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THE GRAIN AMARANTHS AND THEIR RELATIVES: A REVISED TAXONOMIC AND GEOGRAPHIC SURVEY

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Much new information on this species group has accumulated in the years since my initial survey was carried out in the graduate laboratory of the Henry Shaw School of Botany (Sauer, 1950a). Many people have volunteered original field observations and collections from various places in Latin America, Asia, and Africa. Archaeologists have turned up the first material evidence of pre-Columbian grain amaranth cultivation in North America (Bohrer, 1962). Gradually, incidental to other work, I have had chances to study historically important collections in major European herbaria. Experimental plantings have answered some questions about variation patterns. Several long-standing taxonomic problems can now be resolved, classification simplified, and nomenclature corrected.

To make the revised presentation intelligible by itself, some information will be reviewed briefly, but without repeating details or documentation. The previous survey should be consulted for historical geography of the grain crop and for descriptions, illustrations, and lists of exsiccatae of all the species. Sources will be cited for all newly presented information. Specimen citations for the new maps of the grain crop are given in the Appendix.

In both text and Appendix, references to specimens are accompanied by notations of herbaria in which they are deposited, according to the Index Herbariorum of the International Association for Plant Taxonomy.

THE GENUS AMARANTHUS IN RELATION TO MAN

Amaranths were widely distributed through the world's temperate and tropical regions even before man converted some of them into cosmopolitan weeds and domesticates. About 60 species were native to the Americas and a total of about 15 others to Europe, Asia, Africa, and Australia. Most were pioneer annuals of naturally open habitats: mountain and desert canyons, riverbanks, lakeshores, tidal marshes, and ocean beaches. Producing abundant seed that is widely dispersed by water and birds, they survived by constant colonization of sites with

¹I am indebted to all the people referred to in the text who supplied unpublished information, photographs, and new collections. Many of these contributions were inspired by Edgar Anderson and were relayed through the Missouri Botanical Garden. A special Guggenheim Foundation grant to Professor Anderson made possible massive experimental plantings, conducted by George Freytag at the Escuela Agrícola Panamericana, Zamorano, Honduras; these provided adequate population samples grown under uniform and favorable conditions. I am also indebted to the curators of the herbaria and museums cited for making their indispensable collections available for study. Vorsila Bohrer and Joel Andress supplied useful ideas and leads to sources of which I was unaware. The maps were prepared by Jeanne Tsou Liu in the University of Wisconsin Cartographic Laboratory, under the direction of Randall Sale.

disturbed soil, full sun, and little competition. Long natural selection for such a way of life preadapted certain of the species for success in habitats drastically disturbed by man.

The beginnings of their association with man may be cryptically recorded in pollen deposits, but palynology can not yet discriminate amaranth pollen from that of related plants. Even before the origins of agriculture, some amaranths must have flourished around camps and fishing villages. Prehistoric peoples undoubtedly used these conveniently available volunteers in several ways.

Any amaranth seeds, so far as is known, are quite edible when simply toasted and milled, tasting much like true cereals. Analyses and nutrition experiments show the grain to be comparable to true cereals as carbohydrate food and superior in protein and fat content (Hunziker, 1952, p. 78; Singh, 1961, pp. 3-5). Though the seeds average only about 1 mm in diameter, they are obtainable in prodigious quantities, even by primitive gathering techniques (Jones, 1953, p. 90). There are innumerable historical and ethnographic accounts of such gatherings in many regions. Archaeologic amaranth seeds, often in massive caches, are associated with such diverse cultures as Lake Dweller in southern Europe (Thellung, 1914, p. 327), Hopewellian in the Illinois Valley (Struever, 1964, p. 102), Basketmaker in Colorado (Jones & Fonner, 1954, p. 94), a pre-ceramic old dune hearth in New Mexico (Agogino & Feinhandler, 1957, pp. 154-155; Agogino & Hester, 1958, p. 187), and incipient agricultural levels in Tamaulipas and Puebla caves (Kaplan & MacNeish, 1960, p. 36; MacNeish, 1964, p. 534). The species involved are not known, but it seems likely that whatever amaranths were locally available were gathered indiscriminately. Domestication of selected species as grain crops was concentrated in definite regions of the New World, as will be shown below.

Young amaranth leaves and shoots are boiled as greens or potherbs in much of the world. Generally, volunteer weeds are gathered with little discrimination as to species. Careful selection as potherbs leading to domestication evidently took place only in Asia. A variety of cultivated races assigned to *Amaranthus lividus* L. and *A. tricolor* L. (both s.l.) are common potherbs of eastern and southern Asia; these have been introduced to the western world under such names as Chinese spinach, Malabar spinach, and *tampala*, the generic name for amaranths in Ceylon. The American grain amaranths make good potherbs and one is now widely planted as such in the Old World. In their native regions, thinnings from the grain crops are often salvaged as boiled greens but they do not seem to be planted for that reason nor even preferred to their weedy relatives.

Many wild amaranth species have quite noticeable and variable red coloration of inflorescences, leaves, and stems, due to an anthocyanin of the type found in beets. Such pigmentation is intensified in certain forms of all the domesticated grain and potherb species. Selected deep red forms, closely related to some of those grown for grain, are widely scattered as ceremonial, magical, and simply ornamental plants.

Although many amaranths have some role in culture history, a few New World species stand out as especially significant. These belong to a single section (*Amaranthus*) of the genus, with which the rest of this paper is solely concerned.

CHARACTERISTICS OF AMARANTHUS SECT. AMARANTHUS

This section includes all the domesticated grain and dye amaranths, most of the domesticated ornamentals, and most of the common weeds. It has long been recognized as a section under the name *Amaranthotypus* Dumort (Thellung, 1914, p. 230; Sauer, 1950a, p. 594; Grant, 1959b, p. 319; Aellen, 1961, p. 467). Under the present rules of nomenclature, it must bear the same name as the genus, since it includes the type species, *A. caudatus* L. Members of the section form a coherent group, perhaps close to the primitive core from which other sections of the genus radiated.

The section is distinguished from the bulk of the genus by the following combination of characters: plants monoecious; cymes continuing above uppermost leaves to form large, compound terminal inflorescences; tepals and stamens 5 (or varying between 3-5 in flowers of the same plant); utricle circumscissile (indehiscent in occasional mutant and hybrid individuals). As a rule these characters are extremely constant (the parenthetically noted variants are mainly within one species, *A. powellii*.)

Some of the sectional characters are clearly connected with the success of its members as grain crops: the monoecious habit, the dehiscent utricle allowing easy threshing and winnowing, and the large compound inflorescences producing enormous quantities of seed. Estimates of seed production of individual plants in this group have usually been on the order of several tens of thousands, but yields of over 500,000 seeds from a single plant of *A. retroflexus* have been reported (Priszter, 1950, p. 81).

Within the section, discontinuities between species are, as a rule, quite clear-cut. The group has an undeserved reputation of being taxonomically difficult, mainly because of hopeless attempts to recognize taxa by pigmentation, which segregates within populations, and by growth form, which is extremely plastic under different day lengths and other environmental variables. There are abundant constant characters, particularly in shapes and proportions of pistillate flower parts, whose correlated discontinuities reveal genetically isolated species.

However, breeding barriers between the species are by no means always absolute, even when species have different chromosome numbers². An imposing array of hybrids, involving most of the members of this section, have been reported in the literature, recently reviewed by Grant (1959b, p. 321) and Aellen (1961, pp. 512-514). The importance of these hybrids can easily be exaggerated because many are sterile or rapidly eliminated by natural selection. However, some weedy and cultivated populations have variation patterns suggesting effective introgression; these will be noted under the species involved.

²Chromosome counts have so far been of little help in amaranth taxonomy, except in the polyploid *A. dubius* (Grant, 1959a, p. 1064). Diploid numbers of 32 or 34 have been found in all the many other species studied (Grant, 1959b, pp. 315-319). Both counts have sometimes been reported for the same species and the difference shows no apparent connection with relationship or crossability.

- a. Bract much shorter than tepals.
 - b. Tepals acute, shorter than utricule *A. brandegei*
 - bb. Tepals obtuse or retuse, longer than utricule.
 - c. Tepals retuse *A. celosioides*
 - cc. Tepals obtuse *A. pallidiflorus*
- aa. Bract equalling or exceeding tepals.
 - b. Tips of tepals incurved against utricule; bract and all tepals approximately equal in length.
 - c. Lower cymes pistillate, upper staminate; spines in leaf axils *A. spinosus*
 - cc. Each cyme with initial staminate flower and remainder pistillate; plants unarmed *A. dubius*
 - bb. Tips of tepals straight or spreading away from utricule; inner tepals definitely shorter than outer tepals and bract.
 - c. Utricule much shorter than tepals; seed less than 1 mm in diameter.
 - d. Inflorescence very large, much branched; outer tepals obovate *A. scariosus*
 - dd. Inflorescence small, unbranched; outer tepals spatulate *A. bigelovii*
 - cc. Utricule equalling or exceeding some or all tepals; seed at least 1 mm in diameter.
 - d. Inflorescence short, unbranched; style-branches longer than utricule *A. viscidulus*
 - dd. Inflorescence large, branched; style-branches shorter than utricule.
 - e. Inflorescence branches short and thick; tepals all retuse or obtuse *A. retroflexus*
 - ee. Inflorescence branches long or sleniger or both; outer tepals acute or acuminate.
 - f. Fully developed inflorescence moderately large; bract exceeding style-branches; seed dark brown (PROGENITORS OF THE DOMESTICATED SPECIES—coarse, weedy plants, generally green with dull red pigmentation).
 - g. Inflorescence stiff, with few branches; bract about 5 mm long, with extremely heavy midrib; style-branches thick at base; tepals and stamens 3 to 5 *A. powellii*
 - gg. Inflorescence lax, usually with many branches; bract 3 to 4 mm long, with moderately heavy midrib; style-branches slender at base; tepals and stamens 5.
 - h. Tepals straight, the inner oblong, acute *A. hybridus*
 - hh. Tepals recurved, the inner spatulate, obtuse *A. quitensis*
 - ff. Fully developed inflorescence enormous; bract not exceeding style-branches; seed dark brown or pale ivory, often tinged with red in *A. caudatus* (DOMESTICATED SPECIES—attractive, cultivated plants, generally bright green or intense red or various striking combinations).
 - g. Inflorescence stiff; bract equalling style-branches, with moderately heavy midrib; style-branches thick at base *A. hypochondriacus*
 - gg. Inflorescence lax; bract not exceeding utricule, with slender midrib; style-branches slender at base.
 - h. Tepals straight, the inner oblong, acutish; style-branches erect *A. cruentus*
 - hh. Tepals recurved, the inner spatulate, obtuse or emarginate; style-branches spreading *A. caudatus*

WILD SPECIES

Of the 12 wild species listed in the key, the first nine will be passed over briefly; their taxonomy has remained comparatively unconfused and they are not believed to be directly related to the grain species.

Amaranthus brandegei Standley, *A. bigelovii* Uline & Bray, and *A. viscidulus* Greene are minor, non-weedy endemics of the southwestern U.S. and northwestern Mexico.

Amaranthus scariosus Benth. is common and weedy in southern Mexico and Central America, but has not emigrated to other regions.

Amaranthus celosioides H.B.K. has been found at scattered places in western South America from Venezuela and Colombia to Chile, on the Galapagos, and on San Lorenzo Island off Peru. Specimens are few and rather heterogeneous.

Amaranthus pallidiflorus F. Muell. is the only member of the section native to the Old World. It is known only in Australia, except for ephemeral adventives introduced with Australian wool. I have seen it in quite natural habitats on the coastal dunes of Western Australia. The least incredible origin would seem to be by ancient, long range dispersal from South America³.

Amaranthus spinosus L. and *A. dubius* Mart. ex Thell. are the commonest and most widespread weedy amaranths of the New World tropical lowlands, where they presumably originated. *Amaranthus dubius*, the only known polyploid amaranth species, is probably an allotetraploid to which *A. spinosus* contributed one chromosome set (Grant, 1959a, p. 1068); the other progenitor is evidently either *A. quitensis* or *A. hybridus*. By 1700, *A. spinosus* was spreading rapidly through the warmer parts of the world, both as a weed and as a sporadically planted pot-herb. *Amaranthus dubius* followed more slowly, being found at only a few places in the Old World before 1800; it has not spread as widely as *A. spinosus* outside the tropics. Sterile hybrids between the two are common, and have elicited some Latin names, e.g. *A. caracasanus* H.B.K.

Amaranthus retroflexus L. is a native riverbank pioneer of the central and eastern U.S. and adjacent regions of southeastern Canada and northeastern Mexico. In much of this area it has become one of the commonest of all agricultural weeds and thus is often mistaken for an exotic. Peter Kalm sent seeds from Pennsylvania to Linnaeus; the progeny grown at Uppsala, some of which are preserved (LINN 1117.22), may have been the first in Europe. Thellung (1914, p. 258) blamed Linnaeus for inoculating Europe with the species by disseminating it to botanical gardens. By 1800, it was becoming a common weed through much of the continent (Priszter, 1951, p. 261) and soon after spread into the Near East and North Africa. It has since become naturalized throughout temperate regions of the northern and southern hemispheres. In areas of overlap with *A. powellii* and *A. hybridus*, *A. retroflexus* forms many partially sterile hybrids, especially in weed populations of highly artificial habitats.

