oleraceus* (L.) Costea	23051 (a–s)	Germany*
	PI 606 281	Bangladesh
A. *emarginatus* Moq. ex Uline & Bray = A. *blitum* subsp. *emarginatus* (Moq. ex Uline & Bray Carretero, Muñoz Garmendia & Pedrol	22966 (a–j)	Romania
	(k–s)	Spain
	Ames 23387	Brazil
	Ames 14964	India
A. *viridis* L.	23034 (a–j)	Romania
	(k–s)	Spain
A. *blitoides* S. Wats. var. *blitoides*	23045 (a–j)	Romania
	(k–s)	Spain
	PI 553 059	Canada
	PI 608 663	USA
A. *blitoides* S. Wats. var. *reverchonii* Uline & Bray	23046 (a–j)	Romania
	(k–s)	Russia
A. *graecizans* L. var. *graecizans*	23042 (a–j)	Romania
	(k–s)	Germany*
A. *graecizans* var. *sylvestris* (Vill.) Thell.	2632 (a–j)	Romania
A. *crispus* (Lesp. & Thev.) N. Terraciano	22225 (a–j)	Romania
A. *deflexus* L.	22228 (a–s)	Romania
		Spain

varies from 30–33 μm (*A. powellii*) to 7–10 μm (*A. graecizans*) and is more or less constant within a species (Table 3).

The mesocarp has one (Fig. 1, 2, 5, 7, 9, 10, 13, and 15) or two layers of cells (Fig. 3, 8, and 14) de-pending on the species (Table 2). In some species—*A. hybridus, A. quitensis* (Fig. 6), *A. graecizans* (Fig. 12), *A. blitoides* (Fig. 11)—the mesocarp begins as single cell layer but later is crushed and becomes essentially indistinguishable at maturity. As a consequence, the

Table 2. Data matrix of 10 pericarp characters in 17 species of *Amaranthus* (Amaranthaceae). Character abbreviations are explained in the Materials and Methods.

Taxa	1	2	3	4	5	6	7	8	9	10
Amaranthus caudatus	4	VAR	ROU/RAEL	2	—	TRANS	0	STI	1	—
A. cruentus	3	VAR	RAEL	1	LONG	—	0	STI	1	—
A. hypochondriacus	4/3	VAR	ROU/RAEL	2/1	LONG	TLO	+	DET1	1	—
A. powellii	3	VAR	RAEL	1	VARS	—	+	DET1	1	—
A. bouchonii	2	VAR	RAEL	0	—	—	+	DET1	2b	—
A. hybridus	2	VAR	ROU	0	—	—	0	DET1	1	—
A. quitensis	2	VAR	ROU	0	—	—	0	DET1	1	—
A. retroflexus	3	VAR	ROU	1	VARS	—	0	DET1	1	—
A. albus	3	UNI	SQU	1	LONG	—	0	DET1	1	—
A. blitum	4	UNI	RAEL	2	—	TRANS	0	DETp	2a	+
A. emarginatus	3	UNI	ROU	1	LONG	—	0	DETp	2a	+
A. viridis	3	UNI	ROU	1	LONG	—	+	DETp	2a	+
A. blitoides	2	UNI	ROU	0	—	—	0	STI		—
A. graecizans	2	UNI	ROU	0	—	—	0	DET1	1	—
A. crispus	2	UNI	ROU	0	—	—	+	DET1	2b	+
A. deflexus	4	UNI	TAEL	2	—	TLO	0	STI	2b	+
A. rudis	3	UNI	TAEL	1	LONG	—	+	DET1	1	—

pericarp in these species appears two-layered (Table 2). Size and arrangement of mesocarp cells relative to the epidermal cells are variable, thus providing additional characters. When the mesocarp is one-layered, its cells may be longitudinally or variably oriented relative to the epidermal cells. When the mesocarp is two-layered, the cells from the outer layer are always longitudinally elongated, while the cells from the inner layer may be transversely or variably stretched (transversely, longitudinally or obliquely) (Table 2). The thickness of the mesocarp varies from 12–14 μm in *A. graecizans* (Fig. 12) to 50–70 μm in *A. blitum* (Fig. 14) and is also relatively constant within a species (Table 3).

