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CONSPECTUS AND NOTES ON THE GENUS *AMARANTHUS* IN CANADA

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ABSTRACT. The *Amaranthus* spp. collections from the largest Canadian herbaria were reviewed and a conspectus was prepared. The genus is represented in Canada by 14 species (eight naturalized, four cultivated, and two rare adventive) and by six hybrids. New records for the Canadian flora include: *Amaranthus caudatus*, *A. powellii* subsp. *bouchonii*, *A. hybridus* subsp. *quitensis*, *A. blitum* subsp. *emarginatus*, *A. tricolor*, *A. powellii* × *A. hybridus*, *A. powellii* × *A. tuberculatus*, and *A. albus* × *A. blitoides*. The presence of the previously reported dioecious species *A. palmeri* and *A. cannabinus* is not confirmed by herbarium material. The taxonomy of the most problematic taxa is discussed and a key is provided for all Canadian species and subspecies. Morphology of fruits, seeds, and pollen belonging to *A. albus* and *A. californicus* was compared and their taxonomic relationship discussed. The infraspecific variability of *A. tuberculatus* was analyzed and a new nomenclatural combination proposed—*A. tuberculatus* var. *rudis*.

Key Words: *Amaranthus*, Canada, weeds, exotic plants

The genus *Amaranthus* comprises about 70 species, many of them economically important. Some are among the world's worst weeds (Holm et al. 1997) while others are cultivated as cereals, vegetables, and ornamentals (Brenner et al. 2000). The genus is considered difficult by taxonomists, weed scientists, and horticulturists because its taxa are extremely polymorphic and often not easy to identify; additionally the genus has many nomenclatural problems. In Canada, all the species are cultivated or adventive and the genus has never been reviewed. The purpose of this paper is to provide a list of *Amaranthus* species that occur in Canada and to discuss their taxonomy. The most important weed species of the genus in Canada have been treated in detail for the "Biology of Canadian Weeds" series. They include: *A. albus*, *A. blitoides*, and *A. blitum* (Costea and Tardif, in press) and *A. retroflexus*, *A. powellii*, and *A. hybridus* (Costea et al., unpubl. manuscript). Distribution maps as well as relevant biological and ecological information have been included in these papers.

MATERIAL AND METHODS

The following Canadian herbaria were surveyed: ACAD, ALTA, BRS, DAO, HAM, LRS, MMMN, MT, MTMG, NBM, NFLD, NSPM, OAC, OTT, QFA, QK, QUE, SASK, SFS, TRT, TRTE, TUP, UAC, UBC, UNB, USAS, UWO, UWPG, V, WAT, and WIN. Furthermore, the Canadian collections deposited in more than 40 herbaria in the United States (Costea, Sanders, and Waines 2001) were also examined. Detailed notes on the nomenclature and descriptions for most of the species can be found in Sauer (1950, 1955, 1967); Costea, Sanders, and Waines (2001); and Costea, Waines, and Sanders (2001). The morphology of fruits and seeds belonging to *Amaranthus californicus* and *A. albus* was comparatively studied from Canadian herbarium specimens (Appendix). Furthermore, accessions from the U.S.D.A., ARS germplasm collection were examined as well: *A. albus*—Ames 137 888 and Ames 18499; *A. californicus*—PI 595319 (U.S.D.A., ARS 2002). The Scanning Electron Microscopy (SEM) was done with a Hitachi S-570 at 10 and 15 kV, using an Anatech Hummer VII sputter-coater. Twenty-five fruits and seeds were collected from each herbarium specimen or per accession examined (Appendix). The same number of pollen grains per herbarium specimen (25) was analyzed in order to assess the morphology of the pollen grains in the two species (Appendix). A list of representative specimens examined was included in the Appendix for the most problematical taxa. Plants with mature fruits are necessary for accurate determinations. It is important to distinguish between tepals and bracteoles, and floral parts should be examined at magnifications higher than 30×. In the key "tepals" refers to those of female flowers only.

RESULTS AND DISCUSSION

The Canadian species of the genus *Amaranthus*. Based on the herbarium collections surveyed, in Canada there are eight naturalized, four cultivated, and two rare adventive species of *Amaranthus*. The number of *Amaranthus* spp. in Canada is fewer than in floras of significantly smaller countries from the same latitude in Europe. For example, Karlsson (2001) listed approximately 25 *Amaranthus* spp. from cool-temperate northern countries such as Sweden, Denmark, and Norway. The low number of species in Canada may be explained in two ways. Firstly, in Canada the disturbed habitats in which amaranths thrive are not as common comparative to European countries, where the density of human settlements is higher. Secondly, amaranths in Canada

are undercollected; the total number of Canadian specimens deposited in Canadian and United States herbaria does not exceed 3000. Therefore, the number of *Amaranthus* spp. and their inferred distribution from the available herbarium material is probably incomplete, especially if one takes into account that there are about 40 species reported from the United States (U.S.D.A., NRCS 2002).

The dioecious amaranths, *Amaranthus palmeri* S. Watson and *A. cannabinus* (L.) Sauer are mentioned by Scoggan (1978) and might occur in Canada, but their presence is not confirmed by any herbarium evidence. Some monoecious species that are widely distributed in the United States and Europe, such as *A. deflexus* L., if not already introduced in Canada, are very likely to be found in the future.

KEY TO THE *AMARANTHUS* SPECIES OCCURRING IN CANADA

1. Plants dioecious . . . . . 1. *A. tuberculatus*
1. Plants monoecious . . . . . (2)
   2. Flowers in a terminal spiciform or paniculiform inflorescence (axillary clusters may be present as well) . . . . . (3)
      3. Axils of stem leaves bearing a pair of spines; female flowers distributed only at the base of each inflorescence branch . . . . . 8. *A. spinosus*
      3. Axils of stem leaves without spines; female flowers evenly distributed in the inflorescence . . . . . (4)
         4. Tepals 3 . . . . . (5)
            5. Tepals longer than the fruit, with a long, pale awn . . . . . 14. *A. tricolor*
            5. Tepals shorter or equaling the fruit, without an awn . . . . . (6)
               6. Leaves acute; tepals somewhat shorter than or equaling the brownish, strongly muricate fruit . . . . . 13. *A. viridis*
               6. Leaves emarginate to bilobed; tepals much shorter than the green, almost smooth fruit . . . . . 12. *A. blitum*
                  7. Leaves not fleshy, deeply emarginate to bilobed at apex; terminal inflorescence long, thin and flexuous; fruit 1.2–1.8 mm long; seeds 0.8–1.1 mm in diameter . . . . . 12b. *A. blitum* subsp. *emarginatus*

7. Leaves fleshy, emarginate but never bilobed; terminal inflorescence short, thick and dense; fruit 1.7–2.6 (–3) mm long; seeds 1–1.2 mm in diameter . . . . . 12a. *A. blitum* subsp. *blitum*