³A similar enigmatic disjunction occurs between South American and Australian coastal populations of *Carpobrotus* (*Mesembryanthemum*).

The other three wild species will be considered in more detail, as they appear to be directly related to the domesticated grain species. Their taxonomy and nomenclature have been appallingly confused, mainly by attempts to classify continuous intraspecific variations. Synonymy will be limited to basionyms of recently used names.

AMARANTHUS POWELLII S. Wats., Proc. Amer. Acad. **10**: 347, 1875.

Type: United States, grown at Harvard Univ, 1874, seed obtained from Arizona Indians by *Powell s.n.*, US 16163; isotype MO.

A. chlorostachys Willd. var. *pseudoretroflexus* Thell., Vierteljahrsschr. Naturf. Ges. Zürich **52**: 443, 1907.

Type: Switzerland, Derendinger, Solothurn, by worsted yarn factory, 1907, *Probst s.n.* (not seen, but Thellung's description is diagnostic).

A. bouchoni Thell., Monde des Plantes, sér. 3, **45**(160): 4, 1926.

Type: France, Bordeaux, trash dumps by harbor, 25 Sept. 1925, *Bouchon s.n.*, fragment US (Thellung published simultaneously an alternative name *A. hybridus* subsp. *hypochondriacus* var. *chlorostachys* subvar. *genuinus* f. *bouchoni*).

Amaranthus powellii is a pioneer of canyons, desert washes, and other open habitats, ranging through the western Cordilleran system of North and South America, with wide gaps in the wetter regions of Central America. The species has long been a common weed in the West. It began appearing as a rare adventive in eastern North America about 1900; since 1940 it has become a widespread and troublesome weed there. The species also arrived in Germany as an adventive shortly before 1900 and has since become an abundant and still expanding weed of northern and central Europe, where it is usually misidentified as *A. chlorostachys* Willd., a synonym of *A. hybridus*. It has also recently invaded southern India and South Africa.

The species is exceptional in producing flowers with tepal and stamen numbers varying from 3 to 5, even on a single plant. Also, individual plants with indehiscent utricles occur sporadically in native American populations and have formed whole local populations in Europe (Brenan, 1961, p. 270; Aellen, 1961, p. 475), where they have elicited the name of *A. bouchoni*. Such aberrant forms are common among hybrids between other species of *Amaranthus*, but in *A. powellii* they evidently arise without hybridization. The species is involved in partially fertile hybrid swarms in eastern North America, where it is invading territory of *A. retroflexus* and *A. hybridus*, in western North America where the converse is true, and in Europe, where all three are recent immigrants. It also crosses locally with the domesticated grain species, as noted below.

AMARANTHUS HYBRIDUS L., Sp. Pl. 990, 1753.

Linnaeus' phrase-name, *A. racemis pentandris cylindricis horizontalibus, caule inermi*, and the geographic source, Virginia, are appropriate but inconclusive. He also gave two synonyms: (1) *A. sylvestris maximus novae angliae, spicis viridibus*, attributed to John Ray (1686-88, **1**: 201), but Ray's name ended

with . . . *spicis purpureis, carneis, aut viridibus*, and Linnaeus was actually following Tournefort (1719, **1**: 235) in dividing Ray's species into three according to inflorescence color; (2) *A. major, virentibus spicarum paniculis, semine nigro* Barr. (Barrelier, 1714, *fig. 648*). Barrelier's drawing is a fair likeness of the species and all the material available for typification agrees: a specimen bearing Tournefort's polynomial in the Hortus Cliffortianus herbarius (BM), a Clayton specimen from Virginia bearing the same name in the Gronovius herbarium (BM), a specimen labelled *A. hybridus* from the Uppsala Botanic Garden (LINN 1117.19).

A. chlorostachys Willd., Hist. Amaranth. 34, *tab. 10, fig. 19*, 1790.

The only specimen labelled *A. chlorostachys* in the Willdenow herbarium is a collection by *Hermes B 17521*. It agrees well with the (ambiguous) description and plate.

A. patulus Bertol., Comment. It. Neap. 19, *tab. 2*, 1837.

Based on plants found by Bertolini in the plain of Pascone, nr Naples, Italy, which are not known to have been preserved.

A. incurvatus Tim. ex Gren & Godr., Prosp. Fl. France 8, 1846.

Type: France, Tigneu nr Lyon, *Timeroy s.n.* (not seen, but original description fairly diagnostic).

Amaranthus hybridus is evidently a native riverbank pioneer of milder and moister regions from eastern North America through Mexico and Central America to northernmost South America. It has long been a common field weed in this region. Its earliest and most successful emigration was to the Mediterranean region, where it arrived by the early 18th century and became abundant during the 19th century. The species has appeared repeatedly but ephemerally in northern Europe. It has recently become a naturalized weed in western North America, eastern Asia, Australia, and South Africa. At home and abroad, wherever weed populations of *A. hybridus*, *A. powellii*, and *A. retroflexus* mix, partially fertile hybrids appear. Hybrids with the domesticated *A. hypochondriacus* and *A. cruentus* are discussed below.

AMARANTHUS QUITENSIS H.B.K., Nov. Gen. Spe. Pl. **2**: 194, 1817.

Type: Ecuador, banks of Río Guallabamba, alt ca 2000 m, June 1802, *Humboldt & Bonpland 156* (not seen, but the original description is diagnostic).

Amaranthus quitensis is evidently a native riverbank pioneer of South America, both in the mountains of the northwest and at lower elevations in the temperate south. It is also present in the Galapagos, perhaps naturally. Throughout much of South America, the species has become the commonest weed amaranth. It is not known to be naturalized elsewhere, although it has appeared repeatedly in Europe since the late 19th century as an ephemeral adventive, especially around ports and woolen mills.

Forms of this species with stout, intensely red inflorescences grow in Andean gardens and maize fields from Ecuador to northwest Argentina. Called *ataco* or *sangorache*, the plants are semi-cultivated or tolerated as volunteers useful in

coloring *chicha* and ceremonial maize dishes (Sauer, 1950b, p. 412; Heiser, 1964, pp. 137-139). It is not known whether such use is ancient; the earliest available collections are modern (e.g. Peru, Torontay, *jataco achihuite*, 1915, Cook & Gilbert 1893, US; Ecuador, nr Huigra, *ataco, sangorache*, 1918, Rose 22145, US). In aspect the plants look suspiciously like domesticates such as *A. cruentus*, which is used to color ceremonial maize bread in North America. However, if these plants are derived from hybrids between domesticated and weedy amaranths, backcrossing to the weedy *A. quitensis* has obliterated any clearly diagnostic characters of the other species. Another possibility is that the plants are pure *A. quitensis* in a stage of incipient domestication.

DOMESTICATED SPECIES

The three grain species diverge from their closest wild relatives in several similar ways. Bracts are relatively short and weak, perhaps because of selection favoring inflorescences that are less prickly when rubbed between the hands, a common method of extracting the grain. Plants and inflorescences are extremely large, giving greater grain yield with little or no increase in seed size. Pale ivory seeds, preferred for popping quality and flavor, predominate in the grain crops of all three species. The wild type dark brown seeds, characteristic of all other amaranths, are produced by some plants in most grain crops. In the absence of constant artificial elimination, the dark seed type may have the advantage, judging from its frequency among feral plants and those cultivated for non-grain purposes.

The nomenclature of these three fairly coherent and discrete species has been complicated by giving different Latin names to some of the more conspicuous variants that constantly appear within each population and then multiplying these names by shifting them up and down the taxonomic hierarchy. Only partial synonymy will be given, emphasizing basionyms of commonly used names.

AMARANTHUS HYPOCHONDRIACUS L., Sp. Pl. 991, 1753.

The phrase-name, *A. racemis pentandris cylindricis erectis, caule inermi*, is appropriate for this species but rather ambiguous, and the source, Virginia, is implausible. Linnaeus referred the name to his Hortus Cliffortianus of 1737 and Hortus Upsalensis of 1748, where it had been associated with synonyms that Linnaeus transferred to *A. hybridus* in the Species Plantarum. Probably the notation of Virginia should have gone along in this transfer but was left behind as a relic of former lumping of the two species. The only synonym given for *A. hypochondriacus* in the Species Plantarum is *A. sylvestris maximus novae angliae, spicis purpureis* Tournef. (Tournefort, 1719, 1: 235), a name of uncertain meaning derived by splitting a species of Ray (1686-88, 1: 201) that was mainly if not entirely *A. hybridus*. The literature thus establishes that Linnaeus recognized a species similar to *A. hybridus* but distinguishable by its more erect and more intensely colored inflorescences. This hazy distinction becomes clear enough in the presence of a Linnaean herbarium specimen labelled *A. hypochondriacus* (LINN 1117.24).

- A. flavus* L., Syst. Nat. ed. 10. **2**: 1269, 1759.
The original description and a longer one in the 1763 edition of the Species Plantarum are ambiguous. In the latter, the source is given as India. Fortunately there is a Linnaean herbarium specimen labelled *A. flavus* (LINN 1117.23).
- A. frumentaceus* Buch.Hamilt. ex Roxb., Fl. Ind. **3**: 613, 1832.
Buchanan-Hamilton originally applied his unpublished name to a grain crop, called *kiery*, he discovered on the hills of South India between Mysore and Coimbatore, where *A. hypochondriacus* is still a common crop under the same name. Roxburgh's description of the species was at least partly based on a large patch of amaranths planted in the East India Company's Botanical Garden, Calcutta. A specimen labelled *A. frumentaceus* in Roxburgh's herbarium (K) was designated by Sir E. J. Salisbury as the probable type, according to Hunziker (1952, p. 68).
- A. anardana* Buch.-Hamilt. in Wall. ex Moq.-Tand. in DC., Prodr. **13**(2): 256, 1849.
Type: Bhagulpur and Nepal, *Wallich 6903*, Moquin-Tandon herbarium, P; possible isotype: Bhagulpur, Bihar, 2 Nov 1813, *Buchanan-Hamilton 2028-1*, E. In Wallich's catalogue, under 6903, *A. anardana* appeared as a nomen nudum, with collections listed from Bhagulpur, Belaya, and Nepal, 1821. There is no evidence that the Belaya collection was included in Moquin-Tandon's treatment, which is fortunate because it is probably *Buchanan-Hamilton 2028-2* belonging to *A. caudatus*.
- A. hybridus* L. (var) γ *erythrostachys* Moq-Tand. in Dc., Prodr. **13**(2): 259, 1849.
Type: France, seed from Montpellier Bot Gard grown in Toulouse Bot Gard, 17 Sept 1844, Moquin-Tandon herbarium, P.
- A. leucocarpus* S. Wats., Proc. Amer. Acad. **10**: 347, 1875.
Type: United States, grown at Harvard Univ, 1874, seed obtained from Arizona Indians by *Powell, s.n.* US 15163; isotypes GH, MO, US.
- A. leucospermus* S. Wats., Proc. Amer. Acad. **22**: 446, 1887.
Hyponym for *A. leucocarpus*.

Amaranthus hypochondriacus was evidently derived mainly from *A. powellii* by selection as a grain crop within the great region of its aboriginal cultivation in North America. Its distribution as a grain crop in Asia, although perhaps old, is clearly secondary and its wide dispersal as an ornamental is recent.

There has been at least local genetic admixture from another domesticated, *A. cruentus*, and its progenitor, *A. hybridus*. Active hybridization is surprisingly limited considering the great geographic overlap with close relatives. In Mexico both *A. powellii* and *A. hybridus* are common weeds of the *A. hypochondriacus* grain crop, and traces of the domesticated are easy to find in the weed populations. The effect of backcrossing to the crop is probably limited by the fact that hybrids mostly produce dark seeds that are rejected for planting. An exceptional case occurs in a highly aberrant race from Los Reyes, Michoacan, grown to make special black *tamales* and unique among Mexican grain amaranths in being entirely dark seeded (Appendix); this appears to be a stabilized hybrid between *A. hypochondriacus* and *A. hybridus*. In pale seeded grain crops, weed introgression is comparatively subtle, the clearest known case being in a Warihio Indian crop from Rancho Trigo, Chihuahua (Appendix); progeny raised from this grain are heterogeneous and some individuals definitely resemble *A. powellii*. In southern Mexico, particularly Oaxaca, local populations of *A. hypochondriacus* show some resemblances to *A. cruentus*, which is also planted there as a grain crop; similar atypical plants appear in the *A. hypochondriacus* grain crop of Madras, India, where *A. cruentus* has also been introduced (Appendix). Arizona Indian crops of *A. hypo-*

chondriacus, especially a dark seeded archaeological specimen, may also show traces of introgression from *A. cruentus*, but the resemblance is too faint to be sure.

Amaranthus hypochondriacus as a New World Grain Crop (Fig. 1).

In Arizona, well preserved inflorescences and seeds of the species were recently excavated in a cliff-dwelling at Tonto National Monument (Univ of Michigan, Ethnobotanical Laboratory 4024A & 4038—both pale seeded; 4029—dark seeded; deposited at Southwest Archeologic Center, Globe, Arizona; fragments WIS). The occupation, dated at 1350 to 1400 A.D., was by Salado Indians practicing irrigated agriculture with maize, beans, and squash. Their culture was an amalgamation of Hohokam and Anasazi; earlier Hohokam cultivation of grain amaranths is suggested by large caches of charred seeds of an undetermined *Amaranthus* sp. (Bohrer, 1962, p. 108).