The endocarp is adjacent to the seed coat and con-

sists of a single layer of cells in all taxa examined. Generally, the seed coat and endocarp do not fuse, but, in some species with indehiscent fruits, there is a slight concrescence before the fruit dries (Table 2). When the pericarp is separated from the seed coat, the radial walls of the endocarp cells are ruptured (Fig. 8 and 10). Thus, the inner walls of the endocarp cells together with fragments of the radial walls remain in contact. Before the fruit dries the seed coat is visible as a thin membrane on the surface of the seed.

In species with circumscissile fruits, the inner tangential walls and to a lesser extent the radial walls are thickened, whereas the outer tangential walls of the endocarp cells are thin (Fig. 1, 2, 3, 4, 6, 7, 9, 11, and 12). As seen in longitudinal sections, the endocarp is

Table 3. Quantitative pericarp characteristics in 18 *Amaranthus* taxa (Amaranthaceae).

| Taxa	Pericarp thickness [μm]	Epidermis thickness [μm]	Mesocarp thickness [μm]	Endocarp cell thickness [μm]	Width of loops at the base [μm]	Amplitude of loops [μm]
Amaranthus caudatus	49 ± 5	16 ± 5	20 ± 2	12 ± 1	17.5 ± 17.5	13.7 ± 13.7
A. cruentus	44 ± 4	19.5 ± 2.5	14 ± 1	12 ± 1	21.5 ± 21.5	13.7 ± 13.7
A. hypochondriacus	46 ± 2	16 ± 3	17.5 ± 4.5	13 ± 2	97.5 ± 12.5	50 ± 5
A. powellii	35 ± 5	26 ± 0.4	6 ± 1	7.5 ± 0.5	96 ± 9	46 ± 2
A. bouchonii	37.5 ± 4.5	29.5 ± 3.5	6 ± 1	7.5 ± 0.5	45 ± 5	46 ± 2
A. hybridus	23.5 ± 1.5	12.5 ± 2.5	2.5 ± 2.5	5.5 ± 0.5	131 ± 44	107.5 ± 67.5
A. quitensis	24.5 ± 1.5	13 ± 2	2 ± 2	5.5 ± 0.5	117.5 ± 42.5	102.5 ± 72.5
A. retroflexus	26.5 ± 4.5	16 ± 1	5.5 ± 0.5	5.5 ± 0.5	60 ± 20	60 ± 20
A. albus	23.5 ± 1.5	13.5 ± 0.5	6.5 ± 0.5	7.5 ± 0.5	130 ± 50	107.5 ± 67.5
A. blitum subsp. *blitum*	57 ± 7.5	24 ± 2	36 ± 3	12.5 ± 2.5	—	—
A. blitum subsp. *oleraceus*	59 ± 7	26 ± 4	36 ± 4	12.5 ± 2.5	—	—
A. emarginatus	21 ± 3.5	11 ± 1	7 ± 1	5 ± 1	—	—