4. Tepals 3–5 on the same plant, or constantly 5 . . . . . (8)

8. Tepals spathulate to obovate . . . . . (9)

9. Cultivated ornamentals or cereals, sometimes escaped in ruderal places, with large and conspicuous red, yellow, or whitish inflorescences; bracteoles shorter than stigma branches; tepals shorter than fruit . . . . . (10)

10. Inflorescence with a terminal part 10–30 (–40) cm long, thick and pendent; tepals wide-obovate to spathulate, the outer ones overlapping laterally and ± outcurved; fruit gradually narrowed toward apex; stigma branches spreading . . . . . 2. *A. caudatus*

10. Inflorescence usually with many lateral, patent (± perpendicular on inflorescence axis) or ascendant, thin branches; tepals narrow-obovate, straight and not overlapping; fruit abruptly narrowed toward apex in a thin rostrum; stigma branches erect . . . . . 3. *A. cruentus*

9. Weeds with green inflorescences; bracteoles longer than stigma branches; tepals longer than the fruit . . . . . (11)

11. Stem sparsely hairy below inflorescence; inflorescence with many lateral, patent, thin branches; tepal midribs extending beyond apex into the mucro . . . . . 4b. *A. hybridus* subsp. *quitensis*

11. Stem densely hairy below inflorescence; inflorescence usually with short, thick, ascendant or erect branches; tepal midribs ending below apex (although apex often mucronate). . . . . 7. *A. retroflexus*

8. Tepals oblong-linear to lanceolate . . . . . (12)

12. Cultivated ornamentals or cereals, sometimes escaped in ruderal places, with large and

conspicuous red inflorescences; pericarp with 3–4 cell layers; bracteoles shorter than stigma branches . . . . . (13)

13. Fruit abruptly narrowed toward apex in a thin rostrum; stigma branches parallel, erect; inflorescence usually with many lateral, patent or ascendant, thin branches . . . . . 3. *A. cruentus*

13. Fruit apex truncated, rostrum absent, stigma branches divergent from the base; inflorescence usually stiff, with thick, erect or ascendant branches . . . . . 5. *A. hypochondriacus*

12. Weeds with green inflorescences; pericarp with 2–3 cell layers; the bracteoles surpassing the stigma branches . . . . . (14)

14. Inflorescence with a few rigid, erect, and widely spaced branches or with many ascendant or erect, thick branches; leaves broadly elliptic to rhombic or lanceolate; tepals 3–5, very unequal with yellowish midveins; fruit apex gradually narrowed . . . . . (15)

15. Inflorescence stiff and erect, ± unbranched or with a few widely spaced, long branches; bracteoles 5–7.5 (–8) mm long; fruit circumcissile, irregularly wrinkled above the dehiscence line . . . . . 6a. *A. powellii* subsp. *powellii*

15. Inflorescence not strictly erect, more lax, with many lateral branches; bracteoles 3.5–5 mm long; fruit indehiscent or irregularly dehiscent, ± smooth . . . . . 6b. *A. powellii* subsp. *bouchonii*

14. Inflorescence usually with many patent, short and thin branches or with only a few thin, flexuous and long branches; leaves broadly ovate to rhombic-ovate; tepals 5, subequal with green mid veins; fruit apex abruptly narrowed . . . . . (16)

16. Tepals erect, shorter than the fruit . . . . . 4a. *A. hybridus* subsp. *hybridus*

16. Tepals erect or outcurved, longer than the fruit . . . . . 4b. *A. hybridus* subsp. *quitensis*

2. All flowers in axillary cymose clusters, terminal inflorescence absent . . . . . (17)

17. Perianth with (4–) 5 tepals . . . . . 11. *A. blitoides*

17. Perianth with 3 tepals or reduced to 1–2 tepals . . . . . (18)

18. Leaves emarginate or slightly bilobed; bracteoles foliaceous; fruit indehiscent . . . . . (19)

19. Fruit 1.7–2.6 (–3) mm long, pericarp 4-layered; seeds 1–1.2 mm in diameter. . . . . 12a. *A. blitum* subsp. *blitum*

19. Fruit 1.2–1.8 mm, pericarp 3-layered; seeds 0.8–1.1 mm in diameter . . . . . 12b. *A. blitum* subsp. *emarginatus*

18. Leaves not emarginate; bracteoles spinescent; fruit circumcissile . . . . . (20)

20. Stems many from the base, prostrate and mat forming, sometimes ascendant; stem and leaves glabrescent, often fleshy-turgescent; male flowers with 1–2 stamens; bracteoles short, thin, equaling the fruit; perianth of female flowers with 1 linear-lanceolate, membranous tepal and 1 (–2) tepals that are reduced or absent . . . . . 10. *A. californicus*

20. Stems usually single, divaricately branched, ascendant to erect, rigid, bone-like, usually scurfy villous or pubescent; leaves not fleshy; male flowers with (2–) 3 stamens; bracteoles 1.5–2× longer than fruits, spinescent, subulate, rigid; female flowers perianth with 3 membranous tepals . . . . . 9. *A. albus*

TAXONOMIC TREATMENT

I. Subgenus *Acnida* (L.) Aellen *ex* K. R. Robertson, J. Arnold Arbor. 62: 283. 1981.

1. *Amaranthus tuberculatus* (Moq.) J. D. Sauer, Madroño 13: 18. 1955; incl. *A. rudis* J. D. Sauer, Madroño 21: 428. 1972.

Pratt and Clark (2001) showed that *Amaranthus tuberculatus* and *A. rudis* as defined by Sauer (1955) are the morphological extremes of a single variable waterhemp species continuum. However, the authors admitted that the morphologic variation of female flowers exhibits a geographical separation, which follows Sauer's concept of two waterhemp entities (Sauer 1955). The western specimens correspond to the *A. rudis* race, while northern and eastern North American populations can be ascribed to typical *A. tuberculatus*. The two forms have a different ecology. Sauer (1955) observed that although they grow in similar habitats (e.g., margins of inland bodies of water), *A. rudis* (= *A. tamariscinus*) has "a very definite weedy tendency" compared to *A. tuberculatus*. Furthermore, the pericarp of the indehiscent fruits (in typical *A. tuberculatus*) is provided with extensive intercellular air spaces allowing a more effective water dispersal of the seeds than of the plants having circumcissile fruits (in typical *A. rudis*; Costea et al., unpubl. data). Only in the midwestern populations (Iowa, Illinois, and Missouri) might diagnostic traits segregate in populations and form a unique and inseparable morphological, isoenzymatical (Pratt and Clark 2001; Sauer 1955) and, most probably, ecological complex. Uline and Bray (1895) also combined the two waterhemps in a single species, *Acnida tamariscina* (Nutt.) A. W. Wood, but the authors recognized them as varieties. The latter solution seems to be the most appropriate because it would allow a distinction of the two entities (based on the morphology of the female flowers and their ecology) outside the Midwest.