There are hints that the crop may have persisted in this region until recently. About 1890, the custodian of Casa Grande ruin (Whittemore, 1893, p. 52) was told by the Pima that a hundred years before, when they lived some miles west of Casa

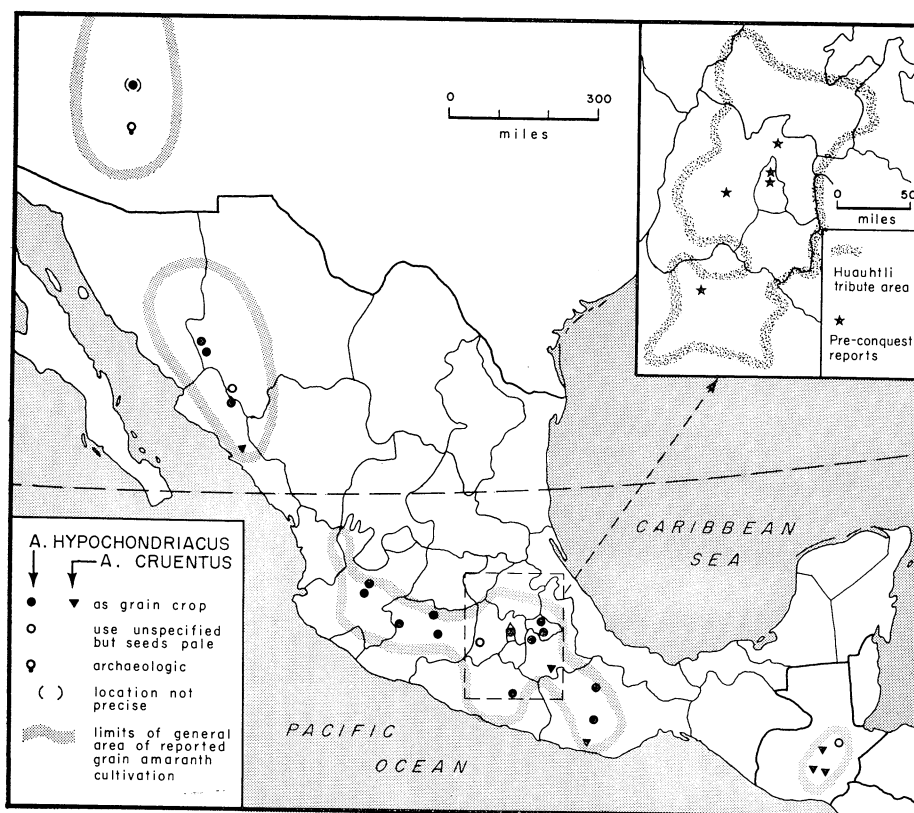


Fig. 1. North American distribution of grain amaranths. Inset: pre-Conquest localities reported and provinces giving tribute of the grain to Moctezuma.

Grande, "they raised cotton, corn, melons, and pumpkins, and a small round seed which they ground and boiled as mush." This may be connected with a report by Russell (1908, p. 74) that the Pima used an unidentified annual plant called *ki'ak*, whose seeds were popped like corn and ground on the metate.

The only tangible historic records of the species among the Arizona Indians are from farther north. Major Powell's mixed bag of domesticated and wild amaranth seeds, from which the types of *A. powellii* and *A. hypochondriacus* were grown, was probably collected during his stay with the Paiute; at any rate, Edward Palmer, who was also with the Paiute in the 1870's, reported they cultivated the latter and milled the seeds for bread and mush.

In Mexico, much of the early history of the grain amaranth crop depends on common names. At the time of the Conquest, the Nahuatl name *huauhtli* was widely used for both amaranths and chenopods, including those used as potherbs; however, *A. hypochondriacus* was probably the main if not the only species cultivated for grain. The paste made from the milled *huauhtli* grain was generally called *zoale*. In several Indian languages of northwestern Mexico, the same crop was called some variant of the word *guegui*. Beginning in the 17th century, the Spanish name *alegria* was applied to confections of popped amaranth grain and was gradually extended to the plants that produce it; the plants have also commonly been called *bledo*, the Spanish name for amaranths in general.

In the northwestern Sierra Madre during the colonial period, the Jova and Tarahumare Indians grew pale seeded grain crops under names similar to *guegui*, identified in Spanish with *zoale* or *alegria*. The grain was used much like maize, popped or toasted and milled. In 1953, Brugge (1954, personal communication) found *guegui* cultivated for *pinole* near the Tarahumare pueblo of Metate in Sinaloa and was told that it is still grown in the mountains of southern Sonora. The Mayo, Wariho, and Tepehuan Indians grow pale seeded *A. hypochondriacus* in the same general region under the name *guegui*, *huauhtli*, *bledo*, or variants (Appendix). Among the Yaqui in Sonora, Spicer (1954, p. 49) was told by the old people that amaranth seeds, called *we'e*, were formerly ground and used much like maize; they remembered the food as a delicacy that was presented to the spirits of the dead in All Soul's Day ceremonies; Spicer reported the seeds were black and were gathered from wild plants, but the name and ceremonial use suggest some traditional connection with the *A. hypochondriacus* crop. In the 19th century farther south in the Sierra Madre of northern Jalisco, the Huichol Indians cultivated a pale seeded amaranth called *wā-vē* that was almost certainly of this species; they milled the grain to make little cakes shaped like animals which played a central role in their greatest annual ceremonial.

In the tropical highlands of central Mexico, *huauhtli* was a major grain crop at the time of the Conquest. Moctezuma collected *huauhtli* tribute totalling about 200,000 bushels a year, nearly equal to maize tribute, from 17 provinces of the Aztec Empire (Fig. 1). During the 16th century, the crop was recorded as a traditional staple in the same region and far beyond, from Jalisco in the west to Oaxaca in the east. The grain was toasted, milled for *zoale*, made into tortillas, rolled into little balls, or powdered and drunk as *atole*.



Fig. 2. Ripening field of *A. hypochondriacus* grown for making *alegrías*, nr San Gregorio Atlapulco, D. F., Mexico. [Photo R. C. West]

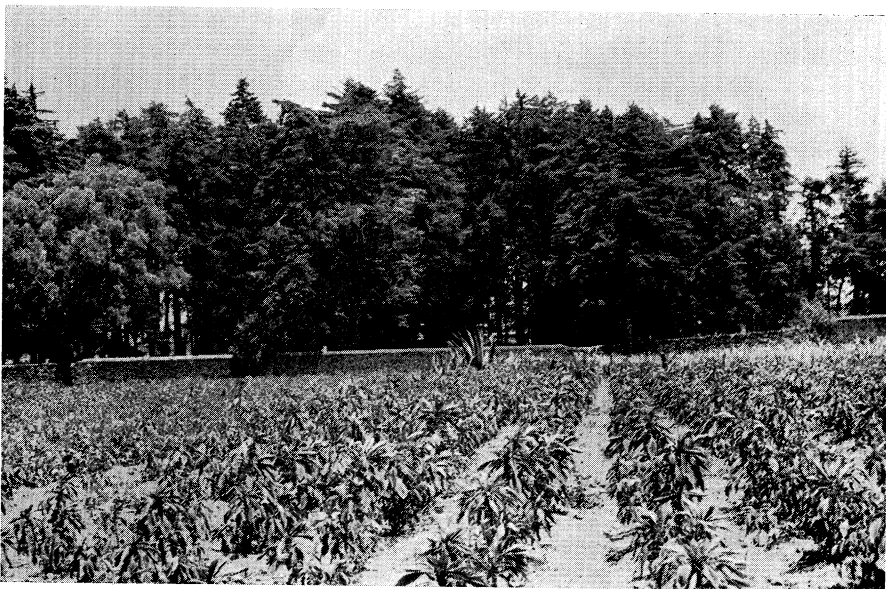


Fig. 3. Young field of *A. hypochondriacus*, same area as Fig. 2. Photo [J. D. Sauer]

Among the Aztecs and their neighbors, the grain had unique religious importance. Idols of *zoale* were the centers of innumerable little household rituals and of the greatest state ceremonies and processions. Far to the south in Oaxaca, the grain evidently also had special significance for the late prehistoric Mixtecs; the famous Tomb 7 at Monte Alban contained a human skull encrusted with turquoise mosaic; the mosaic was set in a paste originally thought to be copal gum (Caso, 1932, p. 510) but shown by later analysis to be *zoale* (Caso, 1966, personal communication).

In Christian eyes the Mexican grain amaranth was the very symbol of heathen idolatry and its cultivation declined drastically during the colonial period. However, even in the valley of Mexico, pagan rituals involving *zoale* persisted into the 17th century. Rosaries with the beads made of *zoale* paste appeared in the late 19th century.

Amaranthus hypochondriacus is still grown here and there through the ancient *huauhtli* area, ordinarily in small patches near houses or in maize fields. The grain is still used as an ordinary food in scattered places, parched and milled much like maize; by far the commonest use nowadays is for *alegria* confections, like little popcorn balls bound with syrup, which have become traditional for certain festivals and saints' days.

There are only a few new records of the crop in central Mexico. In 1962, *alegria* cakes were common in the market at Tehuacán, Puebla (Whitaker & Cutler, 1966, p. 11). West (1966, personal communication) found a small plot of grain amaranths in the old Indian town of Oaxaca near Monte Alban and also saw *alegrias* on sale in the Tlacolula market nearby. Scattered fields of *A. hypochondriacus* have been maintained in the Xochimilco area (Fig. 2-3) to supply *alegrias* for the Mexico City market; some plantings are in *chinampas*, the so-called floating gardens, where legends recorded in the 16th century placed *huauhtli* cultivation before the Conquest.

Amaranthus hypochondriacus as an Old World Grain Crop (Fig. 4-5).

For at least a hundred years, the species has been a far more widespread and important crop in Asia than in its homeland. Early botanists and explorers generally took it for an indigenous domesticate because it was so well established in subsistence agriculture, more often than not in remote regions. There are, of course, other American Indian crops that followed the same pattern, including the Andean *Amaranthus caudatus* L. and perhaps *Chenopodium quinoa* Willd. A tall chenopod of uncertain identity which strongly resembles the latter has long been grown as a grain crop in the hills of northwest India, where it shares the name *bathu* with grain amaranths (Thomson, 1852, p. 49; Singh, 1961, p. 40).

The first known record of *A. hypochondriacus* in Asia was Linnaeus' description of a form from India under the name *A. flavus*. Later in the 18th century, just before the end of the Dutch period in Ceylon, Koenig collected a pale seeded specimen there under a Sinhalese name meaning seed or grain amaranth (Appen-

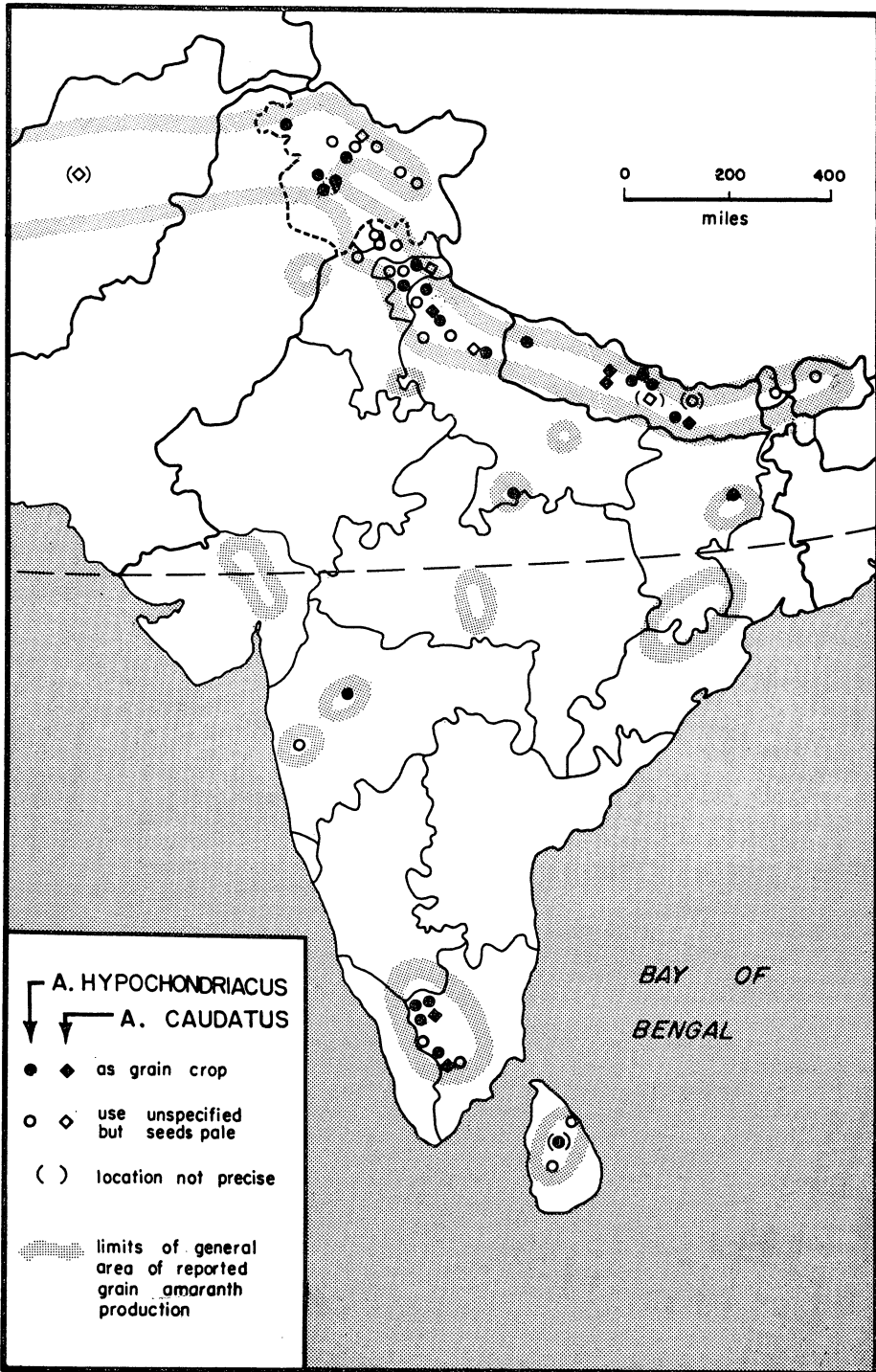


Fig. 4. Grain amaranth distribution in India and adjacent regions.

dix). In the 19th century, grain amaranths were also reported cultivated in Ceylon under the local name *landes* (= *hollandesi*?).