A. viridis	31 ± 3.5	17.5 ± 0.5	5.75 ± 0.75	10.5 ± 0.5	107.5 ± 67.5	82.5 ± 47.5
A. blitoides	19.3 ± 2.5	12 ± 1	2 ± 2	7.5 ± 0.5	55 ± 25	17.5 ± 7.5
A. graecizans	12.5 ± 0.5	8.5 ± 1.5	—	4.5 ± 0.5	67 ± 23	62.5 ± 37.5
A. crispus	20 ± 2.5	11 ± 0.5	3 ± 3	4.5 ± 0.5	85 ± 45	77.5 ± 42.5
A. deflexus	44 ± 4.05	21.5 ± 1.5	21 ± 1	6.5 ± 0.5	—	—
A. rudis	36 ± 3	25.5 ± 2.5	10.5 ± 0.5	10 ± 0.5	80 ± 50	60 ± 30
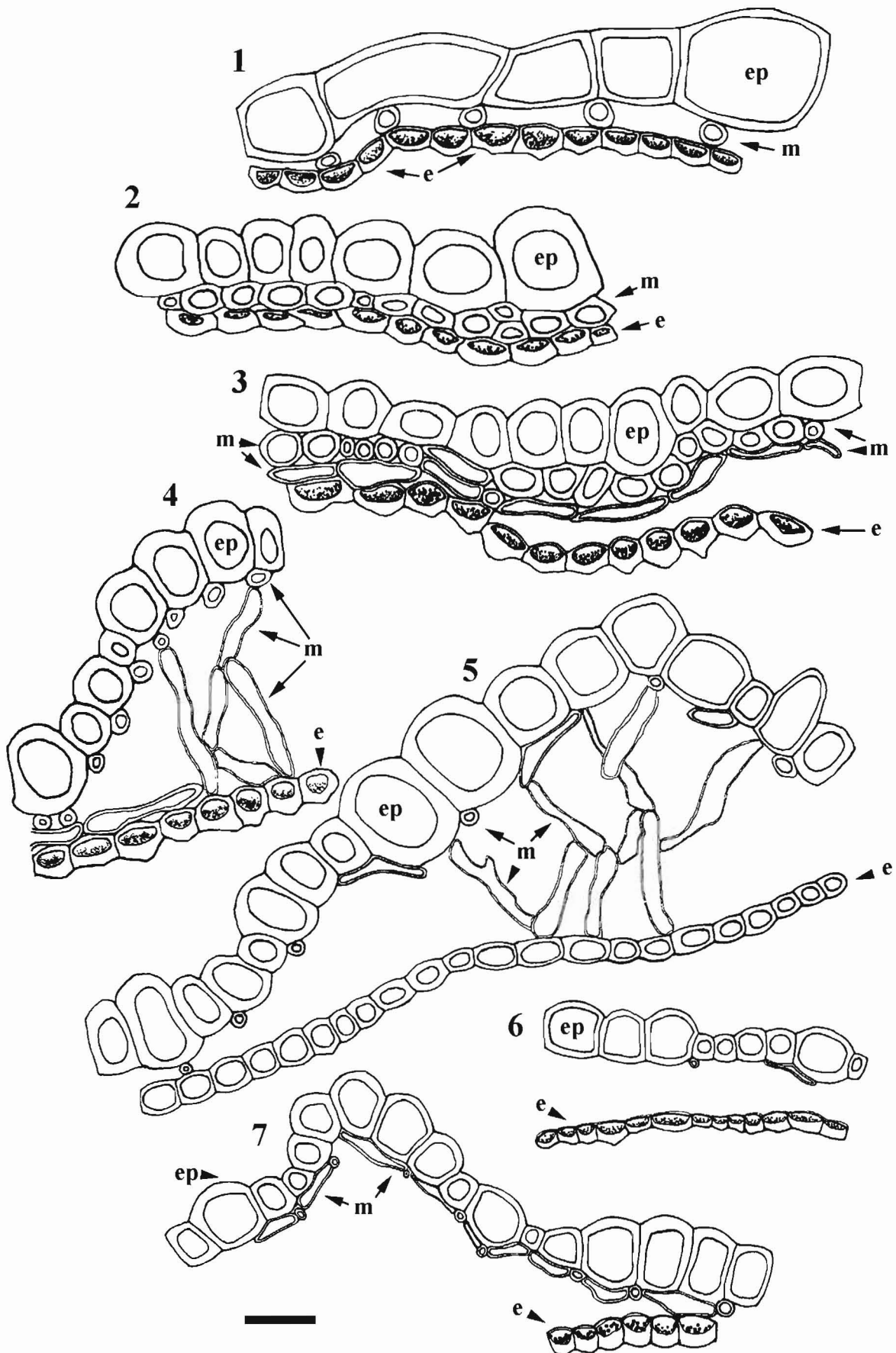
Fig. 1–7. Anatomy of the pericarp.—1. *Amaranthus rudis.*—2. *A. cruentus.*—3. *A. caudatus.*—4. *A. hypochondriacus.*—5. *A. bouchonii.*—6. *A. hybridus.* and *A. quitensis.*—7. *A. retroflexus.* (ep = epidermis; m = mesocarp; e = endocarp; scale bar = 10 μm)
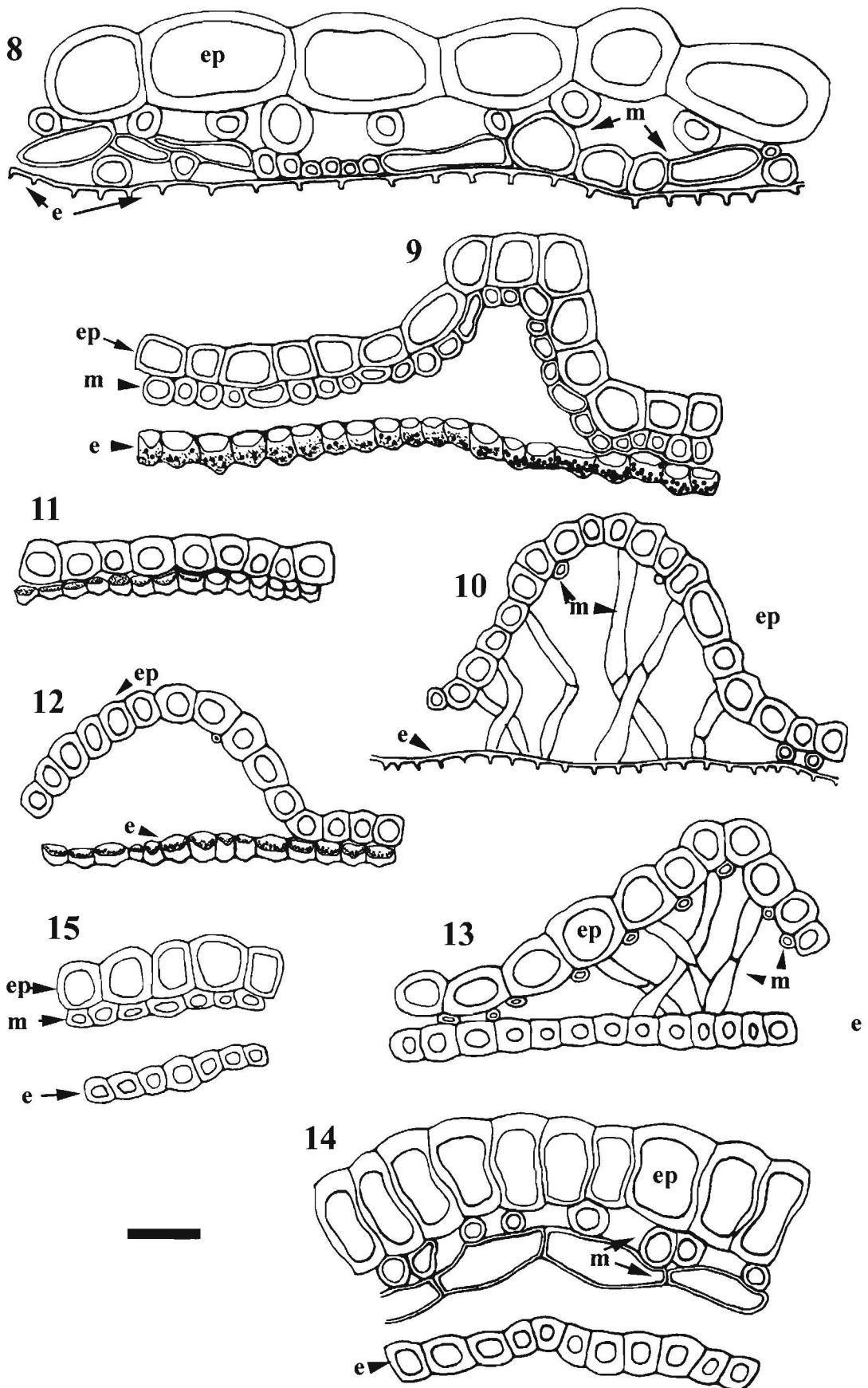
Fig. 8–15.   Anatomy of the pericarp.—8. *Amaranthus deflexus.*—9. *A. albus.*—10. *A. crispus.*—11. *A. blitoides.*—12. *A. graecizans.*—13. *A. viridis.*—14. *A. blitum.*—15. *A. emarginatus.* (ep = epidermis; m = mesocarp; e = endocarp; scale bar = 10 μm).

