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New infrageneric taxa and combinations in *Amaranthus* (Amaranthaceae)

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One new section, one new subsection, one new nothosection, and four new combinations at the sectional level are validated within *Amaranthus* L. (Amaranthaceae). The present state of infrageneric classification of the genus is discussed.

Key words: *Amaranthus*, infrageneric taxa, taxonomy

In recent regional treatments of *Amaranthus* L. (Aellen 1959, Brenan 1961, 1981, Gusev 1972, Frey 1974, Robertson 1981, Carretero 1985), only two or three infrageneric taxa were recognized, usually sections *Amaranthus* and *Blitopsis* Dumort. However, such a taxonomically complicated genus requires a more detailed infrageneric classification. A complete system of the genus can be worked out only as part of a taxonomic revision at species level on a worldwide basis, because proper placement of many taxa, especially those native to South America, Australia and Africa, is not completely clear yet.

In a brief abstract (ca. 90 words) presented at the XII International Botanical Congress, a Bulgarian botanist Kovachev (1975) published several *nomina nuda* for infrageneric groups of *Amaranthus* (names for one section, three subsections, and eight series), and a short Latin description of a supposedly new genus *Galapagosus* Kovachev (for more discussion and rejection of this genus, see Eliasson 1985). No descriptions or any explanations were given in the abstract for the new infrageneric names; their types were not cited either. Consequently, these names are invalid, and we have been unable to trace the subsequent validation of any of these names.

This present article is intended to provide a preliminary outline of the infrageneric classification of *Amaranthus*, mainly of the subgenera *Amaranthus* and *Acnida* (L.) Aellen ex K. R. Robertson, as well as to summarize some results obtained in the course of preparing a treatment of the genus for the forthcoming volume of the Flora of East Europe (formerly Flora of the European part of the USSR), the taxonomic and floristic revision of the genus in the Ukraine and adjacent countries (Mosyakin 1995), and work in progress for the Flora North America. Extensive study of herbarium specimens of *Amaranthus* in American (GH, ILLS, MO, NY, US), Russian (LE, MHA) and Ukrainian (KW, KWHA) herbaria during 1989–1995 was especially helpful for this work.

A modified infrageneric classification of *Amaranthus*

Genus *Amaranthus* L.
- Subgen. *Acnida* (L.) Aellen ex K. R. Robertson
  - Sect. *Acnida* (L.) Mosyakin & K. R. Robertson
  - Sect. *Saueranthus* Mosyakin & K. R. Robertson
  - Sect. *Acanthochiton* (Torrey) Mosyakin & K. R. Robertson
- Subgen. *Amaranthus*
  - Sect. *Amaranthus*
    - Subsect. *Amaranthus*
    - Subsect. *Hybrida* Mosyakin & K. R. Robertson
    - Nothosect. *Dubia* Mosyakin & K. R. Robertson
  - Sect. *Centrusa* Griseb.
- Subgen. *Albersia* (Kunth) Gren. & Godr. (the complete sectional subdivision of subgenus has not been worked out yet; see discussion below)
  - Sect. *Blitopsis* Dumort.
  - Sect. *Pentamorion* (G. Beck) Mosyakin & K. R. Robertson
  - Sect. *Goerziella* (Urban) Mosyakin & K. R. Robertson
  - Sect. *Pyxidium* Moquin in DC.

Key to the infrageneric taxa of *Amaranthus*

Unless noted otherwise, the number and shape of tepals given in the key refers to pistillate flowers. Since the infrageneric classification of subgenus *Albersia* has not yet been adequately developed, only sections of subgenera *Amaranthus* and *Acnida* are included into the key.