During the early and mid 19th century, *A. hypochondriacus* was collected and recorded as a grain crop among the hill tribes of south India, in the Deccan plateau, and in the Himalaya; during the late 19th century it was found through interior China to eastern Siberia (Appendix).

Some important early Himalayan records were not noted in the previous survey (Sauer, 1950a). In the northwest, Vigne (1844, **1**: 36) stated that bread made from a grain of a crop called *batu* was a common food of Himalayan peasants; he identified the crop as a cockscomb or *A. cruentus*; it was almost certainly *A. hypochondriacus*. In 1833, Vigne saw red and yellow patches of the crop on hillsides at Serai near Simla; in 1835 he found it as a grain crop at Skardo and in 1838 in the valley of Kashmir (1844, **1**: 36, 309, **2**: 263). An amaranth had previously been noted among the grain crops of Kashmir by Moorcroft and Trebeck in 1823 (Wilson, 1841, **2**: 132). Some of the earliest collections of *A. hypochondriacus* from Kashmir and the Simla area of Himachal Pradesh were made by Thomson (Appen-

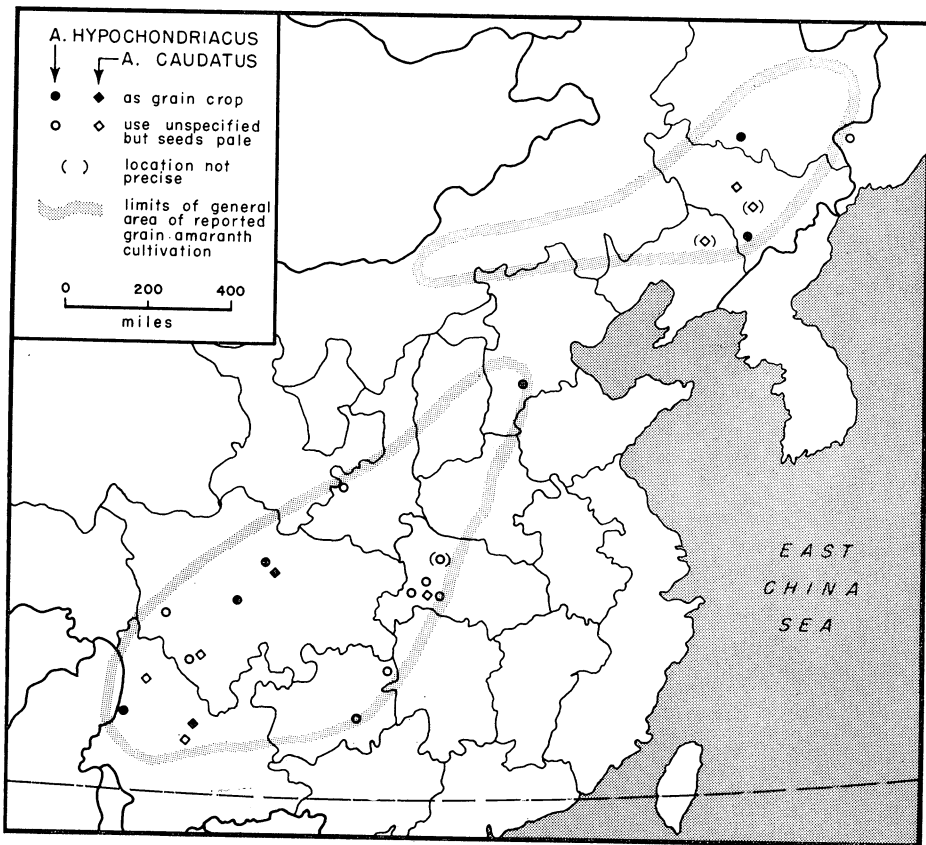


Fig. 5. East Asian distribution of grain amaranths.

dix). He wrote (1852, p. 49) that there were many fields of *Amaranthus* near Simla, on ridges above the Sutlej Valley, and that it was "occasionally cultivated in all parts of the hills, its bright red inflorescence, in autumn, tinging with flame the bare mountain slopes." Also near Simla, Markham (1854, p. 78) saw crops of *batu* clothing the cultivated spots with waving plumes of yellow and vivid crimson; he recognized *batu* as a kind of prince's-feather, the ornamental *A. hypochondriacus* of English gardens. Markham wrote that in the Himalaya it was "extensively grown throughout the hills as a staple grain and the bread made from its seeds is the common food of the people." Farther east, in Uttar Pradesh, the species was collected under the name of *A. anardana* by Madden (Appendix). He listed it (1848, p. 443) among the common grain crops of Kumaon, where it was called *chōoa* or *ramdana*. On the border between Uttar Pradesh and Nepal, Henry Strachey (1848, p. 109) found the Bhotiya people of the Kali Valley growing crops of red and white amaranths; *A. hypochondriacus* was collected nearby, without comment, by his brother and other contemporaries (Appendix).

Through most of its Asiatic range, the species has been cultivated only on a very small scale, scattered through other crops, in rows along field edges, or in gardens by houses. It has been noted as a staple crop only in the Himalaya and the hills of southern India. Mostly it is planted above 1500 m elevation, continuing nearly to the upper limits of agriculture.

As in Mexico, the crop is ordinarily pale seeded where carefully maintained, but dark seeded plants are often present as scattered individuals and may become predominant where the crop is planted in a desultory fashion or allowed to seed itself. Dark seeded specimens without definite notation of grain use are omitted from the maps because they may be weedy volunteers. For example, collections of millet grain from Karakoram (*Nakao 1157, 1159, 1178*) contained dark amaranth seeds as a contaminant; when grown out (*Sauer 2534, 2536, 2537, WIS*), these proved to be *A. hypochondriacus*. Unfortunately, some grain crop specimens are probably thus excluded. In Iran and Afghanistan in the late 19th century, an unidentified amaranth was reported as a very minor grain crop; the only available *A. hypochondriacus* specimens from this region are dark seeded (e.g. *Johnston s.n.*, 1880, nr Shaikhabad, Afghanistan, E; *Koelz s.n.*, 1940, Saidabad, Kerman, Iran, *kharus*—progeny: *Cowgill 2354, GH*). These lack data on use but the Tajic name on the Koelz specimen is like that reported for the grain crop.

The grain is used in Asia much as it is in Mexico; it is parched and milled, the dough patted into thin tortilla-like pancakes called *chapatis*; it is cooked for gruel; it is popped and made into confections with honey or syrup binder. It is also used in peculiarly Asiatic recipes and there is one fascinating account from India of fermenting the grain for beer (Hunziker, 1952, p. 77). Among Hindus, popped amaranth grain soaked in milk is the only food permitted on certain festival days (Singh, 1961, p. 4), which may simply mean that it entered the scene too recently to be covered by traditional taboos.

At present, the crop seems to be spreading out of the back country into the plains of India. It has recently been reported for the first time around Delhi and in the states of Madhya Pradesh and Gujarat (Singh, 1961, pp. 2-4, 8). The common

name in these regions, *rajgira*, is the same reported for the crop in the Deccan early in the 19th century. Singh states that it is now widely grown in the north Indian plains, usually in scattered patches or mixed with chili peppers, eggplant, and other vegetables; he published a photograph (1961, p. 10) of a mixed crop of *A. hypochondriacus* and eggplant in a Delhi village. In eastern Gujarat near Mehsana and Nadiad, amaranth is grown as a pure crop under intensive cultivation and irrigation, 300 acres yielding about 250,000 lbs of grain, which is mainly shipped to Delhi and other big cities of northern India. Much of it is popped for *laddoos*, confections like the *alegrias* of Mexico, which are sold in the Delhi area by a large number of refugee families from West Pakistan as their sole means of livelihood (Singh, 1961, pp. 4, 20). Another area of important recent cultivation is around Fyzabad in the Gogra plains of Uttar Pradesh; there the pale seeds are called *ramdana*, as they were in parts of the Himalaya over a hundred years ago; they are popped to make confections, especially for the September festival of Janam-Ashtami (Panje, 1960, personal communication). The species has also appeared recently in Maharashtra (Appendix), where it is grown along the edges of fields and in small plots near houses; the grain is cooked with milk and sugar (Kelly, 1960, personal communication).

Other recent records show persistence of the species in areas where it was previously reported. In the south Indian hills, it is still grown under the Tamil name *keerai* reported 150 years ago. Singh (1961, p. 10) published a photograph of *A. hypochondriacus* cultivated by the Badagas of the Nilgiri Hills. In 1962, Noble found a few amaranths grown with maize, beans, and squash near almost every Badaga house (Noble, 1962-64, personal communication). He noted that the Badagas mix stone-ground amaranth meal with sweetened milk to make porridge and pop the grain in a shallow iron pan or in an earthenware pot with a hole in the side. The popped grain is eaten plain or in balls made with honey or syrup. Baskets of it and of other popped cereals are placed as offerings on Badaga funeral pyres. Noble also found the species sown on field edges and scattered through millet fields of the Irula and Kurumba tribes in the Nilgiri Hills and among the Maddi and Chettiar tribes in the Pulni Hills (Appendix). Dark seeded forms of *A. hypochondriacus* are evidently grown in the south Indian hills only as potherbs.

There are many new records of the crop in its old Himalayan regions. In Kashmir, Polunin collected it at several places in 1956, mainly from small plantings on verges of maize fields (Appendix). His notes agree with a statement by Randhawa & Nath (1959-61, 1: 218) that in Kashmir the grain, called *ganhar*, is parched, ground, and eaten with milk or water, especially by Hindus on fast days. Polunin collected random samples of 25 plants from each of five different localities; three of these included two or three dark seeded plants and the other two lots were entirely dark seeded. In the Karakoram of Gilgit, Nakao (1956, personal communication) met with the species many times, not in fields but in small garden patches; the grain is eaten by the Hunza. Also in Gilgit, Harlan found the species grown for grain in a Shimal garden in 1960 (Appendix).

In northwest India, the crop is still important in the hills and Himalayan valleys of Himachal Pradesh, the Punjab, and Uttar Pradesh. In the Kullu Valley, Punjab, about 2,000 acres yielding perhaps 400,000 lbs of grain were grown in 1956-57; the boiled grain makes a gruel called *phambra* (Singh, 1961, pp. 4, 20). Singh published a striking color photograph of red and yellow *A. hypochondriacus* in the Kullu Valley. In Uttar Pradesh, particularly around Mussoorie, around Tehri in the Kumaon Hills, and all over Garhwal, the grain is milled for bread and thin *chapati* pancakes; confections of popped grain are sold in local bazaars (Singh, 1961, p. 4; Lal, 1961, personal communication; Andress, 1965, personal communication). Andress found *A. hypochondriacus*, called *chaulai*, one of the staple monsoon crops in the mountains around Mussoorie; it is planted alone or with millets, often on very poor, stony ground; at elevations above 1800 m it yields better than almost any other crop but is considered inferior in taste to true cereals. The 1952 Oxford University Expedition to Tehri-Garhwal found fields of the crop reddening the landscape around Harsil, a village at 2500 m elevation in the Bhagirathi Valley. Harsil is occupied seasonally by Hindu farmers and Bhotiya-related traders who are intermediaries between the Hindus and Tibetans. Photographs of the crop at Harsil (Fig. 6-7) were taken by Tyson, the expedition leader; one has previously been published in color (Tyson, 1953, p. 140). Specimens were collected (Appendix) by an expedition member, Paul Huggins, who died a few days later on a descent from Gangotri peak.