continuous and its cells contain calcium oxalate crystals. Species with indehiscent fruit have endocarp cells either with uniformly thickened walls, or with thin walls, depending on the species (Table 2). The circumscissile dehiscence of fruits is only partly the result of this unequal thickening of endocarp cell walls.

The epidermis and mesocarp always adhere, but usually they detach from the endocarp, resulting in large intercellular spaces (Fig. 4, 5, 7, 9, 10, 12, and 13). Distribution, orientation, form and size of these intercellular spaces, in association with the drying of the pericarp, cause a pattern of wrinkling characteristic for each species. When such intercellular spaces are formed, the mesocarp can exhibit additional loosely arranged cells, variable in form, which probably have a mechanical function (Fig. 5, 10, and 13). The presence or absence of such cells may have diagnostic value (Table 2).

In the mesocarp, along the suture lines of the carpels there are 2–3 colateral bundles. The bundles are surrounded by a sheath of radiate, ± isodiametric cells with thickened walls and large chloroplasts, much like the "Kranz" bundle-sheath that surrounds the minor veins of leaves (e.g., Haberlandt 1914; Fisher and Evert 1982). Because of the existence of this bundle-sheath, the bundles (and consequently the position of the suture lines of carpels) are usually visible on the fruit surface.

Based on the material examined, the pericarp structure is extremely simple but provides characters that allow the recognition of many species. Taxonomic significance of the anatomical features of the pericarp is revealed in the "hybridus" and "blitum" groups. In terms of their general morphology, especially in the A. hybridus complex, the cultivated species and their wild relatives are very much alike (Table 2). However, they differ based on their pericarp anatomy: the grain amaranths (A. hypochondriacus, A. caudatus and A. cruentus) have a more structurally complex pericarp than their wild relatives (A. powellii, A. quitensis and A. hybridus). Thus, A. hypochondriacus has a two-layered mesocarp, while its morphologically closest species, A. powellii, has a one-layered mesocarp. The same situation applies to A. caudatus (Fig. 3) and A. quitensis (Fig. 6), which, beside the different mesocarp, exhibit completely unlike characteristics (Table 2, 3). Similarly, A. cruentus (Fig. 2) and A. hybridus (Fig. 6) have quite distinct qualitative and quantitative anatomical pericarp features (Tables 2 and 3). Regardless of the different hypotheses on grain amaranth evolution (reviewed by Costea et al. 2001a; Xu and Sun 2001), these facts provide reasonable arguments against assembling the cultivated species together with their wild progenitors. In the "hybridus" group, some authors (e.g., Townsend 1988) consider the names A. powellii and A. hybridus taxonomic synonyms. Even

if other morphological characters easily differentiate these taxa, the distinctness of their pericarp anatomy is an additional proof of their individuality (Tables 2 and 3). In contrast, there is an obvious structural resemblance between A. hybridus and A. quitensis (Tables 2 and 3), supporting the idea of a single species including both taxa (Coons 1978; Costea et al. 2001a). In the "blitum" group, A. emarginatus and A. blitum have dissimilar fruits based on both morphological (Costea et al. 2001b) and anatomical characters. Thus, A. emarginatus has a three-layered, thin pericarp (18–25 μm, Fig. 15) while A. blitum has a four-layered, thicker pericarp (50–70 μm; Fig. 14) (Tables 2 and 3). These data support the specific rank for A. emarginatus as proposed by Hügin (1987).

DISCUSSION

Mechanism of Fruit Dehiscence and Wrinkling Pattern

Both dehiscent (irregularly or circumscissile) and indehiscent fruits in Amaranthus originate from the same type of syncarpous, two- or three-carpelar, unilocular and uniovulate gynoecium. In other words, there is no fundamental difference between the ovary of dehiscent and indehiscent fruits. Circumscissile dehiscence is the result of additional elements:

a) As seen in longitudinal section, a band of meristematic cells differentiate in the middle region of the ovary. This zone will constitute a region of mechanical weakness along which the pericarp will rupture producing dehiscence.

b) Mature cells of the endocarp acquire special thickenings in the inner, and to a less extent the radial walls, while the external tangential walls remain thin.

c) Drying of fruits, achieved at maturation.

d) Development of seed within the cavity of the ovary and pressure exercised by the neighboring flowers and fruits.

If the first two structural conditions are not realized, the fruit is always indehiscent. If the weakness line does not differentiate, the fruit will split irregularly or will remain indehiscent. If a weakness area exists but the endocarp cells have evenly thickened walls, the fruit may remain indehiscent (even if the dehiscence line is visible) or will have circumscissile dehiscence. The dehiscence mechanism is very much like the one described for Celosia argentea and Sesuvium portulacastrum (Subramanyam and Raju 1953), Plantago sp. (Rethke 1946) and Anagallis pumila (Raju 1952). The wrinkling pattern of the fruits is the consequence of the interaction between the overall architecture of pericarp in combination with drying.