1. Plants normally dioecious .... *Amaranthus* subgen. *Acnida* … 2
— Plants normally monoecious 4
2. Bracts of pistillate flowers very broad, deltate or rhombic-deltate, foliaceous. Leaves linear or linear-lanceolate. Both bracts and leaves with crisped and/or minutely denticulate margins .... *Amaranthus* subgen. *Acnida* sect. *Acanthochiton*
— Bracts narrowly elliptic to subulate-linear, not foliaceous. Leaves variable. Both bracts and leaves with entire margins 3
3. Pistillate flowers without tepals (perianth segments), or with 1–2 reduced linear or linear-lanceolate tepals less than 2 mm long. Utricle usually indehiscent (dehiscent only in *A. rudis*) .... *Amaranthus* subgen. *Acnida* sect. *Acnida*
— Pistillate flowers with 5 (rarely 4) spathulate or obovate-elliptic tepals (sometimes only inner tepals distinctly spathulate). Utricle usually dehiscent (indehiscent only in *A. greggii*) .... *Amaranthus* subgen. *Acnida* sect. *Saueranthus*
4. Tepals usually (2–)3, but in some species 4–5. Plants ascending, prostrate, or erect; inflorescences in most cases axillary, glomerate or short-spiciform. In some species terminal inflorescences are also developed, but in this case utricles indehiscent, or tepals less than 5 . ..... *Amaranthus* subgen. *Albersia*
— Tepals usually 5, rarely 4–3. Plants normally erect, always with more or less long spiciform-cylindric terminal inflorescences. Axillary inflorescences similar to terminal ones. Fruits transversely dehiscent (except *A. bouchonii* and some forms of *A. spinosus*) .... *Amaranthus* subgen. *Amaranthus* … 5
5. Bracts at the base of inflorescences modified into firm spines. Fruits transversely towards the apex or irregularly dehiscent (rarely indehiscent) .... *Amaranthus* subgen. *Amaranthus* sect. *Centrusa*
— Bracts not modified into spines. Fruits transversely dehiscent in the central (equatorial) part (except for *A. bouchonii*, which has indehiscent fruits) ..... *Amaranthus* subgen. *Amaranthus* sect. *Amaranthus* … 6
6. At least inner tepals spathulate, with obtuse, truncate, emarginate, or at least broadly triangular apex; in some species abruptly narrowed toward a protruding bristle formed by the central vein ..... Subsect. *Amaranthus*
— Tepals gradually narrowed into acute, often spinulose or bristle-like apex ..... Subsect. *Hybrida*

Discussion and validation of new taxa and combinations

Amaranthus subgen. ***Acnida*** (L.) Aellen ex K. R. Robertson

J. Arnold Arbor. 62(3): 283. 1981. [Aellen in Hegi, Illustr. Fl. Mitteleur., ed. 2, 3/2: 467, 474. 1959, *nom. inval.*]. — *Acnida* L., Sp. Pl.: 1027. 1753. — Type: *Acnida cannabina* L. (= *Amaranthus cannabinus* (L.) Sauer), the only species originally included by Linnaeus in the genus *Acnida*.

Acnida L. was widely recognized as a separate genus by most authors until 1955, when Sauer (1955) presented his considerations and convincing evidence in favor of its inclusion within *Amaranthus*. He, however, did not propose any formal nomenclatural combination for this group at either subgeneric or sectional levels. Aellen (1959) introduced the combination *Amaranthus* subgen. *Acnida* (L.) Aellen but did not cite the basionym; the combination was validated later by Robertson (1981). Since dioecious amaranths definitely represent a natural and morphologically distinct group originally endemic to North America, we maintain the subgeneric status of the group. The subgenus can be subdivided into three natural sections, each possessing a rather distinctive combi-

nation of characters with regard to fruits (dehiscent or indehiscent), bracts (foliaceous or not), and tepals of pistillate flowers (completely absent, reduced to 1–2 small linear or lanceolate tepals, or all 5 tepals well developed and spathulate).

Amaranthus subgen. *Acnida* sect. *Acnida* (L.) Mosyakin & K. R. Robertson, *comb. nov.*

Acnida L. sect. *Acnida*, an autonym created by publication of *Acnida* L. sect. *Montelia* Moquin in DC., Prodr. 13/2: 277. 1849. — Type: *Acnida cannabina* L. (= *Amaranthus cannabinus* (L.) Sauer).

Acnida L. sect. *Montelia* Moquin in DC., Prodr. 13/2: 277. 1849 (in part). — *Montelia* (Moquin) A. Gray, Manual of Bot., ed. 2: 369. 1857.

Acnida L. sect. *Acnidastrum* Moquin in DC., Prodr. 13/2: 277. 1849 (in part).