In western Nepal in 1953, Tyson found the species at Biunera, an unmapped village 25 miles due east of Baitadi, and also at Chainpur, 20 miles farther east in the Seti Valley; at both places the crop is called *marcha* and flour made from the grain is called *ata* (Appendix; Tyson, 1954, personal communication). Hagen (1960, p. 388) published a fine color photograph of a field of *A. hypochondriacus* in the Kuwari Valley of western Nepal, where the grain is popped and ground for flour. In central Nepal in 1952-53, the Japanese Himalayan Expedition found little patches of grain amaranths were a characteristic feature of the agricultural landscape, especially on newly cleared mountain slopes. The mixed red and yellow spikes were very colorful when the crop was maturing in the fall. Photographs taken on this expedition by Nakao show *A. hypochondriacus* as an aftercrop in a maize field near Jagat in the Marsyandi Valley, about 20 miles southeast of Annapurna (Nakao, 1956, p. 101, *plate 14*; Nakao & Sauer, 1956, p. 143). Nakao also collected the crop 40 miles farther east at Tsumje and Thomje in the Shiar Kola Valley (Appendix). It is generally called *nana* by the Nepalese, *pilim* by the Sherpa; the grain is boiled for gruel and ground for flour.

I have no new information on the species in China except from Manchuria. In 1956, Hanelt saw small plots of grain amaranths there, particularly near Harbin and Chiamussu in Heilunkiang; they were cultivated at the margins of fields of farmers and cooperatives (Hanelt, 1958, personal communication). Hanelt also obtained a specimen from an agricultural experiment station in Kirin (Appendix). Nakao (1957, p. 409) saw a field of *A. hypochondriacus* in the Kirin area in 1944.

A surprising outpost of *A. hypochondriacus* appeared recently in Uganda, where it was collected in 1945 and 1946 as a grain crop in the Masaka District



Fig. 6. Walled field of *A. hypochondriacus*, Harsil, Tehri-Garhwal, India. [Photo J. Tyson]



Fig. 7. Patch of mature *A. hypochondriacus* in garden, Harsil, Tehri-Garhwal, India. [Photo J. Tyson]

(Appendix). According to Pursglove (1964, personal communication), during World War II, when imported Indian food grains, mainly pulses and amaranth, became increasingly scarce in east Africa, the local Indian population provided seed for planting by African cultivators. The first small amaranth crop was sold in 1943 at a shilling per lb. By 1945, 66 tons of the grain were sold in Masaka at a much lower price. The grain was used primarily on Hindu fast days and was not known to have been eaten by Africans.

Amaranthus hypochondriacus as a Cosmopolitan Ornamental.

There is no record that the American Indians ever planted this species primarily for its color or as a dye plant, but they evidently favor red and yellow forms in the grain crop. Such pigmentation was the main reason the species was taken into European gardens. Selected forms, scarcely gaudier than those of the aboriginal grain crop, have been widely disseminated as ornamentals, particularly in temperate regions with a European gardening tradition. These ornamentals are invariably dark seeded, as are all specimens of *A. hypochondriacus* known from European botanical gardens, even those from the 18th century.

It is uncertain how long the species had been in Europe before Linnaeus encountered it in Clifford's garden in Holland early in the 18th century. It may be represented in some puzzling earlier descriptions of amaranths grown in European gardens, some dating back to the 16th century, but it is possible that all of these were forms of *A. caudatus*. Older common names for ornamental amaranths in Europe, such as flower-gentle, *floramour* and *Mayer*, were highly ambiguous and even shared with ornamentals in other genera, *Celosia* and *Gomphrena*. The distinctive English name for *A. hypochondriacus*, Prince-of-Wales'-feather or prince's-feather, appeared in the early 19th century.

AMARANTHUS CRUENTUS L., Syst. Nat. ed. 10. 2: 1269, 1759.

The phrase-name, *A. racemis pentandris compositis patulo-nutantibus, fol. lanceolata-ovatis*, is appropriate but inadequate for identification. In the 1763 edition of the *Species Plantarum*, Linnaeus inserted China as the habitat and cited *A. sinensis foliis variis* Mart. (Martyn, 1728-37, pl. 6) as a synonym. Martyn's plate, a fair likeness of the species, was drawn from "Chinese" plants cultivated in gardens around London. There is a specimen in the Linnaean herbarium labelled *A. cruentus* (LINN 1117.25).

A. paniculatus L., Sp. Pl. ed. 2, 2: 1406, 1763.

The phrase-name, *A. racemis pentandris supradecompositis, partialibus patentibus*, is compatible with but not diagnostic of the species. Linnaeus noted that *A. paniculatus* resembled *A. cruentus*, but was taller, and gave the habitat as America. There is a specimen in the Linnaean herbarium labelled *A. paniculatus* (LINN 1117.20).

A. sanguineus L., Sp. Pl. ed. 2, 2: 1407, 1763 (pro parte).

Linnaeus' description is ambiguous. He cited a description and plate of a plant grown by Miller from Bahamas seed; I have seen only a later reproduction (Miller, 1768), which is evidently *A. cruentus*. A specimen in the Linnaean herbarium labelled *A. sanguineus* (LINN 1117.21) belongs to *A. caudatus*.

A. speciosus Sims, Curtis Bot. Mag. 48: 2227, 1821.

The plate, which is a fair likeness of *A. cruentus*, is based on plants grown in England in the garden of Sir George Staunton, Leigh Park, from Nepal seeds obtained from H. I. Colebrook. There is no doubt that *A. cruentus* was in Nepal at the time; specimens collected there by N. Wallich in 1821, labelled *A. speciosus*, are in the Moquin-Tandon herbarium (P) and the de Candolle herbarium (G).

Amaranthus cruentus evidently originated as a domesticated grain crop somewhere in southern Mexico or Guatemala, the only region where it is found in aboriginal cultivation within the range of its probable progenitor, *A. hybridus*. Its wide range as a dye plant, ornamental, and potherb is certainly secondary, although not necessarily entirely modern.

As a rule, the species is extraordinarily homogenous but there is some diversity in pigmentation within the grain area and some other local variation attributable to hybridization with other species. The *A. cruentus* grain crop is often intimately associated with weedy populations of its probable progenitor, *A. hybridus*, and it is easy to find traces of introgression on both sides. However, interbreeding has evidently been limited by natural selection against hybrids in the weed populations and artificial elimination of hybrids, especially those with dark seeds, from the crop. Crossing with the other North American grain crop, *A. hypochondriacus*, has more pervasive effects; the few collections of *A. cruentus* as a Mexican grain crop all show definite traces of such crossing (Appendix). Where *A. cruentus* is grown as a Pueblo dye plant within the native range of *A. powellii*, hybridization with the latter occurs (Bohrer, 1960, p. 199). As a cosmopolitan ornamental, *A. cruentus* has occasionally mixed with weedy populations of *A. powellii*, *A. hybridus*, and *A. retroflexus*. The resulting hybrids are partly sterile and usually ephemeral, but some have developed into locally successful weeds (Tucker and Sauer, 1958, p. 260; Grant, 1959b, p. 320).

Amaranthus cruentus as a New World Grain Crop (Fig. 1).

The species has not been identified archaeologically. It is, of course, not certain that the *zoale* paste found in the prehistoric Mixtec tomb at Monte Alban was made from *A. hypochondriacus* grain, as suggested above, rather than from *A. cruentus*. The former species is more important in Oaxaca today, but Kaplan recently collected *A. cruentus* among the Mixtec near the Pacific coast (Appendix). Called *chian*, which ordinarily refers to *Salvia*, it is grown only by the Indians, who sow it as a minor crop in milpas with maize or by itself; the milled grain is used for *atole* and mixed with maize for tortillas (Kaplan, 1954, personal communication). The few previous records of the species from Mexico (Appendix) suggest it was locally a minor component of the grain amaranth crop, indistinguishable in historical records from the dominant *A. hypochondriacus*.

In Guatemala the situation was reversed, *A. cruentus* being the more important of the two, although it is now a declining relic. In 1947, it was regularly grown in a few temperate zone villages in the departments of Guatemala and Chimaltenango and in a lower-lying region in Alta Verapaz, usually on a very small scale. Both pale and dark seeded forms were present; both were called *bledo* in Spanish



Fig. 8. Semi-cultivated plant of *A. cruentus*, edge of milpa, nr San Juan Sacatepequez, Guatemala. [Photo J. D. Sauer]

and variants of *tez* in the Maya dialects. Dark seed was used only for tortillas; the pale seed was much preferred for tortillas and was prepared in various other ways, much like maize, for home consumption. It was also popped for confections identical to the *alegrias* of Mexico, but here called *niguas*, which were peddled widely at certain seasons.

Revisiting some of these areas in 1966, I could find only vestiges of the crop. Between San Juan Sacatepequez and San Raimundo in the department of Guatemala and near El Tejar in Chimaltenango, plants of *A. cruentus* are still conspicuous along the edges of some milpas and in a few dooryard gardens (Fig. 8). However, all the plants seen were said to be volunteers or planted simply by scattering some seed at the time of harvest. Moreover, all the plants were dark seeded and I could find nobody that had a supply of the pale seed. The farmers all knew about *niguas* but said they were now not often made, being more expensive than a similar confection, *alborotos*, made of popped sorghum grain.

I have not been back to Alta Verapaz to see whether the crop persists there, but in 1965 small scale cultivation was encountered not far away by Barbara Denton and Alan Covich; they found *A. cruentus* grown, under the name *ses*, at Ensenada and El Estor in the lowlands of Izabal, the grain being milled and made into little cakes as confections (Covich, 1966, personal communication).

Amaranthus cruentus as a New World Dye and Ceremonial Plant.

The domesticators of the species may have been at least incidentally interested in coloration of the plants from the start and forms evidently selected for striking

pigmentation were carried in the Central American grain crop. However, the only American Indian peoples known to have planted the species primarily for its pigment were the Pueblos of the Southwest. A special form with the whole plant body as red as a beet was grown by the Hopi, Zuñi, and Rio Grande pueblos. A water extract of the entire inflorescence was used to dye the pink maize wafer bread for ceremonial dances. The seeds, invariably dark, were apparently not eaten. The Hopi had their own name, *komo*, for this plant but the Mexican name *alegria* was used in the eastern pueblos. The only hints of a possible aboriginal track northward from Central America are an old collection of *A. cruentus* grown for unknown reasons in the Tarahumar area of Chihuahua and a report of an unidentified bright red amaranth used to color maize dough in Guerrero (Sauer, 1950b, pp. 412-414).

During the 19th century, the Pueblo dye amaranth was carefully cultivated in irrigated terrace gardens but the Hopi have lately neglected it, substituting vegetable coloring bought from the trader (Farmer, 1953, personal communication). In Zuñi gardens it is now mostly allowed to reseed itself and it is gradually being lost by crossing with the weedy *A. powellii* (Bohrer, 1960, p. 199).

Amaranthus cruentus as a Cosmopolitan Ornamental and Potherb.

Dark seeded forms of the species, some approaching the Pueblo dye form in intensity of plant color, are now commonly grown in the wet tropics and some temperate regions. Ordinarily they are planted in gardens as ornamentals and potherbs; occasionally they have magical, imaginary medicinal, or other esoteric functions.

The present range of planting as an ornamental and potherb includes the grain crop region; in fact, *A. cruentus* is the commonest garden amaranth of Central America in general. How much of this range was aboriginal is unknown. By the time the species distribution began to be revealed by extensive botanical collecting, it had already been adopted into non-indigenous cultivation throughout Latin America and far beyond.

As noted in the discussion of nomenclature, the species reached Europe in the early and mid 18th century via China, the Bahamas, and other unspecified New World sources. The original European descriptions show that bright red or deep red forms were introduced at the start. Martyn (1728-37) praised it as elegant and colorful. Miller (1768) said the plants were beautiful and gay the first two years they were sown in England but afterward the seed degenerated. However, stabilized color forms are still widely grown in European style gardens, often called cockscomb like the distant relative, *Celosia argentea*.

In the Old World tropics, the chronology and geography of the species' immigration are quite mysterious. As already noted, it was attributed to China and India in 18th century literature and collected in Nepal in 1821. By 1850, it was common in south India (e.g. Madras collections by Buchanan-Hamilton, Elliott, Thorison, & Wight, all E). It is still commonly planted as a potherb there and the seeds are sold in commercial packets. The Badagas, who cultivate *A. hypochondriacus* as a grain crop high in the Nilgiri Hills, plant *A. cruentus* as a potherb

in lower sites (*Noble s.n.*, 1963, Marakari, WIS). Asiatic cultivation of *A. cruentus* is mostly outside the grain amaranth regions, and extends through the tropical and warm temperate parts of India, Indo-China, China, Japan, the Philippines, and Indonesia. In New Guinea, it has been found as a fetish planted among the crops (*Stoner s.n.*, 1949, nr Lae—progeny: *Sauer 1536*, WIS). There are collections from a few Pacific islands, the earliest (1860) from Fiji (*Seemann 367*, GH).