The dehiscence-indehiscence character involves

probably two or a few Mendelian genes (reviewed by Brenner et al. 2000) but further research should clarify this point. The indehiscence character state is also an important breeding objective for grain amaranths because amaranth seeds are prone to shatter (Brenner and Hauptli 1990). In this respect, some results have already been obtained. The indehiscence trait has been transferred from *A. powellii* (*A. bouchonii*?, PI 572261) to *A. cruentus* and *A. hypochondriacus* using traditional breeding techniques (Brenner et al. 2000).

The Fruit in Amaranthus and its Taxonomic Significance

These new data illuminate the following questions: what is the fruit type in *Amaranthus* and what is the significance of dehiscence for the taxonomy of the genus? Using the categories provided by some systems of fruit classification (e.g., Gusuleac 1939; Winkler 1939, 1940; Egler 1943; Baumann-Bodenheim 1954; Judd 1985; Spjut 1994), *Amaranthus* fruits always fall into one of two categories. The indehiscent fruit is called "utricle" in the American literature or usually "achene" in the European literature (e.g., Aellen 1959; Ciocarlan 1988; Stace 1991). The circumscissile fruit is commonly called "pyxidium (pyxis)" or sometimes "capsule" (Townsend 1988) or "one-seeded capsule" (Stace 1991). The irregularly dehiscent condition is not named separately but is considered a derivative of the abovementioned types.

The problem is that in *Amaranthus* the gynoecium is invariant and anatomical differences between indehiscent and circumscissile fruits are extremely small. The best example is offered by *A. powellii* and *A. bouchonii*. The first has circumscissile fruits, while the second has indehiscent ones. Structurally, they differ by formation of a transverse zone of weakness and by the different manner of wall thickenings in the endocarp cells. Except for these anatomical peculiarities achieved at maturity, there are no other differences between the circumscissile and indehiscent fruits in *Amaranthus*. Therefore, on the basis of the ontogeny and the structural organisation of the pericarp, the two fruit "types" in *Amaranthus* are only functional variants of a single fruit type. However, choosing terms for the *Amaranthus* fruit is not simple. In *Amaranthaceae* and *Chenopodiaceae* many genera have irregularly dehiscent fruits. Sometimes, (as in *Chamissoa*) all intermediates between irregularly dehiscent fruits and circumscissile dehiscent fruits may be observed (Eliasson 1988). The same spectrum of circumscissile, irregularly dehiscent, and indehiscent fruits occurs in populations of *A. hybridus* from Mexico (Costea et al. 2001a). In such situations, circumscissile dehiscence should be considered more as a tendency than as a constant character. Some species with usually circum-

scissile fruits (e.g., *A. powellii, A. hybridus, A. retroflexus* and *A. albus*) can also form irregularly dehiscent and indehiscent fruits even on the same plant (Tucker and Sauer 1958; Costea et al. 2001a). In contrast, species with indehiscent fruits never produce plants with circumscissile or irregularly dehiscent fruits. Therefore, indehiscence in *Amaranthus* could be viewed as plesiomorphic and circumscissile transversal dehiscence as derived. However, in some situations (e.g., *A. bouchonii*) indehiscence may have evolved again from circumscissile dehiscence. As Cronquist (1988) stated, the advantages of circumscissile dehiscence are obscure since the entire fruit could act as a single unit of dispersal. There is apparently no correlation between fruit dehiscence and indehiscence and the success of various amaranth species as weeds. Species with dehiscent fruits are noxious weeds (e.g., *A. retroflexus, A. hybridus, A. powellii* and *A. palmeri*), but the same is also true of some species with indehiscent fruits (e.g., *A. viridis* and *A. blitum*). In some instances, the dehiscence mechanism is easily lost because the genetic causes of indehiscence are not selected against (Cronquist 1988). In such cases, irregular dehiscence can be regarded as an intermediate step between circumscissile dehiscent and indehiscent fruit variants.