Species: *Amaranthus cannabinus* (L.) Sauer, *A. australis* (A. Gray) Sauer, *A. tuberculatus* (Moquin) Sauer, *A. floridanus* (S. Watson) Sauer, and *A. rudis* Sauer (*A. tamariscinus sensu auct., non* Nutt., see Sauer 1972).

This section includes dioecious species with greatly reduced tepals in pistillate flowers and mostly indehiscent fruits. Three species belonging to this section, *Amaranthus cannabinus*, *A. australis*, and *A. tuberculatus*, usually completely lack tepals in pistillate flowers or occasionally have 1 (rarely 2) very small, rudimentary tepals less than 1 mm long. The two other species, *Amaranthus rudis* and *A. floridanus*, have pistillate flowers with 1–2 linear or narrowly lanceolate tepals to 1.5–2 mm long and thus they show a morphological transition toward the following section. Moreover, the fruits of *A. rudis* are dehiscent, but all other characters of both *A. rudis* and *A. floridanus*, such as greatly reduced non-spathulate tepals, shape of inflorescences, and general habit, provide good reason for their inclusion in section *Acnida*.

Amaranthus subgen. *Acnida* sect. *Saueranthus* Mosyakin & K. R. Robertson, *sect. nova*

Type: *Amaranthus palmeri* S. Watson.

Plantae dioeciae. Flores pistillati pentameri (rarissime tetrameri). Perianthii phylla spathulata, ca. 2–3.5 mm longa, in apice rotundata, truncata vel acuminata. Utriculus plerumque circumscisse dehiscens; species typica A. palmeri *S. Watson.*

Plants dioecious. Pistillate flowers with 5 (rarely 4) spathulate tepals (sometimes only inner tepals distinctly spathulate) ca. 2–3.5 mm long, rounded, truncate, or acuminate at apex. Utricle usually dehiscent, type species *A. palmeri* S. Watson.

Species: This section includes four dioecious species: *Amaranthus palmeri* S. Watson, *A. watsonii* Standley, *A. arenicola* I. M. Johnston, and *A. greggii* S. Watson. These have five well-developed spathulate tepals in pistillate flowers and usually dehiscent fruits (with the exception of *A. greggii*, which has indehiscent utricles). The section is named for Jonathan D. Sauer, American botanist and author of several perceptive articles on the grain and dioecious amaranths.

Amaranthus subgen. *Acnida* sect. *Acanthochiton* (Torrey) Mosyakin & K. R. Robertson, *comb. nov.*

Basionym: *Acanthochiton* Torrey, Report on an expedition down the Zuni and Colorado Rivers by Captain L. Sitgreaves — Botany: 170. 1853. — Type: *Acanthochiton wrightii* Torrey (= *Amaranthus acanthochiton* Sauer), the only species included by Torrey in *Acanthochiton*.

Species: This is a monotypic section represented only by the morphologically deviate species *Amaranthus acanthochiton* Sauer (often incorrectly cited as *A. acanthochiton* (Torrey) Sauer). Extensive discussion and justification for inclusion of *Acanthochiton* in *Amaranthus* was provided by Sauer (1955) and Eliasson (1988). For dioecious amaranths these plants combine several quite unusual characters, such as extremely broad, deltate, foliaceous bracts of pistillate flowers and narrowly lanceolate to linear leaf blades with crisped margins.

Amaranthus subgen. ***Amaranthus***

Type: *Amaranthus caudatus* L., lectotype of the genus designated by Britton and Brown (1913) and supported by Hitchcock and Green (1929).

Amaranthus subgen. *Euamaranthus* (Moquin) Gren. & Godr., Fl. France 3: 4. 1856.