1a. *Amaranthus tuberculatus* var. *tuberculatus*.

Female flowers with one or two lanceolate or linear tepals; the fruit is indehiscent. It has been collected since the last century from Ontario and Québec, where it is native. It grows along lake shores, ponds, and rivers (Appendix).

1b. **Amaranthus tuberculatus** var. **rudis** (J. D. Sauer) Costea & Tardif, *comb. nov. Amaranthus rudis* J. D. Sauer, Madroño 21: 428. TYPE: U.S.A. Kansas: Riley Co., 6 Aug 1895, *J. B. Norton 428* (HOLOTYPE: MO 1740436!).

Female flowers with absent or vestigial tepals; the fruit is dehiscent. This invasive weed, often resistant to various herbicides, has been recently introduced in southern Ontario, in Lambton County, and a few specimens were collected from ruderal places in Burnaby, British Columbia (Appendix).

II. Subgenus *Amaranthus*.

The most problematic group of species in this subgenus is referred to in the literature as the *Amaranthus hybridus* aggregate. It includes six extensively studied species, today almost cosmopolitan in distribution (*A. hybridus*, *A. powellii*, *A. hypochondriacus*, *A. cruentus*, *A. caudatus*, and *A. quitensis*), and a number of other species, poorly known, restricted to the southern parts of North America and to Central and South America (Costea, Sanders, and Waines 2001; Sauer 1950, 1967). *Amaranthus retroflexus* is usually separated from this complex. In our opinion, it should be included here as well because it hybridizes readily with all of the above-mentioned species. Cytological studies indicate a close genomic homology between *A. retroflexus* and other members of the *A. hybridus* complex (e.g., *A. cruentus* and *A. powellii*; Pandey 1999). Molecular (Xu and Sun 2001) and morphological studies (Costea and DeMason 2001; Costea, Sanders, and Waines 2001) have, in general, proved the distinction of the six (seven with *Amaranthus retroflexus*) species. However, such studies have necessarily based their conclusions on a limited number of populations and/or accessions. A worldwide survey of thousands of *Amaranthus* herbarium specimens has revealed that, especially in some subtropical and tropical regions, an overlapping pattern of variation may occur between species (Costea, unpubl. data). Nonetheless, including these six (or seven) species in a broadly defined *A. hybridus* may be a premature solution. Other concepts of *A. hybridus* in which only one or several species are included in *A. hybridus*, while the others are separately maintained or combined in various ways, are also unacceptable because they provide an arbitrary classification. Therefore, until the pattern of variation within this group, including the less known species, is properly understood, the best solution is to maintain them at specific rank.

2. *Amaranthus caudatus* L., Sp. Pl. 990. 1753.

This distinctive South American species, reported here for the first time in Canada, is sometimes cultivated as an ornamental (Appendix). The grain amaranths—*Amaranthus caudatus*, *A. hypochondriacus*, and *A. cruentus*—have generated a great interest in recent years as agricultural crops in the United States and other regions of the world, due to the exceptionally high nutritional value of their seeds and leaves. For a comprehensive review of the genetic and breeding resources of these species, see Brenner et al. (2000).

3. *Amaranthus cruentus* L., Syst. Nat. ed. 10, 1269. 1759.

This species is native from Central America, and in Canada the name has been frequently misapplied to *Amaranthus hypochondriacus*. It is cultivated as an ornamental (but less frequently than *A. hypochondriacus*) and sometimes it escapes in ruderal places in Alberta, Ontario, and Québec (Appendix). In Canada, it has usually been treated as a variety of *A. hybridus* (Boivin 1966; Scoggan 1978).

4. *Amaranthus hybridus* L., Sp. Pl. 990. 1753.

4a. *Amaranthus hybridus* subsp. *hybridus*. *A. patulus* Bertol., Comment. Itin. Neapol. 19. 1837. *A. incurvatus* Timeroy *ex* Gren. & Godr., Fl. France Prosp. 8. 1846.

Originally from eastern North America, Mexico, and Central America, this taxon is now widespread all over the world as a weed in cultivated or ruderal places. In Canada, it is confined to southwestern Ontario (Appendix). Scoggan (1978) also mentioned that it was recorded in western Québec, and that a specimen was found in Winnipeg (Scoggan 1957). We were unable to prove this from herbarium material, although the presence of this taxon in other provinces is likely to be expected.

4b. *Amaranthus hybridus* subsp. *quitensis* (Kunth) Costea & Carretero, Sida 19: 955. 2001. *A. quitensis* Kunth, Humb., Bonpl. & Kunth, Nov. Gen. Sp. 2, folio: 156; ed. 4: 194. 1817.

This is a new record for Canada, based on a single collection: Toronto, Bull grounds, 10 Sep 1904, *W. Scott s.n.* (TRT). A native of tropical South America, where it is a noxious weed, this plant tends to be more restricted to warm climates than subsp. *hybridus*, and it is unlikely to become a permanent part of the Canadian flora in the future.

5. *Amaranthus hypochondriacus* L., Sp. Pl. 991. 1753. *A. hybridus* L. subsp. *hypochondriacus* (L.) Thell. [rankless] *erythrostachys* (Moq.) Thell., Asch. & Graebn., Syn. Mitteleur. Fl. 5: 241. 1914.

In Canada, *Amaranthus hypochondriacus* has been considered a synonym of *A. hybridus*, but the description of the latter species (e.g., Scoggan 1978) did not include the characteristics of the former. It is the most frequent grain amaranth cultivated in Canada and sometimes it escapes in ruderal places in British Columbia, Alberta, Manitoba, Ontario, and Québec (Appendix).

6. *Amaranthus powellii* S. Watson, Proc. Amer. Acad. Arts. 10: 347. 1875.

6a. *Amaranthus powellii* subsp. *powellii*. *A. retroflexus* var. *powellii* (S. Watson) B. Boivin, Naturaliste Canad. 93: 641. 1966.

This subspecies is native to North and South America and has previously been shown to be frequent in Québec and Ontario (Doyon et al. 1986; Frost 1971). The subspecies was also reported from British Columbia to Saskatchewan, and from Prince Edward Island (Boivin 1966). Moss (1983) mentioned that *Amaranthus powellii* was "rare on waste ground" in Alberta. Based on the early reports of this species in British Columbia and Alberta (which date from the late 1800s), *A. powellii* may be much more frequent in these provinces than is currently believed and the same situation may occur in Saskatchewan, Nova Scotia, and New Brunswick. A few specimens of *A. powellii*, previously identified as *A. retroflexus*, were examined from these provinces.