In tropical Africa, *A. cruentus* has had a remarkable distribution as a potherb, ornamental, and for superstitious medicine. It was collected on Livingstone's expeditions in the Zambesi and Nyassa regions in 1859 and 1861, on Speke and Grant's expedition in the Lake Albert and Lake Victoria regions in 1862, by Burton in the Congo in 1863, Schweinfurth on the Sudan-Ethiopian border in 1865, Welwitsch in Angola in 1879 (all K), and by innumerable later explorers from French Guinea through the heart of the continent to the east coast and Zanzibar. The only record suggesting cultivation as a grain crop is a note on one collection that the seeds are edible (*Scott-Elliott 4653*, 1891, Sierra Leone, K). *Amaranthus cruentus* is almost certainly the source of the beloved red dyestuff that Dammer (1895, p. 402) reported was obtained from the large blood red inflorescences of an amaranth much cultivated in the Lake Region of East Africa. Dammer called the species *A. caudatus*, which is actually scarcely known in tropical Africa outside Ethiopia. In African botanical literature and herbarium collections, *A. cruentus* usually masquerades as *A. caudatus*.

AMARANTHUS CAUDATUS L., Sp. Pl. 990, 1753.

The phrase-name, *A. racemis pentandris cylindricis pendulis longissimis*, which is diagnostic, derives from Linnaeus' Hortus Cliffortianus of 1737. Evidently he first became acquainted with the species in Clifford's garden in Holland, where it was recognized as a South American native. Linnaeus later connected it by citations in his Hortus Zeylanicus of 1747 with Ceylon plants collected by Hermann in the 1670's, and in his Hortus Upsalensis of 1748 with plants grown in Sweden. Other synonyms cited in the Species Plantarum are *A. maximus* Bauh. (Bauhin, 1623, p. 120) and *Blitum majus peruvianum* Clus. (Clusius, 1601, 4: 81). Linnaeus gave Peru, Persia, and Ceylon as habitats, the first evidently after Clusius, the others after Hermann, who called his Ceylon plants *Blitum persicum maximum*, for reasons unknown. All these cited names probably are actually synonymous, although not all are positively identified. There is a specimen bearing Bauhin's name, *A. maximus*, in the Hortus Cliffortianus herbarium (BM) and a specimen labelled *A. caudatus* from the Uppsala Botanic Garden (LINN 1117.26).

A. sanguineus L., Sp. Pl. ed. 2. 2: 1407, 1763 (pro parte see synonymy under *A. cruentus*).

A. caudatus L. (var.) δ *alopecurus* Moq.-Tand. in DC., Prodr. 13(2): 256, 1849.

Type: Ethiopia, nr Aduwa, ruderal, 1 Nov 1844, *Schimper 1535*, Moquin-Tandon herbarium, P; isotypes G, GH, K, MO, US. Another collection was cited from the same locality: 10 Nov 1838, *Schimper 1077*, G, MO, US. (*A. alopecurus* Hochst. ex A. Br. et Bouché, Ind. Sem. Hort. Berol. App. 1, 1872, is based on the same specimens as Moquin-Tandon's variety; in both cases, the name was taken from Hochstetter's nomen nudum on the printed labels of Schimper's collections).

A. mantegazzianus Passerini, Ind. Sem. Hort. Bot. Parma, 4, 1865.

Based on plants grown in Italy; seed obtained by Mantegazza from grain crop, *quinoa blanca*, in Salta and Jujuy, Argentina. Neotype designated by Hunziker (1951, p. 105): Argentina, Colalao del Valle, Tucuman, grain crop, *chacion*, *quinoa de Castilla*, 23 Mar 1943, *Hunziker 2555*, CORD (not seen); duplicates K, S, SI, US.

A. edulis Spegazzini, Physis 3: 163, 1917.

Type: Argentina, plants grown at La Plata from seeds of Indian grain crop, *trigo inca*, collected in 1897 at Amblayo, Salta, *Spegazzini, s.n.*, LP 16.325 (not seen, but Hunziker's description of the type (1943, pp. 322-323) is meticulous).

Amaranthus caudatus probably originated by domestication of *A. quitensis* as an ancient Andean grain crop. Its wide introduction elsewhere as a grain crop and ornamental is certainly secondary and probably post-Columbian.

The species, like other grain amaranths, has a spectrum of plant color forms. It also has some variations in inflorescence structure and seed color not found in any other *Amaranthus* species. The *A. caudatus* grain crop includes a variety of inflorescence types, some resembling those of other domesticated amaranths, some with peculiar drooping branches; the commonest ornamental has an almost unbranched, pendulous inflorescence like a long, red tail. An even more bizarre form has inflorescence branches with determinate growth, each tipped by an abnormal polymerous staminate flower; as a result, the inflorescence branches become club shaped rather than tapering toward a continuously growing tip. This form is known only from northwest Argentina, where it is planted as a grain alone or together with ordinary *A. caudatus*. It has been given species rank, as *A. edulis* or *A. mantegazzianus*, but is probably merely a conspicuous mutant. No possible progenitor other than *A. caudatus* is known.

Some forms of *A. caudatus* have ordinary wild type dark seeds or plain ivory seeds like the other grain species, but the commonest forms have ivory seeds flushed with red around the rim. Unfortunately, this unique character of *A. caudatus* usually cannot be detected on older specimens because the red tinge fades.

In its native area, the species has some variation attributable to local interbreeding with weedy populations of *A. quitensis*. In its wide migrations as a crop and ornamental, *A. caudatus* has repeatedly mixed with various weed relatives and may have contributed to some complex hybrid weed populations (Tucker and Sauer, 1958, p. 260). However, most forms of *A. caudatus* show no trace of hybridization with weeds or other domesticates. Even in Asia, where *A. caudatus* and *A. hypochondriacus* now share an enormous range as grain crops, only a few sterile hybrids are known (e.g. *Hooker s.n.*, Sikkim, L).

Amaranthus caudatus as a New World Grain Crop (Fig. 9).

The oldest record of the species is from an urn found in a late pre-historic site in Salta, Argentina; it contained flowers and both pale and dark seeds of *A. caudatus*, together with maize, beans, and chenopod seeds. The crop is not usually distinguishable in early chronicles from the superficially similar *Chenopodium quinoa*; both often share the common name *quinoa* and are grown as grain crops by the same Andean peoples. Hunziker (1952, p. 74) points out that *A. caudatus*

had an advantage over *Chenopodium* in mountainous regions where water was scarce, because its grain is free from the bitter saponins that must be leached out of chenopod grain.

The first recognizable reference to *A. caudatus* as a grain crop was the description and illustration of *Quinoa sive Blitum majus peruvianum* by Clusius (1601). In 1635 in Ayacucho, Peru, red and white amaranths were very common foods of the Indians, and the seeds of the white form were also made into confections.

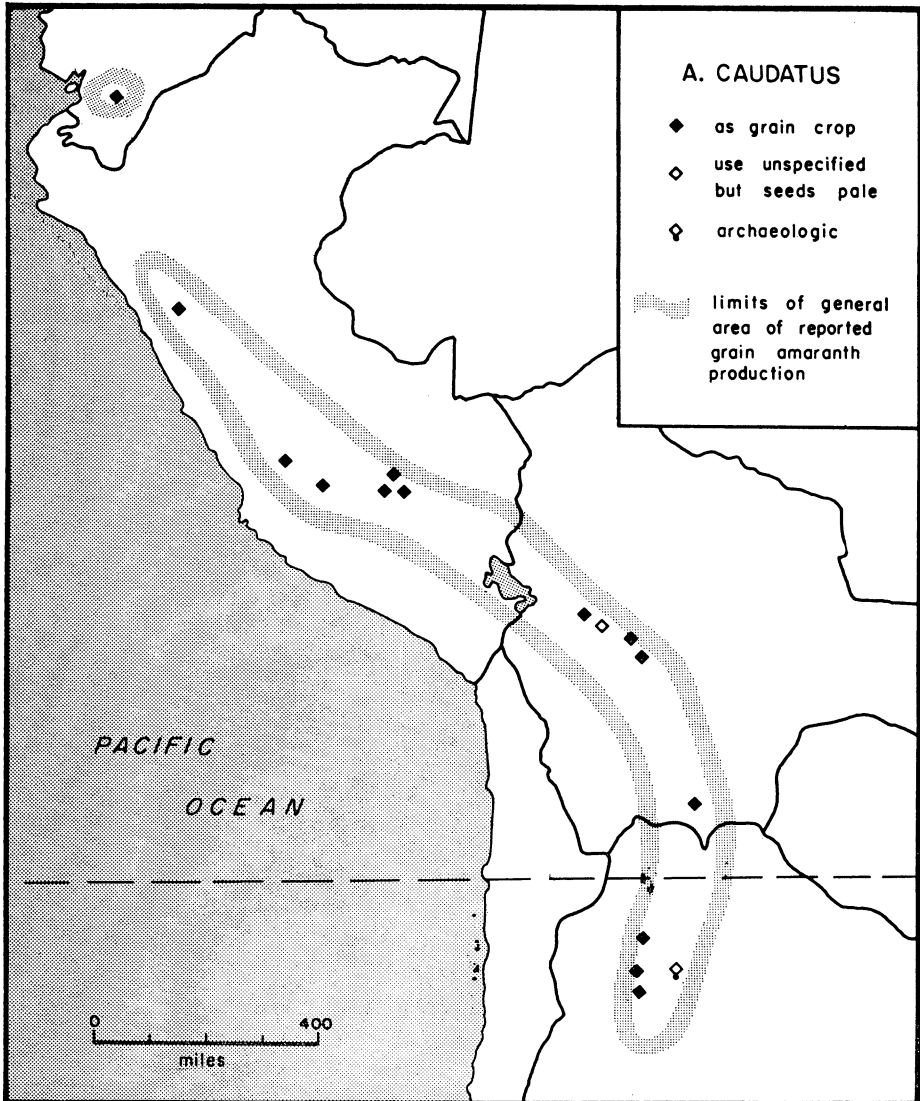


Fig. 9. South American distribution of grain amaranths.

Modern botanical exploration, beginning late in the 19th century, has turned up many cases of cultivation in temperate and cool temperate valleys of Peru, Bolivia, and Argentina. The crop is grown only by Indian peoples, usually in very small plantings near houses or on the edges of maize fields. The grain is toasted and popped, boiled for gruel or stews, or ground into flour. Pale seeds, reddish tinged or plain, are preferred but some dark seeds are often mixed in the harvested grain.

The crop is obviously a declining relic and there are few new records. In Bolivia, Urquidi (1954, p. 151) and Henkel (1966, personal communication) report persistent cultivation in the department of Cochabamba; a row of plants is grown along the edges of maize fields, the toasted grain being used especially for children or invalids and the stalks being useful in fencing and roof construction. There are recent collections of the species as a minor grain from several places in Bolivia and Peru (Appendix). Commerce in the grain in the Cuzco region has been described (Hunziker, 1952, pp. 74-75) as conducted by witch-doctors from the Altiplano; they carry bags of amaranth flour for sale to the natives, who mix it into *chicha* and consider it excellent food.

In Ecuador, the first known record of the crop was a note by Luis Cordero in 1950 (cited by Heiser, 1964, p. 137) that the grain of an amaranth called *quinua de tostar* was eaten in the provinces of Azuay and Cañar. In 1966, Heiser found several Indian families in this region cultivating *A. caudatus* for grain under the name *quinua* (Appendix; Heiser, 1966, personal communication).

Amaranthus caudatus as an Old World Grain Crop (Fig. 4-5).

The species had been introduced to Asia before 1700, if Linnaeus identified Hermann's Ceylon plants correctly. The oldest available Asiatic specimens were collected in northern India and Nepal in the early 19th century. By the middle of the century it had been found scattered widely through the Himalaya and into Afghanistan; before 1900 it was in China as far north as Manchuria (Appendix). The listed specimens have pale, sometimes reddish, seeds; dark seeded forms were also collected early but more rarely in Asia (e.g. *A. von Schlagintweit* 5720, 1856, Baltistan, E; *H. & R. von Schlagintweit* 1482, 1856, Ladak, GH).

None of the early collections bear data on purpose of cultivation, but in the present century pale seeded forms have been recorded as a grain crop at several places in the Himalaya and China. Uses are similar to *A. hypochondriacus*, which is grown at more places and in larger quantities over the same general range.

There are some additional records from Asia. The Japanese Expedition to Nepal Himalaya found *A. caudatus* grown for grain at three villages on the slopes of Annapurna in 1953 (Appendix; Nakao & Sauer, 1956, p. 142). It was recently photographed growing with millet in the Kullu Valley, Punjab; there and in India in general, it is grown only as scattered plants or in very small plots and is less common and important than *A. hypochondriacus* (Singh, 1961, pp. 12-14). In the Nilgiri Hills of Madras, the Kurumbas, who commonly cultivate *A. hypochondriacus*, occasionally also plant *A. caudatus* for grain and as a potherb (Appendix; Noble, 1963, personal communication). Nearby in the Pulni Hills, Noble

obtained a lot of amaranth seeds intended for popping; when grown out, they proved to be a mixture of *A. hypochondriacus* and *A. caudatus* (Appendix). In Suiyan province, Inner Mongolia, a field planted to *A. caudatus* was seen in 1944 (Nakao, 1957, p. 409).