This subgenus can be subdivided into several sections, two of which are discussed below, to-

gether with a new nothosection. Sauer (1967) also included *A. brandegei* Standley, *A. bigelowii* Uline & Bray, *A. viscidulus* Greene, and *A. scariosus* Bentham in section *Amaranthus*. However, the proper subsectional placement of these species, as well as of the South American *A. asplundii* Thell. (see Hunziker 1965) is not yet clear and requires additional study. The Australian *A. pallidiflorus* F. von Muell. was also included by Sauer (1967) in *Amaranthus* sect. *Amaranthus*. However, judging from its floral morphology, this species (as well as *A. clementii* Domin segregated from it) is closely related to another Australian taxon, *A. mitchellii* Bentham, which has axillary inflorescences typical of *Amaranthus* subgen. *Albersia* (Kunth) Gren. & Godr. (see note below). The resemblance of the habit of *A. pallidiflorus* to American species of section *Amaranthus* is most probably a result of parallel evolution within different infrageneric groups of the genus. Independent development of terminal inflorescences similar to those of *Amaranthus* sect. *Amaranthus* can be traced in such phylogenetically distant taxa as *A. tricolor sensu lato*, *A. viridis* L., and *A. blitum* L. Thus, the presence of well-developed terminal inflorescences is not an absolute diagnostic character for subgenus *Amaranthus* and neither are dehiscent fruits (see discussion in Eliasson 1988); these characters should be used in combination with others.

Amaranthus subgen. *Amaranthus* sect. *Amaranthus*

Amaranthus sect. *Amaranthotypus* Dumort., Florula Belgica: 19. 1827.

Amaranthus sect. *Euamaranthus* Moquin in DC., Prodr. 13, 2: 255. 1849 (excluding *A. gangeticus* L. and *A. mangostanus* L.).

This section can be subdivided into at least two subsections.

a. *Amaranthus* subsect. *Amaranthus*

Species: *Amaranthus caudatus* L., *A. quitensis* Kunth, *A. retroflexus* L., *A. celosioides* Kunth, ? *A. asplundii* Thell.

b. *Amaranthus* subsect. *Hybrida* Mosyakin & K. R. Robertson, *subsect. nova*

Type: *Amaranthus hybridus* L.

Perianthii phylla in apice acuta, subulato-acuminata vel subulato-mucronulata.

Tepals gradually narrowed into acute, often spinulose or bristle-like apex.

Species: *Amaranthus hybridus* L. (*A. patulus* Bertol.), *A. powellii* S. Watson (*A. hybridus p.p. sensu auct.*), *A. bouchonii* Thell., *A. hypochondriacus* L., and *A. cruentus* L.

Amaranthus bouchonii, the only species with indehiscent fruits in this subsection, is occasionally regarded as a mutant form of *A. powellii* or *A. hybridus*. Whatever its origin was, now this taxon probably deserves recognition as a separate species (see Wilkin 1992). Some authors accept *A. hybridus* in a very broad sense, submerging into it many taxa of both subsections mentioned above (see Coons 1977, 1978).

Amaranthus subgen. *Amaranthus* nothosect. *Dubia* Mosyakin & K. R. Robertson, *nothosect. nova*

Amaranthus sect. *Amaranthus* × *Amaranthus* sect. *Centrusa* Griseb.

This nothosection is proposed here to house the deviate allopolyploid species *Amaranthus dubius* Mart., which is very close morphologically and genetically to both *A. spinosus* L. and members of section *Amaranthus*. This stabilized hybridogenous species most probably has originated as a result of ancient hybridization between *A. spinosus* and either *A. hybridus* or *A. quitensis* (for more details see Clifford 1959, Grant 1959, Pal & Khoshoo 1965, Sauer 1967, Khoshoo & Pal 1972, Srivasta *et al.* 1977).

Amaranthus subgen. *Amaranthus* sect. *Centrusa* Griseb.

Fl. British West Indian Islands: 68. 1859. — Type: *Amaranthus spinosus* L. (the only species originally included by Grisebach into the section).

Amaranthus sect. *Acanthophora* G. Beck in Reichenb., Icon. Fl. Germanicae et Helveticae 24: 177. 1909.

Species: This section includes only the very polymorphic species *Amaranthus spinosus*, which is widespread in the tropics and subtropics of both hemispheres; it is probably native to South Ameri-

ca. It shows some degree of morphological transition toward dioecious amaranths, or, better, toward developing a dioecious habit. However, it is not completely clear yet whether this indicates a phylogenetic relationship or parallel evolution.