6b. *Amaranthus powellii* subsp. *bouchonii* (Thell.) Costea & Carretero, Sida 19: 964. 2001; *A. bouchonii* Thell., Monde Pl. 27(160): 4. 1926.

This first record for Canada was described from France (Thellung 1926), but it has spread as an agrestal weed in several western and central European countries, where it has frequently been accepted at the specific rank. In Europe, *Amaranthus bouchonii* is thought to have evolved as a colonist of nitrophilous river banks because of the water dispersal advantage conferred by its indehiscent fruits. Afterwards, it has invaded irrigated fields, where it may compete efficiently with other amaranths such as *A. retroflexus*. Costea, Waines, and Sanders (2001) reported it from the United States and, based on its morphology, reduced it to a subspecies of *A. powellii*. The latter authors suggested two hypotheses regarding its presence in North America. The first one suggests that *A. powellii* subsp. *bouchonii* was introduced from Europe; the second hypothesis assumes that the indehiscence character had developed simultaneously in both North America and Europe. This second hypothesis is supported by the early records and by the wide and scattered distribution observed for these plants in North America (Costea, Sanders, and Waines 2001; Appendix). However, this taxon has apparently not acquired here the consistency observed in Europe. A study using molecular markers would be necessary to clarify the relationships between these two subspecies using both European and North American source material.

7. *Amaranthus retroflexus* L., Sp. Pl. 991. 1753.

This is the most common species of the genus and is distributed in all the Canadian provinces. *Amaranthus retroflexus* was probably the first species of the genus introduced to Canada by the early colonists from the more southern regions of America, between the 17th and 18th centuries. Evidence for this includes the macrofossil seeds of *A. retroflexus* excavated from various sites in Québec, which are estimated to be approximately 250 years old (Richard 2001).

8. *Amaranthus spinosus* L., Sp. Pl. 991. 1753.

This distinctive tropical species is not naturalized in Canada and is unlikely to be in the future because of its cold sensitivity. Its presence in Canada is based on two collections from Manitoba (Fort Garry, 14 Jul 1931, *Hutchinson s.n.*, DAO) and Ontario (Swansea, 23 Aug 1912, *A. L. Bennes s.n.*, DAO).

III. Subgenus *Albersia* (Kunth) Gren. & Godr., Fl. France (Grenier) 3: 3. 1856.

9. *Amaranthus albus* L., Syst. Nat. ed. 10: 1268. 1759. *A. graecizans* auct., non L.

This species is a common weed, native to the plains of central North America. In Canada it occurs in all provinces except the coldest ones: Yukon Territory, Northwestern Territories, Nunavut, Newfoundland, and Labrador. It grows in both ruderal and agrestal habitats, and it is the second most frequent species after *Amaranthus retroflexus*.

10. *Amaranthus californicus* (Moq.) S. Watson, Bot. California 2: 42. 1880.

This species is a native of the western United States, but was also reported from Nebraska, Wyoming, and Texas; in Canada it is known from southern Alberta and western Saskatchewan (Boivin 1966; Scoggan 1978). *Amaranthus californicus* has been misidentified in herbaria as *A. albus* (and vice versa) and the relationship between the two taxa needs resolution. Besides the differences already mentioned in the key, the SEM study of the fruits and seeds revealed the following:

1. Fruit abruptly narrowed in a beak toward the stigma branches, with more or less smooth pericarp; stigma branches thin, erect (Figure

1C); seeds obovate, with the radicle zone prominent (Figure 1A) . . . . . *A. californicus*

1. Fruit gradually narrowed and truncated toward the stigma branches, with the pericarp coarsely wrinkled; stigma branches thick, spreading from the base (Figure 1D); seeds round to nearly round, with the radicle zone not prominent (Figure 1B) . . . . . *A. albus*

These differences (including those mentioned in the general key) represent the extremes between which intermediates may occur. Thellung (1914) described in *Amaranthus albus* the form *monosepalus* based on a "forme aotomnale" observed by Sennen in Barcelona, Spain. Occasionally we examined specimens of *A. albus* with a reduced perianth formed of 1 (2) tepals from Europe and eastern North America (where *A. californicus* does not occur). The morphology of bracteoles can also vary in the populations of *A. albus* located outside the distribution range of *A. californicus*; sporadically, individuals with short, thin bracteoles may be encountered. The morphology of fruits and seeds examined on Canadian specimens, although often reliable in differentiating the two taxa, may also show an overlapping pattern in some cases (e.g., round seeds and/or wrinkled fruits in *A. californicus* and obovate seeds and/or smooth pericarp in *A. albus*). These observations suggest that the normal range of variation in *A. albus* may include many of the differentiating characteristics of *A. californicus*. Howell (1970) observed that typical plants of *A. californicus* at Alpine Lake, California were growing together with a similar amaranth, which differed in having female flowers with 3 tepals. The author suggested that these forms might represent a hybrid between *A. californicus* and *A. albus*.

Costea, Waines, and Sanders (2001) and Costea, Sanders, and Waines (2001) found differences in pollen morphology among the taxa of *Amaranthus hybridus* and *A. blitum* complexes. The specimens of *A. albus* and *A. californicus* examined (Appendix) were identical with respect to their pollen morphology, suggesting a close relationship. The pollen grains are pantoporate, apolar, 18–28 μm in diameter, with 22–36 uniformly distributed apertures, and the tectum is provided with granules.

It is probable that *Amaranthus californicus* evolved from *A. albus* in western North America as an ecological segregate of moist mud or sand and in beds of dried-up lakes around ponds and lake shores, habitats from which it has been recorded by all authors (Abrams 1944; Correll and Johnston 1970; Hickman 1993; Hitchcock and Cronquist 1964; Moss 1983; Munz and Keck 1959). The