The only other area where the species is known in folk cultivation is Ethiopia. The older specimens are all dark seeded and are not known to represent a regular grain crop. The earliest known collection (*Pearce s.n.*, ca 1815, Tigre, BM) was said by Pearce to be the most beautiful flower he had seen in Abyssinia. He noted that the Abyssinians parched the seeds and ate them for complaints in the stomach and breast; the name was *Tsellal Enno Mariamm* (parasol of the Virgin Mary). This name was reported for other specimens from Tigre (*Schimper* 359, 1077, 1513, 1535, 1837-44, nr Aduwa, BM, G, GH, K, MO, P, US). There have been later collections of the same dark seeded form from Ethiopia (e.g. *Cooper s.n.*, 1926 Addis Alam, Shoa Prov, K) and from the Sudan (*Lynes* 596, 1921, Darfur Prov, US), but none have data on use. Finally, near Jimma in 1957, Anderson found that *A. caudatus* grain is eaten popped and milled and the inflorescences are used to decorate the cross for Mascal Day processions; forms with both dark and pale, reddish tinged seeds were collected (Anderson, 1957, personal communication; Appendix). The plants are allowed to seed themselves and also sown along field edges and in rubbish heaps by houses. The seed was said to have been brought originally from the Maji forest region, where the Ghimera regularly cultivate it as an important grain. Meyer subsequently collected pale, reddish tinged seeds of *A. caudatus* in the forest districts of southwestern Ethiopia, where it is a grain of Negro tribesmen (Appendix).

Amaranthus caudatus as a Cosmopolitan Ornamental.

It is certain that some pale seeded American grain amaranths had been introduced to European gardens during the 16th century (Gesner, 1561, p. 246; Gerarde, 1597, p. 254,) and were soon widely grown as ornamentals and for medicinal uses inspired by their blood red color. It is possible that *A. caudatus* was the only American amaranth planted in Europe during the 16th and 17th centuries, but this is not certain. The distinctive form of *A. caudatus* that was to become the common ornamental was first clearly described by Parkinson (1640, p. 753) and Ray (1686-88, I: 202). This has since gone around the world, often in commercial seed packets, and is still widely planted, especially in temperate zone gardens. Its peculiar English name, love-lies-bleeding, seems to be a Victorian invention. In other languages it shares names such as red-hot-cattail, fox-tail, or scourge-of-the-nun with the unrelated but curiously similar chenille plant, *Acalypha hispida*.

DISCUSSION AND CONCLUSIONS

Amaranth domestication may have begun, as has been repeatedly suggested, with the very beginnings of American Indian agriculture. Some arguments for early domestication, such as the central role of the crop in pre-Conquest Mexican ceremonials, are fairly convincing but they are not based on direct evidence. So

far, archaeological amaranth seeds that are known to be very ancient may have been merely gathered. In both North and South America, finds of definitely domesticated grain go back only to late prehistoric times.

It has been more or less taken for granted that each grain species was separately domesticated in a particular region and period, then carried into other regions and passed down through time like a uniquely invented culture trait. Some alternative possibilities have not been ruled out, one being multiple domestications of the same wild species. The progenitors of the grain amaranths would seem to be ideal candidates for repeated domestication, being naturally wide ranging, weedy, and obviously useful plants. However, what little variation there is within the domesticated species does not suggest an old heritage from distinct geographic races so much as it does recent introgression.

Another conceivable possibility is derivation of two or even all three grain species from a single primary domesticate. For example, *A. cruentus* might have been domesticated from *A. hybridus* in humid regions of Central America and then carried northwestward into drier highlands, where it picked up *A. powellii* as a weed. By continued crossing with *A. powellii*, the Mexican grain crop might eventually have come to resemble it more than its original progenitor. Similarly, southward carriage of *A. cruentus* followed by repeated crossing with *A. quitensis* might have produced the distinctive Andean grain crop, assuming that *A. cruentus* and *A. quitensis* can interbreed, which is not proven.

The main reason for considering such a speculative connection between domesticated species is that it would account very simply for some peculiar characters shared by all three. Of these, the pale seed character seems hardest to explain by convergent evolution in three independent evolutionary lines. Mutants producing pale seeds have never been recorded in any wild amaranth species nor in the dark seeded ornamental forms of the grain species. It would be worth knowing whether the pale seed character is genetically homologous in the domesticated species, but this has not been investigated.

Thus, although alternatives should be kept open, it is still possible to maintain the simplest, most obvious hypothesis, namely that the three grain species were independently domesticated by different prehistoric peoples of North and South America.

As for the intriguing problem of when and how the species were introduced to the Old World, the evidence remains inconclusive. There is no proof that any of them were in the Old World before Columbus. On the other hand, their spread in Asiatic and African cultivation certainly outran European contacts and could scarcely have been initiated by any direct transfer between Old and New World colonies of the same European power. Introduction through Europe itself seems most likely in the case of the Andean *A. caudatus*. Pale seeded forms evidently were taken there directly from South America in the 16th century, long before they were found in Asia or Africa. However, dark seeded forms that are minor components of the Andean crop somehow became established in remote parts of Asia and Africa before they were known in Europe.

The Mexican *A. hypochondriacus* and the Central American *A. cruentus* evi-

dently reached Europe in the 18th century, both arriving via Asia and directly from America. Europe got only dark seeded forms that are inferior as grain and grown mainly as potherbs and ornamentals. The pale seeded forms of *A. cruentus* apparently never left Central America but pale seeded *A. hypochondriacus* had reached Asia by the 18th century. At least since the early 19th century, *A. hypochondriacus* has been a widespread and locally important grain crop there. At present, India alone undoubtedly harvests more grain from this one species than is produced by all the relics of grain amaranth cultivation in the New World.

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APPENDIX: GRAIN AMARANTH SPECIMENS EXAMINED

Specimens cited are either reported as grown for grain or are pale seeded forms from known grain amaranth regions. (The only other pale seeded specimens belong to the common ornamental race of *A. caudatus*.) Collections of the author are indicated by J.D.S.

Notations between hyphens:

- G: grain use specified
- N: grain use not noted
- d-: seeds dark
- p-: seeds pale
- i-: seeds immature
- @: strongly atypical, apparently hybrid

Amaranthus hypochondriacus

AMERICA. GUATEMALA. ALTA VERAPAZ: *Pittier 197* (in 1905), nr Secanquim -Np- (US).

MEXICO. CHIHUAHUA: *Gentry 1843, 1844* (in 1935), Warihio Indian village, Guasaremos, *guegui* -Gp- (MO, UC, US); *Gentry s.n.* (in 1948), seed from Rancho Trigo, Sierra Chamco, *bledo* or *guegui*—progeny: *J.D.S. 1193* -Gp- @ (MO, WIS). *Pennington 269* (in 1960), Tepehuan settlement nr Santa Rosa, *giage* or *guatle* -Np- (WIS). DISTRITO FEDERAL: *Martinez s.n.* (in 1917), *alegria* -Gp- (US). *Bravo s.n.* (in 1940), seed from Valley of Mexico, *alegria*—progeny: *Hunziker 2948* -GP- (GH). *Kelly s.n.* (in 1947), betw Xochimilco & Tlahuac -Gp- (UC). *J.D.S. 1171* (in 1947), San Gregorio Atlapulco, *alegria* -Gp- (F, GH, MO, UC, US, WIS). GUERRERO: *Hernandez X. 3166* (in 1947), seed from Chilapa, *alegria*—progeny: *J.D.S. 1162* -Gp- (F, GH, MO, UC, US, WIS). JALISCO: *Palmer 694, 695* (in 1886), Guadalajara, *alegria* -Gp- (K, MICH, US). *J.D.S. 1174* (in 1947), Tlajomulco, *alegria* or *zoale* -Gpd- (F, GH, MO, UC, US, WIS). MEXICO: *Hinton 2137* (in 1932), Temascaltepec, *alegria* -Np- (K, MO, US). MICHOACAN: *West s.n.* (in 1946), seed from Teremendo, Zacapu *pati* or *alegria blanca*—progeny: *J.D.S. 1170* -Gp- (DS, MO, UC, US, WIS); *West s.n.*, seed from Opopeo, *alegria blanca*—progeny: *J.D.S. 1274* -Gp- (WIS); *West s.n.*, seed from Los Reyes highlands, Pomatacuaro, *alegria negra*—progeny: *J.D.S. 1355* -Gd- @ (MO, WIS). OAXACA: *C. O. Sauer s.n.* (in 1945), seed from Zapotec village of San Juan nr Ixtlan de Juarez, *alegria*—progeny: *Reed s.n.* -Gp- @ (UC) and *J.D.S. 1161* -Gpd- @ (MO, TENN, WIS). *J.D.S. 1266* (in 1947), Clavillones in Zimatlan area, *alegria* -Gp- @ (MO, WIS). PUEBLA: *C. O. Sauer s.n.* (in 1948), seed from San Jeronimo Teocuzmanalco nr Tezmelucan, *alegria*—progeny: *J.D.S. 1239* -Gp- (WIS). SINALOA: *Gentry 6547* (in 1941), Quebrada de Manzana, Sierra Surotato, *bledo* -Gi- (MO). TLAXCALA: *J.D.S. 1173, 1277* (in 1947), San Miguel del Milagro, *alegria* -Gp- (DAV, F, GAT, GH, MO, UC, US, WIS). *Hernandez X. 3715* (in 1948), seed from San Bernabé Amaxac, *alegria*—progeny: *J.D.S. 1535* -Gp- (F, GH, MO, UC, US, WIS).

UNITED STATES. ARIZONA: (Archaeologic specimens noted in text.) *Powell s.n.* (ca 1870), seed from Arizona Indians—progeny grown at Harvard Univ -Gp- (GH, MO, US).

ASIA. BHUTAN. *Cooper 2759* (in 1914), Punakha -Np- (E); *Cooper 2501, 3363*, s. loc. -Np- (E).

CEYLON. *Koenig 29* (ca 1780), s. loc., *ette tampala* -Gp- (L). *Macrae 837* (ca 1830), s. loc. -Np- (BM). *Brodie 101* (ca 1850), *101* s. loc. -Np- (E). *Thwaites s.n.* (in 1860), Tricomalee -Np- (K). *Deschamps s.n.* (in 1890), Teldeniya, *rana tampala* -Np- (G).

CHINA. HEILUNGKIANG: *Dorsett & Dorsett* 4089 (in 1925), Hsiaoling -Np- (UC, US). HOPEH: *Beach s.n.* (in 1948), Hsin Chi -Gp- (UC). HUPEH: *Henry* 2390 (ca 1885), Patung dist, *jua-ku* -Np- (K); 2732, Ichang, *jua-ku* -Np- (BM, K, US); *Henry* 4808, s. loc. -Np- (GH). *Chow* 1294 (in 1934), *Chienshih* -Np- (E). KIREN: *Hanelt* 6014 (in 1958), experiment station, Tung Hua -Gp- (GAT, WIS). KWEICHOW: *Tsiang* 5946 (in 1930), Yunfou-shan, Tuyan -Np- (K). *Steward et al.* 784 (in 1931), Fan Ching Shan, Ta Ho Yen -Npd- (GH, K, L, US). SHENSI: *Rev. Fr. Hugh s.n.* (about 1900), Isay Toe, Pao Chi -Np- (BM). SZECHWAN: *Hosie s.n.* (in 1904), betw Batang & Tachienlu -Np- (K). *Yü* 14480 (in 1937), Muli, Wachin, Shawan -Np- (E). *Chang s.n.* (in 1948), seed from Muping—progeny: *J.D.S.* 1489 -Gp- (F, GH, MO, UC, US, WIS); *Chang s.n.*, seed from Mowhsien—progeny: *J.D.S.* 1484, 1499 -Gpd- (DAV, F, GH, MO, UC, US, WIS). YUNNAN: *Ward* 3522 (in 1919), Imaw Bum to Hpimaw, *yü-mi* -Gp- (E).