Amaranthus subgen. ***Albersia*** (Kunth) Gren. & Godr.

Fl. France 3: 3. 1856. — *Albersia* Kunth, Fl. Berolinensis 2: 144. 1838. — Type: *Albersia blitum* (L.) Kunth (= *Amaranthus blitum* L.).

The genus *Albersia* was established by Kunth (1838) to accommodate the species of *Amaranthus sensu lato* with indehiscent utricles. He mentioned several taxa belonging to this genus: "*Hujus generis sunt praeter sequentem Amarantus lividus* L., *prostratus* Balb., *oleraceus* L., *polystachyus* Willd. et *polygonoides* L." (Kunth 1838, p. 144). However, the only combination at the species level validated in the protologue was *Albersia blitum* (L.) Kunth, which consequently should be regarded as the type. Kunth's generic name is antedated by names published by Rafinesque (1836), particularly *Euxolus* (type: *Euxolus deflexus* (L.) Rafin. = *Amaranthus deflexus* L.), but *Amaranthus* subgen. *Albersia* (Kunth) Gren. & Godr. seems to be the earliest available combination at the subgeneric level.

This subgenus, as provisionally accepted here, includes all species traditionally included by many previous authors in *Amaranthus* sect. *Blitopsis sensu lato*. It still remains a rather polymorphic group, which can be more easily delimited by exclusion of the two above subgenera than by description of its crucial morphological characters. However, most of the species of subgenus *Albersia* are less closely related to typical representatives of subgenus *Amaranthus* than even dioecious species. Thus, accepting *Acnida* as a subgenus, we should consequently accept subgenus *Albersia* as well. Additional justification for the naturalness of these two polymorphic groups (subgenera *Amaranthus* and *Albersia*) was provided by cytogenetic studies (Khoshoo & Pal 1972).

Carretero (1985), following Moquin-Tandon (1849), justified the segregation of dehiscent-fruited species in the separate section *Pyxidium*. But even after this segregation, the resulting infrageneric taxa of this subgenus still represent groups too polymorphic and geographically widespread to be natural. The dehiscence/indehiscence of fruits is not the best character for segregating infrageneric taxa. For example, such species as *Amaranthus graecizans* L. and *A. californicus* (Moquin) S. Watson may have fruits both dehiscent and indehiscent, often even on the same plant. The character is also variable within groups of closely related species, e. g. *A. scleropoides* Uline & Bray (with dehiscent fruits) and *A. crassipes* Schlecht. (with indehiscent fruits).

The best taxonomic solution for the subgenus *Albersia* seems to be the recognition of several narrower sections and subsections based on the whole of their morphological characters. However, the taxonomic relationships within subgenus *Albersia* require additional study. Therefore, at present we refrain from providing a complete account of the infrageneric taxonomy of this subgenus and from describing new infrageneric taxa, as well as from citing complete lists of species belonging to the sections mentioned below. The following information is included in this article mostly in order to show problems existing in the traditional subdivision of the subgenus and to try to outline some possible solutions. However, we prefer to divide the indehiscent-fruited species (sect. *Blitopsis sensu* Carretero 1985) into three sections differing from each other in number and shape of tepals and some other characters.

Amaranthus subgen. *Albersia* sect. *Blitopsis* Dumort.

Florula Belgica: 19. 1827 (*pro parte, excl. sp.*). — Lectotype: *Amaranthus blitum* L. (see Carretero 1985)

Pentrius Rafin., Fl. Tellur. 2: 42. 1836.

Euxolus Rafin., Fl. Tellur. 2: 42. 1836. — *Euxolus* sect. *Pentrius* (Rafin.) Moquin in DC., Prodr. 13, 2: 273. 1849. — *Euxolus* sect. *Trimorion* G. Beck in Reichenb., Icon. Fl. Germanicae et Helveticae 24: 180. 1909.