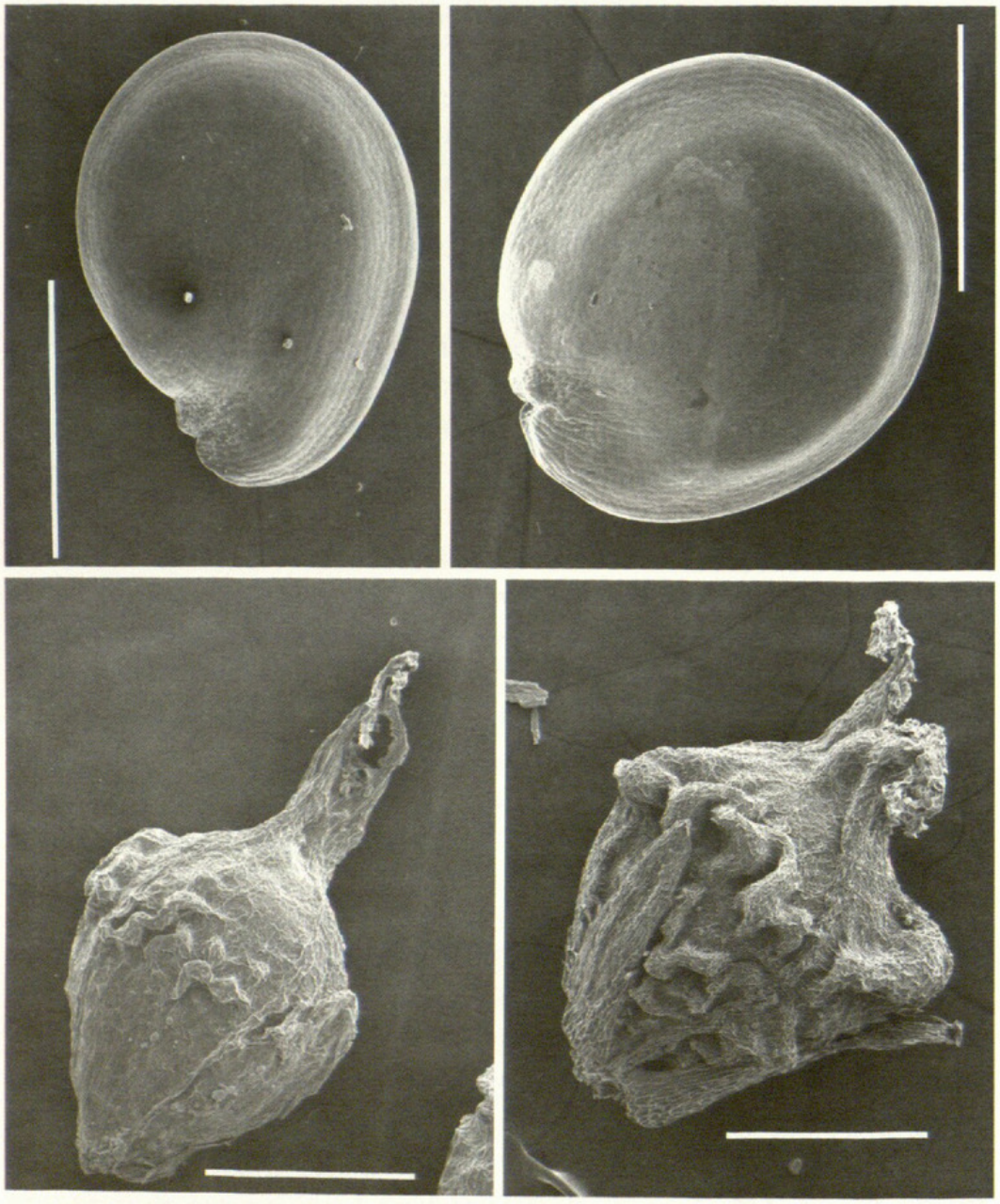

Figure 1. Morphology of seeds and fruits of *Amaranthus californicus* (left) and *A. albus* (right). Scale bar = 0.50 mm for seeds and 0.60 mm for fruits.

expansion of *A. californicus* to disturbed habitats with *A. albus* might eventually obscure the limits between the two taxa. For example, Hartman and Nelson (2000) included both *A. californicus* and *A. albus* on the list of invasive species in Wyoming. *Amaranthus californicus* in Canada often occurs in ruderal places where *A. albus* has been long-established. Nevertheless, the change in rank of *A. californicus* to an infraspecific taxon (subspecies) of *A. albus* would require more study

of the United States populations. Until then it should retain its current status at specific rank.

11. *Amaranthus blitoides* S. Watson, Proc. Amer. Acad. Arts 12: 273. 1877. *A. graecizans* auct., non L.

This species is considered by most authors to be a native of western North America. In Canada it occurs with *Amaranthus albus* in many of its habitats. The provinces where it was not documented by herbarium material were Yukon Territory, Northwestern Territories, Nunavut, Newfoundland, Nova Scotia, New Brunswick, and Prince Edward Island. The binomial *A. graecizans* has been widely misapplied in North America to either *A. albus* or *A. blitoides*. *Amaranthus graecizans* (subsp. *graecizans*) is a taxon native to Europe, North Africa, and Asia that superficially resembles *A. blitoides* var. *reverchoni* Uline & Bray (Costea, Waines, and Sanders 2001).

12. *Amaranthus blitum* L., Sp. Pl. 990. 1753.

This species has been known in North America as *Amaranthus lividus* L. (for details on nomenclature see Costea, Waines, and Sanders 2001). Two of the three subspecies of *A. blitum* (Costea, Waines, and Sanders 2001) occur in Canada.

12a. *Amaranthus blitum* subsp. *blitum*; *A. lividus* L. subsp. *ascendens* (Loisel.) Thell. *ex* Wachter, Heukels, Geill. Schoolfl. Nederl., ed. 11, 169. 1934.

This subspecies is native to the Mediterranean region, Eurasia, and North Africa where it is a frequent weed in vegetable gardens and in ruderal places. In the United States, *Amaranthus blitum* subsp. *blitum* occurs as a rare adventive (Costea, Waines, and Sanders 2001) and the same situation seems to exist in Canada. A few specimens of this subspecies were collected from Ontario and Québec (Appendix).

12b. *Amaranthus blitum* subsp. *emarginatus* (Moq. *ex* Uline & Bray) Carretero, Munoz Garm. & Pedrol, Anales Jard. Bot. Madrid 44: 599. 1987; *Amaranthus emarginatus* Moq. *ex* Uline & Bray, Bot. Gaz. (Crawfordsville) 19: 319. 1894.

This subspecies is native to and very widespread in the tropics, but it has also been introduced into the temperate regions of North America and Europe. It is a thermophyte, which prefers humid, nitrophilous

alluvial sands (on river banks, lakes) or fertile light horticultural substrates. It is naturalized as a ruderal and agrestal weed in the United States (Costea, Waines, and Sanders 2001). In Canada, *Amaranthus blitum* subsp. *emarginatus* is a new record and it appears to be naturalized in British Columbia and Québec (Appendix).

13. *Amaranthus viridis* L., Sp. Pl. (ed. 2) 1405. 1763.

According to the majority of authors, this species is native to South America. Previous records of this species from Canada were based on misidentifications of *Amaranthus blitum*. The only valid Canadian specimen is from Québec, Cté. de Rouville, St-Césaire, champ de tomates, 25 Jul 1983, *D. Tanguay 83-703* (QUE).

14. *Amaranthus tricolor* L., Sp. Pl. 989. 1753.

This distinctive species is native to Asia, where it is widely cultivated as a vegetable. In Canada we encountered it in Ontario as an ornamental. The most frequent cultivated ornamental forms are 0.6–1 (–1.5) m tall and their leaves are green or variegated, displaying bright white, purple-red, or yellow shades.