INDIA. Without province: *Roxburgh s.n.* (ca 1800), -Gp- (K). *Wallich* 238 (in 1815), -Gp- (BM). *Royle s.n.* (about 1830), NW India -Np- (K). *Ritchie* 631 (ca 1840), -Np- (E, GH). *Simpson s.n.* (ca 1840), Himalaya -Np- (G). *Wight s.n.* (ca 1840), -Np- (UC, W). *Edgeworth s.n.* (in 1844), NW India, *batou* -Gp- (K). *Falconer* 823 (ca 1850), -Np- (K). *Gamble* 2028A (in 1876), -Np- (K). BIHAR: *Buchanan-Hamilton* 2028-1 (in 1813), (*Wallich* 6903), Bhagalpur -Gp- (E, P). HIMACHAL PRADESH: *Lady Dalhousie s.n.* (in 1831), Simla -Np- (E). *Thomson s.n.* (in 1847), Serahan, Sutlej Valley -Gp- (K). *Grant s.n.* (about 1850), Kunamer, Sutlej Valley -Np- (K). *Drummond* 26070 (in 1886), Simla Hills -Np- (K). *Lace* 1483 (in 1896), Chamba -Np- (E). *Harsukh s.n.* (in 1899), Pangi, Sauch Valley, Chamba -Np- (K). *Koelz* 7279 (in 1933), Li, Bashahr -Gd- (G, US). MADRAS: *Wight s.n.* (ca 1850), s. loc. -Np- (E); *Wight* 1787, Dindigul Hills -Np- (E); *Wight* 2436, Koathagerry -Np- (K). *Cleghorn s.n.* (in 1859), Kalhatti -Np- (E). *Barber* 8603, (in 1910), Dhimbar, Coimbatore -Npd- (K). *Noble s.n.* (in 1962-63), seed and plant collections from six Badaga villages, Upper Nilgiri Hills—progeny: *J.D.S.* 3954, 3955, 3965 -Gpd- (WIS); *Noble s.n.*, seed and plant collections from three Kurumba villages, Manjankombai area, Upper Nilgiri Hills—progeny: *J.D.S.* 3949, 3950, 3953, 3956, 3960, 3961 -Gpd- (WIS); *Noble s.n.*, seed and plant from Kodomalai Estate, nr Coonor, Upper Nilgiri Hills—progeny: *J.D.S.* 3952 -Gp- (WIS); *Noble s.n.*, seed from Irulas tribe, Caricure, Nilgiri Hills—progeny: *J.D.S.* 3957, 3959 -Gpd- @, 3958 -Gp- (WIS); *Noble s.n.*, seed from Vilpatti, Pulni Hills—progeny: *J.D.S.* 3963 -Gp- (WIS). MAHARASHTRA: *Tyson* 30 (in 1953), seed from Poona—progeny: *J.D.S.* 1703 -Np- (MICH, MO, UC, WIS). *Gentry* 37440 (in 1954), seed from Poona—progeny: *J.D.S.* 2538 -Np- (WIS). *Kelly s.n.* (in 1960), nr Ajanta, Aurangabad, *raj-gira* -Gp- (WIS). PUNJAB: *Stewart* 1790 (in 1917), nr Pathankot, Ravi Valley -Np- (K). UTTER PRADESH: *von Hügel* 158, 409 (in 1832), Mussoorie -Np- (W). *Ritchie s.n.* (ca 1840), Saharampore -Np- (E). *Madden* 583 (ca 1845), Bashahr to Kumaon -Gp- (E). *Anonymous s.n.* (in 1846, 1848), Saharampore -Np- (K). *Strachey & Winterbottom* 2b (ca 1850), Kumaon -Np- (GH, K). *von Schlagintweit* 9707 (in 1855), Nelong to Ussila, Garhwal -Np- (E). *Gamble* 27404, 27432 (in 1898), Jaunsar, *chaulai* -Np- (K). *Bell s.n.* (in 1902), Banda, *ramdana* -Gp- (K). *Anderson s.n.* (in 1915), Mussoorie -Np- (E). *Huggins s.n.* (in 1952), seed from Harsil, Tehri Garhwal, *marcha*—progeny: *J.D.S.* 1702 -Gp- (MICH, MO, WIS). *Lal s.n.* (in 1961), Mussoorie, *chaulai*—progeny: *J.D.S.* 2845 -Gp- (WIS). *Andress s.n.* (in 1963), Mussoorie, *chaulai*—progeny: *Frenkel* 889, 890 -Gd- (WIS).

KASHMIR. BALTISTAN: *von Schlagintweit* 871 (in 1856), nr Skardo -Np- (L, UC); *von Schlagintweit* 872, nr Skardo -Np- (BM, US); *von Schlagintweit* 5789, Kunes via Kiris to Neru -Np- (BM, US); *von Schlagintweit* 5850, Kunes via Kiris to Neru -Np- (E); *von Schlagintweit* 6407, Das via Goltore/Naugaum to Hasora/Astor -Np- (US). GILGIT: *Harlan* 806 (in 1960), seed from Shimal garden nr Gupis, Teru, *gunerie*—progeny: *J.D.S.* 3966 -Gp- (WIS). KASHMIR: *Thomson s.n.* (in 1848, 1849), s. loc. -Np- (K). *Aitchison s.n.* (in 1875), s. loc. *ganhar* or *sil* -Gpd- (K). *Polunin* 300 (in 1956), Tangmarg -Gd- (MO, WIS); *Polunin* 617, Rezan, Sind Valley -Gpd- (MO, WIS); *Polunin* 759, Khanan, Wangat Nullah -Gd- (MO, WIS); *Polunin* 804, nr Miragund -Gpd- (MO, WIS); *Polunin* 819, Srinagar -Gpd- (MO, WIS). LADAK: *H. & R. von Schlagintweit* 1771 (in 1856), Himis lamasery, nr Leh -Np- (BM); *H. & R. von Schlagintweit* 1958, Yugah to Leh -Np- (GH); *H. & R. Schlagintweit* 12075, Gures across Uri plain to Bandipur -Np- (GH).

NEPAL. *Wallich s.n.* (in 1821), s. loc. -Np- (K, P, W). *Janaki-Ammal 1482* (in 1948), seed from Makwanpur, nr Sirsagarhi—progeny: *J.D.S. 1495* -Gpd- (F, GH, MO, UC, US, WIS). *Nakao 194* (in 1953), seed from Tsumje, S slope of Sringi Himal—progeny: *J.D.S. 1713* -Gp- (MICH, MO, WIS); *Nakao 203*, seed from Thomje, Shiar Kola Valley—progeny: *J.D.S. 1714* -Gp- (MO, UC, WIS). *Tyson 20* (in 1953), Chainpur, Seti Valley, *marcha* -Gp- (MO).

SIKKIM. *Hooker s.n.* (in 1849), Lachen, Lachoong -Np- (K); *Hooker s.n.*, s. loc. -Npd- (BM, E, GH, K, W).

SOVIET RUSSIA IN ASIA. MARITIME TERRITORY: *Bohnhof s.n.* (in 1898-99), Lake Khanka -Np- (E, K).

AFRICA. UGANDA (not mapped). MASAKA: *Purseglove 1775* (in 1945), Kakuto, Buddu -Gp- (K). *Thomas 4494* (in 1946), Bawanga -Gp- (K).

Amaranthus cruentus

AMERICA. GUATEMALA. ALTA VERAPAZ: *J.D.S. 1265* (in 1947), nr Coban, *bledo* or *tses* -Gd- (DAO, F, GH, MO, UC, US, WIS). CHIMALTENANGO: *J.D.S. 1168* (in 1947), San Martin Jilotepeque, *bledo blanco* -Gpd- (DS, F, GAT, GH, TENN, UC, US, WIS); *J.D.S. 1240, 1267*, San Martin Jilotepeque, *bledo morado* -Gd- (DAV, MO, WIS). GUATEMALA: *J.D.S. 1176* (in 1947), San Juan Sacatepequez, *nigua negra* -Gpd- (DAO, GH, MO, US, WIS); *J.D.S. 1177*, San Juan Sactepequez, *nigua blanca* -Gp- (DAV, F, UC); *J.D.S. 3972* (in 1966), San Juan Sacatepequez, *nigua negra* -Gd- (WIS).

MEXICO. OAXACA: *Kaplan s.n.* (in 1954), seed from Mixtec village, Jicatepec, *chian*—progeny: *J.D.S. 2529* -Gp- @ (WIS). PUEBLA: *J.D.S. 1172* (in 1947), Acatlan, *alegría* -Gp- @ (GH, MO, UC, US, WIS). SINALOA: *Palmer 1718* (in 1891), Ymala, *guaute* -Gp- @ (US).

Amaranthus caudatus

AMERICA. ARGENTINA. SALTA: *Mintzer s.n.* (in 1938), seed from San Carlos, *quinoa*—progeny: *Hunziker s.n.*, 1085 -Gp- (G, GH, US). *Lovaglio 1449* (in 1941), seed from Cachi, *quinoa*—progeny: *Hunziker 2127* -Gp- (G, GH). *Hunziker 3003* (in 1943), San Carlos, *quinoa* -Gp- (MO). *Anonymous DEIP-17007* (in 1958), seed from Coronel Moldes experiment station, *chaclion*—progeny: *Grant 336* -Np- (WIS). TUCUMAN: *Hunziker 2550, 2555*, (in 1943), Colalao del Valle, *chaclion* or *quinoa de Castilla* -Gp- (G, K).

BOLIVIA. COCHABAMBA: *Cardenas 3512, 3514, 3515*, (in 1944), Cochabamba, *millmi* -Gp- (GH, US); *Cardenas s.n.* (in 1947), seed from Sacaba, *millmi*—progeny: *J.D.S. 1314, 1315* -Gpd- (UC, WIS). *Cutler s.n.* (in 1947), seed from Hacienda Chihuni, nr La Angostura, *millmi*—progeny: *J.D.S. 1179, 1241, 1298* -Gpd- (DAV, DS, F, GAT, GH, MO, TENN, UC, US, WIS). *Fuller s.n.* (in 1947), nr Cochabamba, *millmi* -Gp- (ILL). LA PAZ: *Kelly 1006* (in 1958), seed and plant from betw Chulumani & Irupana, *kwimi*—progeny: *J.D.S. 2540* -Gpd- (UC, WIS); *Kelly s.n.*, Chirca—progeny: *J.D.S. 2539* -Np- (WIS); *Kelly s.n.*, Tajma, Chulumani region, *quinoa*—progeny: *J.D.S. 2542* -Np- (WIS). TARIJA: *Figueroa s.n.* (1941), Tarija, *coimi*—progeny: *Hunziker 2128* -Np- (GH).

ECUADOR. AZUAY: *Heiser 6554* (in 1966), nr Cuenca, *quinoa* -Gp- (IND, WIS).

PERU. ANCASH: *Bradford s.n.* (in 1956), Hacienda Vicas above Chancos, *achi* or *achita* or *cuiipa* -Np- (USM). AYACUCHO: *Gade s.n.* (in 1964), nr Ayacucho, *achita* -Gd- (WIS). CUZCO: *Cook & Gilbert 256* (in 1915), Urubamba, *quihuicha* -Gp- (US). *Vargas s.n.* (in 1939), seed from Cuzco, *quihuicha*—progeny: *Hunziker 810* -Gp- (US); *Vargas s.n.* (in 1943), seed from Cuzco, *quihuicha*—progeny: *Cardenas 3513* -Gp- (GH). *Gade s.n.* (in 1964), Naihua, bottom of Apurimac gorge, *quihuicha* -Gd- (WIS). HUANCABELICA: *Arevalo s.n.* (in 1948), seed from La Mejorada, *achita*—progeny: *J.D.S. 1283* -Gpd- (DAV, F, GH, MO, UC, US, WIS).

ASIA. AFGHANISTAN. Without province: *Griffith 4184* (about 1840), -Np- (GH).

CHINA. HUPEH: *Henry 7517* (about 1885), Changyang -Np- (K). KIRIN: *Komarou II-165* (in 1896), s. loc. -Np- (K). *Kozlow 14486* (in 1929), s. loc. -Np- (W). *Chen 369* (in 1931), nr Kirin -Np- (GH). LIAONING: *Webster 230* (in 1884), Mukden to Yalu River -Np- (K). SZECHWAN: *Yü 14479* (in 1937), Muli, Wachin—progeny: *Cowgill 2087* -Np- (E, GH). *Chang s.n.* (in 1948), seed from Mowhsien, progeny: *J.D.S. 1503* -Gp- (F, GH, MO, UC, US, WIS). YUNNAN: *Maire 319* (in 1906), Yunnansen -Np- (E). *Handel-Mazzetti 8479* (in 1915), Mekong Valley, 27½° N.L. -Np- (E). *Ten 1429* (in 1919), Pai Yen Ching -Gp- (W).

INDIA. Without province: *Edgeworth 85* (in 1844), NW India -Np- (K). HIMACHAL PRADESH: *Lace s.n.* (about 1900), Bashahr -Np- (E). MADRAS: *Noble s.n.* (in 1962), seed from Kurumba villages, Manjakombai, Upper Nilgiri Hills—progeny: *J.D.S. 3951, 3962* -Gp- (MO, WIS); *Noble s.n.*, seed from Vilpatti, Pulni Hills—progeny: *J.D.S. 3964* -Gp- (WIS). UTTAR PRADESH: *Buchanan-Hamilton 2028-2* (in 1813), Belaya -Np- (E). *Jameson 776* (in 1845), Mussoorie -Np- (K). *Madden s.n.* (about 1850), Mussoorie -Np- (E). *Strachey & Winterbottom 2a* (about 1850), Kumaon -Np- (GH). *King s.n.* (in 1869), nr Mussoorie -Np- (L). *Anderson s.n.* (in 1915), Mussoorie -Gp- (E).

KASHMIR. BALTISTAN: *von Schlagintweit 5787* (in 1856), NE of Skardo -Np- (US).

NEPAL. *Wallich s.n.* (in 1821), s. loc. -Np- (G, K, P). *Janaki-Ammal 1481* (in 1948), seed from Makwanpur, nr Sirsagarhi—progeny: *J.D.S. 1505* -Gp- (MO, UC, WIS). *Nakao 188, 191, 201, 205* (in 1953), seed from Ulleri, SW slope of Annapurna—progeny: *J.D.S. 1707-1710* -Gp- (F, GH, MICH, MO, UC, US, WIS); *Nakao 204*, seed from Ghasa, W slope of Annapurna—progeny: *J.D.S. 1712* -Gp- (MICH, MO, WIS); *Nakao 210*, seed from Sikha, SW slope of Annapurna—progeny: *J.D.S. 1711* -Gp- (WIS).

AFRICA. ETHIOPIA: (not mapped). ILUBABOR: *Meyer 8905* (in 1964), Tukle, nr Teppi -Gp- (WIS). KEFA: *Anderson & Getachew s.n.* (in 1957), nr Jimma, *lishalisho* or *kettila* -Gdp- (WIS). *Mengesha s.n.* (in 1957), Missan Tefferi -Gp- (WIS).