Species: The section includes species with indehiscent utricles and mostly trimerous flowers, such as *Amaranthus blitum* (incl. *A. lividus* L.), *A. emarginatus* Moquin ex Uline & Bray, *A. viridis* L. (*A. gracilis* Desf.), and *A. deflexus* L. Some other species with indehiscent fruits and mostly trimerous flowers, such as Central American *A. acutilobus* Uline & Bray and Australian

A. macrocarpus Bentham, could be formally placed in this section as well. However, their relationships with other taxa are still insufficiently known, and their proper placement in the infrageneric system is not so evident, at least for now. For example, *A. macrocarpus* is probably related to some Australian taxa of the following section that have pentamerous pistillate flowers (see Brenan 1961); *A. acutilobus* seems to be related to the South American species of *Amaranthus* sect. *Pentamorion*.

In the future this section should be subdivided into several more natural subsections, or even segregate sections. For example, the study of seed morphology and anatomy of *Amaranthus* by Kowal (1954) has revealed differences in the sculpturing of the seedcoat between *A. gracilis* (= *A. viridis*) and *A. acutilobus* and the rest of the species he examined. The new section *Puncticulatae* Kowal was proposed for these two species. Unfortunately, this name is invalid since no Latin description or diagnosis was provided. A detailed study of fruit and seed morphology and anatomy (Klopper & Robel 1989ab) did not support the separation of *A. viridis* and *A. acutilobus* into a distinct section of their own. Also, from the point of view of macromorphology, these two species do not seem to be closely enough related to form a natural unit.

Amaranthus subgen. *Albersia* sect. *Pentamorion* (G. Beck) Mosyakin & K. R. Robertson, *comb. nov.*

Basionym: *Euxolus* Rafin. sect. *Pentamorion* G. Beck in Reichenb., Icon. Fl. Germanicae et Helveticae 24: 182. 1909. — Lectotype (here designated): *Euxolus crispus* Lesp. & Thev. (= *Amaranthus crispus* (Lesp. & Thev.) N. Terrac.).

Species: This section includes species with indehiscent utricles and five (occasionally four) spathulate or at least distinctly obovate tepals. Most of the species belonging to this section are native to South America (*A. crispus, A. standleanus* Parodi ex Covas, *A. vulgatissimus* Spegaz., *A. crassipes* Schlecht., and *A. muricatus* (Moquin) Hieron.) or Australia (*A. mitchellii* Bentham and *A. interruptus* R. Br.). Some other Australian taxa, including *A. pallidiflorus* F. von Muell. and *A. clementii* Domin, are probably also related to this section despite the similarity of their habits to some representatives of *Amaranthus* sect. *Amaranthus* (see discussion above, under *Amaranthus* sect. *Amaranthus*). Probably the Australian taxa mentioned above deserve recognition at least at subsectional level.

Amaranthus subgen. *Albersia* sect. *Goerziella* (Urban) Mosyakin & K. R. Robertson, *comb. nov.*

Basionym: *Goerziella* Urban in Feddes Repert. Sp. Nov. 20: 301. 1924. — Type: *Goerziella minima* (Standley) Urban (= *Amaranthus minimus* Standley), the only species included in *Goerziella* by Urban.

This monotypic section includes the unique Cuban endemic, *Amaranthus minimus* Standley, which differs from all other taxa of *Amaranthus* in its very peculiar floral morphology and habit (for more details see Standley 1917, Urban 1924, Hunziker 1965).

Amaranthus subgen. *Albersia* sect. *Pyxidium* Moquin in DC.

Prodr. 13, 2: 262. 1849. — Lectotype: *Amaranthus tricolor* L. (see Carretero 1985).

Dimeianthus Rafin., Fl. Tellur. 2: 41. 1836.

Amaranthus sect. *Blitopsis sensu auct. plur., pro parte*.

Species: This section traditionally includes *Amaranthus tricolor* aggr. (incl. *A. mangostanus* L., *A. melancholicus* L., and *A. gangeticus* L.), *A. graecizans* L., *A. blitoides* S. Watson, *A. albus* L., *A. scleropoides* Uline & Bray, *A. capensis* Thell., *A. thunbergii* Moquin, and other species of the subgenus with dehiscent (circumscissile) utricles (see Carretero 1985). In its present outline, it remains probably the most unsatisfactory grouping of taxa in the whole genus, both from the point of view of morphology and phytogeography. After additional study, which is beyond the scope of the present article, the section *Pyxidium* should be subdivided into several natural subsections.

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