Hybrids. Hybridization is one of the most important sources of taxonomic difficulty in *Amaranthus*. Hybrids are known to occur naturally between the species within each of the three subgenera and also between the species of the subgenera *Amaranthus* and *Acnida*. Hybridization between the species of subgenera *Amaranthus* and *Albersia* or between *Acnida* and *Albersia* is unknown. Introgression rates have been reported only for the grain amaranths and they vary between 3.5–34%, depending on the environmental factors (Costea, Sanders, and Waines 2001). Experimental hybridizations have shown that F_1 hybrids are usually 89–90% sterile (Greizerstein and Poggio 1992; Greizerstein et al. 1997; Murray 1940). The introgression rates explain the formation of hybrid swarms, while the predominant inbreeding nature of amaranths may account for the relative stability of the hybrid products.

The F_1 hybrids within the subgenus *Amaranthus* are often not morphologically intermediate between the two parents. They have abnormally shaped inflorescences with very dense, crowded (and sometimes twisted or fan-shaped) branches. They can easily be recognized by the great number of densely packed and larger bracteoles that subtend the sterile female flowers. The best way to identify them is to note which potential parent species are present in the field where the hybrids were

collected and to perform molecular tests. Franssen et al. (2001) showed that the hybrids between monoecious and dioecious species have an intermediate number of apertures in the pollen grains. The F_1 hybrids within the subgenus *Albersia* are usually morphologically intermediate between the two parents. The survey of Canadian herbarium specimens revealed the following F_1 hybrids:

1. *Amaranthus* ×*soproniensis* Priszter & Karpati, Index Horti Bot. Univ. Budapest. 7: 140. 1949 (*A. retroflexus* × *A. powellii*).

The plants are often purplish-colored, with the leaves resembling those of *Amaranthus powellii* in shape. Most commonly, the terminal inflorescence has many crowded, thin branches (occasionally fan-shaped, or a long and pendent terminal inflorescence may be encountered). The tepals of the female flowers are obovate or spathulate and much longer than the sterile ovaries (as in *A. retroflexus*; Appendix).

2. *Amaranthus* ×*ozanonii* Thell., Asch. & Graebn., Syn. Mitteleur. Fl. 5: 263. 1914 (*A. retroflexus* × *A. hybridus*).

The plants are usually green-gray. The inflorescence has many thick lateral branches, and the tepals of female flowers are like those of *Amaranthus retroflexus* (Appendix).

3. *Amaranthus hybridus* × *A. powellii* (the hybrid has not been formally named).

This hybrid is a new record for Canada. Plants are monoecious with the leaves resembling those of *Amaranthus powellii* in shape. The inflorescence has many ascendant branches. The bracteoles are thin, acicular, and 3–4.5 mm long (Appendix).

4. *Amaranthus hybridus* × *A. tuberculatus* var. *tuberculatus* (the hybrid has not been formally named).

The plants are monoecious. The inflorescence is very branched, and has many thin and patent branches. The female flowers have reduced tepals and long stigma branches, as in *Amaranthus tuberculatus* (Appendix).

5. *Amaranthus powellii* × *A. tuberculatus* var. *rudis* (the hybrid has not been formally named).

This hybrid is a new record for Canada. The plants are monoecious, they are somewhat intermediate between the parents, and they have a much more branched inflorescence than *Amaranthus powellii*, but the many, thin branches are rigid (as in the latter). The bracteoles are spinescent and 2.5–3.5 mm long. The female flowers have 1–3 tepals and long stigma branches (Appendix).

6. *Amaranthus* ×*budensis* Priszter, Index Horti Bot. Univ. Budapest. 7: 125. 1949 (*A. albus* × *A. blitoides*).

This hybrid is reported here for the first time in Canada. It is more or less intermediate between its parents. It differs from *Amaranthus albus* by its shorter bracts and larger fruits and seeds, and from *A. blitoides* by its ascendant or erect stems, the longer bracts, and the smaller fruits and seeds (Appendix).

The presence of *Amaranthus retroflexus* × *A. tuberculatus* is also possible in Canada. The hybridization between the species examined in the present account and the grain amaranths (*A. caudatus*, *A. cruentus*, and *A. hypochondriacus*) in Canada is feasible but improbable due to the infrequent cultivation of the grain species.

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APPENDIX

REPRESENTATIVE SPECIMENS EXAMINED.

1a. *Amaranthus tuberculatus* var. *tuberculatus*. Ontario: Essex Co., Pelee Twp., Middle Island, on the shore of Lake Erie, 27 Jul 1988, *M. J. Oldham et al. 8416* (DAO, MICH, TRTE); Haldimand Co., waste ground by Lake Erie, 21 Aug 1960, *H. J. Scoggan 14935* (MTMG); Hastings Co., Salmon River, 1 Oct 1865, *J. Macoun s.n.* (MTMG); Middlesex Co., Lobo Twp., 2 km S of Komoka, Komoka Swamp, 31 Aug 1993, *M. J. Oldham 15550* (QFA, MICH); Ottawa Co., Ottawa, 20 Aug 1892, *W. Scott s.n.* (DAO); Ottawa, Rockcliffe Park, on the shoreline of Ottawa River, 1 Sep 1951, *J. J. Basset & D. R. Lindsay 3061* (DAO). Québec: Cté. Jacques Cartier, Mount Royal, 11 Sep 1960, *G. & P. H. Du Boulay 1636* (HAM); Montréal, Pointe St-Charles, 24 Aug 1976, *J.-P. Bernard B 76-736* (DAO, QFA, MTMG); Cté. Missisquois, Stanbridge Station, 10 Sep 1959, *J.-P. Bernard 59-316* (DAO, QFA, QUE).

1b. *Amaranthus tuberculatus* var. *rudis*. British Columbia: Greater Vancouver Regional Distr., Burnaby, growing between rails of railroad tracks in ballast, 18 Oct 1992 and 3 Nov 1992, *F. Lomer 92-317* (UBC). Ontario: Lambton Co., Petrolia, 15 Sep 2002, *M. Costea & F. Tardif 8638–8643* (OAC).

2. *Amaranthus caudatus*. Saskatchewan: Regina Distr., Regina, 2352 Athol Street, 8 Sep 2001, *G. F. Ledingham 13980* (USAS). Ontario: Welland Co., Stamford, summer 1940, *W. R. Ellis 1844* (OAC). Québec: Cté. Laval, Laval University, cultivated, 5 Aug 1968, *R. Van den Hendle 068-265* (OAC); Cté. Portneuf, Deschambault, 16 Sep 1983, *R. Neron 83-3020* (QUE).