The absence of a generally accepted system of fruit classification is regrettable. However, it is beyond the scope of this paper to resolve the carpological nomenclature for *Amaranthus*. The following considerations are only a survey of the available possibilities. "Amaranthocarpium" of Kaden and Kirpieznikov (1965) with its two variants: "dehiscens" (in *A. albus*) and "indehiscens" (in *A. blitum* = *A. lividus*), is difficult to accept—even if correct from a phylogenetic perspective—because this would involve the acceptance of many hundreds of names for the fruits of other plants. The other available terms are "utricle" and "achene." The definition of utricle of Judd (1985) and Spjut (1994; without the word "dehiscent") would be appropriate for the fruit of *Amaranthus*. For example, the characterisation of *Amaranthus* fruit as given by Gleason and Cronquist (1991)—"a thin-walled to coriaceous utricle, indehiscent or bursting irregularly, or commonly circumscissile at the middle, crowned by the persistent stigmas"—is satisfactory. Unfortunately, as Spujt (1994) showed, "utricle" is a confusing term because as a fruit type it was, and still is, used to refer either to the one-seeded capsule with circumscissile dehiscence, or to the one-seeded, indehiscent bladdery fruit, or even both situations together. More than that, the term "utricle" is also often used for the sac that surrounds the fruit of *Carex*. European authors preferred the term "achene", because of the above confusion regarding the name "utricle" and because the thickness of pericarp is not considered sufficient to warrant the distinction of two different types of fruits

("utricle" and "achene"). The symmetrical variant would be a "circumscissile" (transversally dehiscent) "achene." If adjectival terms that contradict the common definition of a carpological nomenclatural type are not to be used (Spjut 1994), the simplest approach would be to avoid naming the fruit in *Amaranthus* (and *Amaranthaceae*) entirely, as an increasing number of authors have done lately (e.g., Eliasson 1988; Akeroyd 1993), referring to it as circumscissile, irregularly dehiscent or indehiscent as appropriate.

In Europe, the dehiscence character is apparently constant within a line. Mixed European populations of *A. bouchonii, A. powellii, A. hybridus* and *A. retroflexus* were observed to maintain their original character (Costea et al. 2001a). Segregation is possible, but occurs at low frequencies. In North America, individuals of *A. powellii* and *A. hybridus* with indehiscent fruits are more variable than in Europe. In both, a single plant may bear only indehiscent fruits (especially *A. powellii*) or both dehiscent and indehiscent fruits (especially *A. hybridus*). Sometimes the dehiscence zone is partially visible but the fruit does not open (weakness zone present, but cell endocarp with no special thickenings in the walls). After surveying the most important herbarium collections in the United States it became obvious that European-like *A. bouchonii* occurs here too (Costea et al. 2001a). Perhaps the process of evolution of this taxon has been taking place simultaneously in North America and Europe, acquiring more stability and consistency on the latter continent. It is obvious that the dehiscence character cannot support recognition of taxa such as *A. bouchonii* at the species level. Pratt and Clark (2001) reached the same conclusion in a similar case: *A. tuberculatus* (Moq.) Sauer and *A. rudis* Sauer. However, the dehiscence character may be significant at the infraspecific level. For example, Costea et al. (2001a) proposed *A. bouchonii* as a subspecies of *A. powellii*. The two variants of *A. powellii* in Europe have a different ecology: subsp. *bouchonii* occurs primarily along riverbanks as pioneers, while subsp. *powellii* is a ruderal or agrestal weed. The seeds of subsp. *bouchonii* can be water-dispersed at longer distances than the seeds of subsp. *powellii* because of the extensive intercellular spaces present in the pericarp, which insure a better buoyancy. Additionally, the indehiscent fruits of subsp. *bouchonii* may enhance the imbibition of seeds during germination.

In conclusion, based on the material studied, the structural characteristics of the pericarp support the separate recognition of cultivated grain amaranths from their wild relatives. The anatomical features of the pericarp can supplement the morphological characteristics of fruits described by Costea et al. (2001a) in the identification of *Amaranthus* species. The dehiscence character in closely related *Amaranthus* taxa

(e.g., *A. powellii* and *A. bouchonii*) may be significant only at the infraspecific level. However, because the genus *Amaranthus* comprises approximately three times more species than were examined in the present study and some of these species are very variable and widespread, more material should be examined before definite conclusions can be reached.

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