3. *Amaranthus cruentus*. Alberta: Edmonton Distr., Fort Saskatchewan, grown as ornamental, 2 Sep 1945, *G. H. Turner 4716* (ALTA). Ontario: Middlesex Co., London, Watson Street, "dump", 2 Sep 1950, *J. F. Calvert s.n.* (WAT); Waterloo, Beechwood estate, waste sandy ground, 20 Aug 1969, *J. K. Morton 3298* (WAT); Ottawa Co., Ottawa, 46°26′30″N 75°40′W, rubble and sand of basement ruins, 14 Oct 1991, *D. F. Brunton 11025* (TRT). Québec: Cté. de Vaudreuil, Ile Perrot, 26 Jul 1937, *Fr. Cléonique 9385* (MT); Montréal, cultivated, 29 Sep 1947, *J.-P. Bernard 44468* (MT).

4. *Amaranthus hybridus* subsp. *hybridus*. Ontario: Brant Co., S of New Scotland, 43°21′N 81°51′W, corn field, 29 Sep 1973, *A. Reznicek 2619* (TRTE); Elgin Co., 5 mi. NW of Dutton, weed of soybean with *A. powellii*, 29 Aug 1967, *R. A. Frost 36* (DAO, UWO); Essex Co., Pelee Island, 27 Sep 1988, *M. J. Oldham 8844, 8853* (DAO, TRTE); Leamington, 0.4 mi. Mersea Twp., field survey 725, tomato field, 23 Sep 1969, *J. F. Alex 4221* (DAO, OAC, TRT); Elgin Co., 2 mi. E of Westhome, weed of tobacco field, 29 Aug 1967, *R. A. Frost 36* (DAO, UWO); Lambton Co., Sarnia, 6 Sep 1960, *L. O. Gaiser 2884* (DAO); Kent Co., Ridgetown, 43°23′N 81°55′W, bean field, 18 Sep 1966, *R. A. Frost 23* (UWO); Dresden, Camden Twp., 43°35′N 82°11′W, 18 Sep 1977, *P. M. Catling s.n.* (TRTE).

5. *Amaranthus hypochondriacus*. British Columbia: Greater Vancouver Regional Distr., Burnaby, near Brenwood Mall, 8 Nov 1993, *F. Lomer 93-334* (UBC). Alberta: Edmonton Distr., Fort Saskatchewan, "flower garden," 4 Aug 1936, *G. H. Turner 337* (ALTA). Manitoba: Winnipeg, Aug 1921, *J. F. Higham s.n.* (WIN). Ontario: Elgin Co., St. Thomas, spreading after cultivation, 1 Sep 1958, *L. E. James 3281, 3163, 3164* (DAO, UWO); Hastings Co., 15 Aug 1875, *J. Macoun s.n.* (MTMG); Huron Co., Wingham, roadsides and gardens, Sep 1890, *J. A. Morton s.n.* (UWO); Middlesex Co., London, "fields", 8 Aug 1880, *T. J. W. Burgess & J. Macoun s.n.* (MTMG); Ottawa Co., Ottawa, School grounds, Aug 1891, *W. Scott s.n.* (DAO); Rideau River bank below White Bridge, 10 Aug 1954, *W. G. Dore & D. Erskine 15253* (DAO). Québec: Cté. Charlevoix, St-Joseph, "naturalisé depuis un an ou deux à la suite de cultures", 100 m, 22 Jul 1937, *B. Boivin 1612* (DAO); Cté. Hyacinthe, St. Damase, 3 Sep 1958, *L. Cinq-Mars & G. Samoisette 198* (QFA); Cté. Labelle, Nomininque, 1 Aug 1932, *E. Roy 2667* (MT); Cté. Laval, Bout-De-L'Ile, fossé de la route 2, 3 Sep 1937, *B. Boivin 1612* (MT).

6a. *Amaranthus powellii* subsp. *powellii*. British Columbia: Greater Vancouver Regional Distr., Vancouver, 49°16′N 123°15′W, 24 Sep 1978, *P. Bowen s.n.* (UBC); Okanagan Valley, 12 mi. NW of Penticton, fairly common in irrigated orchards, 5 Aug 1955, *G. A. Mulligan & W. Woodbury 1926* (DAO); 27 mi. of Osoyoos, fairly common in grain field, 11 Aug 1955, *G. A. Mulligan & W. Woodbury 1927* (DAO); Popcum Distr., N of Agassiz, sandy banks, 2 Sep 1912, *W. Taylor s.n.* (UBC). Saskatchewan: Regina Distr., Melford, 15 Sep 1946, *H. Groh 3182* (DAO). Ontario: Essex Co., 4 mi. SE of Leamington, weed in tomato, 30 Jul 1965, *J. F. Alex 765*

(DAO, OAC); Haldimand-Lambton Co., Forest, along James Street, 2 Oct 1963, *L. O. Gaiser 3373, 3374* (MTMG); Norfolk Co., Rock Point Provincial Park, 17 Sep 1988, *M. J. Oldham 8244* (DAO, TRTE); Middlesex Co., London, 0.5 mi. W of Hwy. 4, 24 Sep 1966, *R. A. Frost & P. B. Cavers 30* (UWO); Greater Toronto Region, Mississauga, 43°34′N 79°38′W, on clay, 22 Aug 1980, *J. M. Webber 3082* (DAO, TRTE); Ottawa Co., Ottawa, 300 m SE of Woodroffe High School, 45°22′N 75°46′W, 5 Oct 1984, *D. F. Bruno & C. Franckton 5373* (DAO). Québec: Cté. Missisquois, Clarenceville, 18 Aug 1976, *J.-P. Bernard 76-701* (DAO, QFA); Cté. Ste-Foy, Ste-Foy (Québec City), Laval University, 46°47′N 71°16′30″W, 12 Sep 1977, *J.-P. Bernard 77-772* (QFA). Nova Scotia: Kings Co., Wolville, 13 Sep 1968, *Taschereau 317* (NSPM); Lunenburg, Martin Brook Settlement, 21 Sep 1968, *Taschereau 332* (NSPM). Prince Edward Island: Queens Co., near Stanhope, on reddish sandy loam, 4 Aug 1950, *J. J. Basset s.n.* (DAO).

6b. *Amaranthus powellii* subsp. *bouchonii*. British Columbia: Greater Vancouver Regional Distr., Vancouver, Locarno Park, 21 Sep 1937, *J. W. Eastham s.n.* (UBC); Kootenays Valley, 2 mi. NW of Creston, 15 Aug 1955, *G. A. Mulligan & W. Woodbury 2051* (DAO). Ontario: Bruce Co., Walkerton, 2 Aug 1944, *H. Groh 2282* (DAO); Hulton Co., Burlington, clay disturbed area, 5 Aug 1984, *W. J. Crins 6549* (TRTE); Peel Co., Streetsville, 25 Aug 1957, *A. F. Coventry 57-155* (TRTE). Québec: Cté. L' Assomption, Ville-des-Laurentides, pommes de terre, 19 Aug 1984, *R. Néron 84-3006* (QUE); Cté. Bellechasse, St-Gervais, sur sable graveleux pierreux, 31 Aug 1984, *J.-G. Denis & L. Guay 84-443, 84-447* (QUE); Cté. Laval, Ile-Jésus, 15 Sep 1999, *R. Néron 99-250, 99-246* (QUE); Cté. Napierville, Sherrington, oignons, terre noire, 27 Aug 1981, *R. Néron 81-610-5* (QUE).

9. *Amaranthus albus*—specimens used for the SEM study. Alberta: Peace River Distr., Spirit River, 13 Sep 1939, *H. Groh 970* (DAO); Watino, 14 Sep 1939, *H. Groh 988* (DAO). Saskatchewan: Saskatoon, 15 Sep 1979, *J. H. Hudson 3859* (DAO); Asquith, Rice Lake, 23 Sep 1979, *J. H. Hudson 3868* (DAO). Manitoba: Marquette Distr., Rivers Twp., 21 Aug 1957, *I. J. Basset & J. W. Kemp 3674* (DAO). Ontario: Dundas Co., Winchester, Railroad Station, 1 Sep 1954, *W. Shumovich & G. McCann 1523* (OAC); Essex Co., 13 mi. SE of Leamington, 23 Sep 1969, *J. F. Alex 4197* (OAC); Lambton Co., Squirrel Island, 2 Oct 1957, *L. O. Gaiser & C. Gaiser s.n.* (OAC); Middlesex Co., Dorchester, tobacco field behind high school, 6 Aug 1973, *C. & B. Chamberlain 88* (OAC). Québec: Montréal, 2 Sep 1962, *G. & P. H. Du Boulay 2827* (DAO). Nova Scotia: Pictou Co., New Glasgow, 14 Sep 1951, *E. G. Anderson 1593* (DAO).

10. *Amaranthus californicus*—specimens used for the SEM study. Alberta: Herraton, 7 Aug 1933, *H. Groh s.n.* (DAO); Manyberries, 1928, *S. C. Clarke s.n.* (DAO). Saskatchewan: Cypress Distr, Cypress Hills, roadside, 20 Aug 1947, *A. J. Breitung 5695* (DAO); Grassland National Park, 10 mi. SE of Val Marie, disturbed area near Frenchman River, 6 Aug 1989, *E. R. Hooper & G. F. Ledingham 10851* (USAS); Moose Distr., 3 mi. W and 4 mi. S of Rockglen, with *Rorippa tenerrima*, prostrate on the trampled shore of stock-watering pond, 14 Sep 1984, *G. F. Ledingham 8919* (USAS); Regina Distr., 20 mi. N of Regina, dry depression in native prairie, top of south bank of Qu'Appelle Valley, 25 Jul 1988, *G. F. Ledingham 10397* (USAS); Saskatoon Distr., Dundurn, farm garden, 17 Aug 1974, *E. W. Sullivan s.n.* (USAS).

12a. *Amaranthus blitum* subsp. *blitum*. Ontario: Simcoe Co., Muck Research Station, Holland Marsh, 20 Sep 1970, *J. F. Alex 4428* (OAC). Québec: Montréal, sur le Mont-Royal, 4 Sep 1938, *Frère Cléonique 11423* (MT); Ile de Montréal, Jul 1890, *Soeur Amélie s.n.* (MT).

12b. *Amaranthus blitum* subsp. *emarginatus*. British Columbia: Coquitlam, waste sandy ground landfill, old Terra Nova dump site, 12 Aug 1993, *F. Lomer s.n.* (UBC); Greater Vancouver Region, Annacis Island, "many plants", 15 Aug 1990, *F. Lomer 90-113* (UBC). Québec: Cté. de Brome-Missisquoi, Quest, 45°04′N 73°06′W, 16 Sep 1989, *A. Sabourin & D. Paquette 363* (MT); Cté. de Chambly, Richelieu, 20 Aug 1988, *P. Guertin 3296* (QFA); Cté. de Missisquoi, Lac Selby, 15 Sep 1987, *P. Guertin 3015* (QFA); Cté. de Papineau, Montebello, 51 Rue Notre-Dame, 31 Aug 1972, *J. E. Charlebois s.n.* (QFA); Ile aux Bois Blanc, Sain-Laurent River, sect. alluviale à l'est de Montréal, 22 Aug 1966, *L. Deschamps 1374* (QFA); Francheville, Pointe-du-Lac, Saint-Laurent River, 46°17′N 72°42′W, dans le sable du rivage humide, 5 Oct 1999, *M. Blondeau 99028* (QFA); Saint-Lambert, oblique de la Voie Maritime du côté du fleuve, près des écluses, rivage graveleux, 29 Sep 2001, *S. G. Hay 01-055* (MT).

Hybrids. 1. *Amaranthus ×soproniensis*. Ontario: Elgin Co., 5 mi. N of Rodney, apparently sterile plant as weed of corn with *A. retroflexus* and *A. powellii*, 5 Sep 1967, *R. A. Frost 45* (DAO, UWO). Québec: Cté. Laval, Laval, Ile Jésus, *R. Neron 99-250a* (QUE); Cté. de Lac-St-Jean, Métabetchouan, Ferme Antoine Langevin, 26 route 168, champ de mais sucré, *R. Neron 83-2795*, 7 Sep 1983 (QUE).

2. *Amaranthus ×ozanonii* Thell. Ontario: Essex Co., N of Leamington, in vegetable gardens with *A. hybridus* and *A. retroflexus*, 26 Sep 2002, *M. Costea 8991* (OAC).

3. *Amaranthus hybridus* × *A. powellii*. Ontario: Essex Co., N of Leamington, in vegetable gardens with *A. hybridus* and *A. powellii*, 26 Sep 2002, *M. Costea 8998* (GH, OAC, QUE).

4. *Amaranthus hybridus* × *A. tuberculatus* var. *tuberculatus*. Ontario: Essex Co., Kingsville beach, ca. 0.5 km W of harbour, 29 Sep 1988, *M. J. Oldham 8882* (DAO).

5. *Amaranthus hybridus* × *A. tuberculatus* var. *rudis*. Ontario: Lambton Co., Petrolia, in soybeans infested with *A. powellii* and *A. rudis*; a few plants in the whole field, 13 Sep 2002, *M. Costea 8880* (GH, OAC, QUE).

6. *Amaranthus ×budensis*. British Columbia: Greater Vancouver Distr., Fraser Surrey Docks, Surrey, 17 Oct 1993, *F. Lomer s.n.* (UBC).