ABERRANT AMARANTHUS POPULATIONS OF THE SACRAMENTO-SAN JOAQUIN DELTA, CALIFORNIA

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In the early 1890's W. L. Jepson found some tall, brightly colored amaranths growing among other rank vegetation on the riverbanks and small islands of the lower Sacramento River (Jepson, 1893, p. 243; 1914, p. 449; also Table 1). Although these were growing in natural habitats, he interpreted them as feral derivatives of an introduced cultigen which he identified as *Amaranthus hypochondriacus* L. We believe that Jepson was right in looking toward cultivated ornamental species for an ancestor of these striking plants, but their ancestry is different and more complex than he thought.

At present similar robust amaranths, on occasion attaining heights of as much as nine feet, often with gaudy anthocyanin pigmentation and great compound inflorescences, grow widely through the lowlands above the junction of the two major Central Valley rivers. They can still be found along the river side of levees but are now far more abundant as weeds in cultivated fields. It is apparent that they occur in very large part on the highly organic, peaty, basin soils—Staten peaty muck, Venice peaty muck, and Egbert muck—occupying the bulk of the delta country, as well as on more limited areas of alluvium—Burns clay loam, Ryde clay loam, Sacramento loam. They are abundant up to the edge of the peat soil and then peter out rapidly on the generally more alkaline alluvial loams along the periphery of the delta area.

Morphology

Field observation and examination of the few conventional herbarium specimens available from the area (Table 1) established that the delta amaranths are highly variable and include individuals that resemble various recognized species but rarely appear identical with any of them. In one population or another through this region characters of five different species are discernible, although in no population yet studied are the characters of all five present. These are all rather closely related members of the section *Amaranthotypus* Dumort. Descriptions and diagrammatic figures illustrating diagnostic features of these species are presented elsewhere (Sauer, 1950). It will suffice here to tabulate briefly the typical condition, or norm, of each species in four important structures (Table 2).

Population Samples

In order to get beyond the frustration and uncertainty that come with attempts to understand taxonomically difficult populations from a few isolated specimens, mass collections were made at widely scattered localities through the delta (Table 1). Individuals were collected at random in sufficient numbers to give a respectable sample of the actual popula-

TABLE 1. ABERRANT AMARANTHUS COLLECTIONS FROM THE DELTA AREA

COLLECTOR AND NUMBER (DATE)	HERBARIUM (ACCESSION)	HABITAT AND LOCALITY	POSTULATED PARENTAGE
		Conventional Herbarium Specimens	
W. L. Jepson (Oct. 4, 1893)	JEPS	Tyler Island, Sacramento County	*A. cruentus* x *A. retroflexus*
W. L. Jepson (Oct., 1895)	UC (7574)	Lower Sacramento	*A. cruentus* x *A. retroflexus*
R. N. Raynor (Aug. 11, 1941)	DAV (51)	Asparagus field, near Clarksburg, Yolo County	*A. caudatus* x *A. retroflexus*
C. O. Sauer and J. D. Sauer *1502* (Oct., 1947)	WIS	Roadside levee, Sherman Island, Sacramento County	*A. cruentus* x *A. powellii* x *A. retroflexus*
J. D. Sauer *1643* (Aug. 14, 1953)	DAV, WIS	Farmyard ditch, Roberts Island, San Joaquin County	*A. caudatus* x *A. hybridus* x *A. powellii*
		Population Samples	
J. M. Tucker *2314* (Oct. 31, 1951) 14 individuals	DAV, WIS	Periphery of cornfield, Staten Island, San Joaquin County	*A. caudatus* x *A. powellii* x *A. retroflexus*
J. M. Tucker *2335* to *2343* (March 29, 1952)	DAV	Progeny of certain individuals from previous collection (2314) grown in greenhouse.	
J. M. Tucker *3277* (Oct. 27, 1956) 17 individuals	DAV	Milo field 1 mile west of Thornton, San Joaquin County	*A. cruentus* x *A. powellii* x *A. retroflexus*
J. M. Tucker *3278* (Oct. 27, 1956) 47 individuals	DAV, WIS	Asparagus field 2½ miles west of Thornton, San Joaquin County	*A. cruentus* x *A. powellii* x *A. retroflexus*
J. M. Tucker *3279* (Nov. 10, 1956) 16 individuals	DAV	Asparagus field, Roberts Island, San Joaquin County	*A. cruentus* x *A. powellii* x *A. retroflexus*
J. M. Tucker *3280* (Nov. 10, 1956) 21 individuals	DAV, WIS	Open field, Union Island, San Joaquin County	*A. hybridus* x *A. powellii* x *A. retroflexus*

tion. In most cases only a few inches of the terminal portion of the inflorescence was collected and pressed. From some of these open-pollinated individuals progenies were grown in the greenhouse which, in cases where the number of individuals was small, were studied in their entirety, or, where the number of individuals was large, in random samples.

Each individual specimen was scored for its degree of resemblance to the five species in Table 2 in the characteristics tabulated. Discrimination between these taxa relies heavily on shape differences in the almost microscopic flower parts. It is practically impossible to abstract these effectively by simple measurements, but they can be scored by comparison with a graded series of specimens used as standards. These scorings have been rechecked and found to be repeatable with only minor variation.

TABLE 2. DIAGNOSTIC CHARACTERISTICS OF THE SPECIES INVOLVED IN THE DELTA AMARANTH COMPLEX

	TEPAL	BRACT	UTRICLE	INFLORESCENCE
A. caudatus	Long, very broadly obovate or spatulate, tip obtuse or emarginate, recurved.	Short or medium length, midrib very slender, rather long excurrent.	Style-branches recurved with slender bases forming shallow saddle.	Thick and pendulous, terminal spike extremely long, laterals few and short or absent.
A. cruentus	Extremely short, oblong, tip acute, straight.	Extremely short, midrib extremely slender, long excurrent.	Style-branches erect with slender bases forming sharp cleft at summit of very narrow tower.	Moderately thick, very lax, terminal spike short, laterals long, extremely numerous and crowded.
A. hybridus	Medium length, oblong, tip acute, straight.	Moderately long, midrib medium thick, long excurrent.	Style-branches erect with slender bases forming sharp cleft at summit of moderately narrow tower.	Moderately slender, lax, terminal spike short, laterals short, numerous, and crowded.
A. powellii	Very long, oblong, tip acute, straight.	Extremely long, midrib very thick, excurrent.	Style-branches recurved with stout bases forming cleft at summit of broad tower.	Thick and stiff, terminal spike long, laterals long, few and widely spaced.
A. retroflexus	Very long, narrowly obovate, tip emarginate, recurved.	Extremely long, midrib extremely thick, barely excurrent.	Style-branches erect with moderately stout bases forming saddle or shallow cleft.	Extremely thick and stiff, terminal spike short, laterals short, numerous, and crowded.

Data obtained in this way are presented in figures 1 to 3. Each small triangle represents an individual plant; its position relative to the apices of the grid indicates in a relative way resemblance to any of three species; the barbs on each symbol show scoring of separate diagnostic characters; shading inside the symbol indicates a peculiarity which is not taxonomically diagnostic. A detailed legend is given with figure 1. For example, in collection *2314* there are four plants shown in the lower left corner; all of these resemble *A. powellii* S. Wats. in all four characters studied, more than they resemble the other two species involved, but one plant slightly resembles *A. retroflexus* L. in all four characters and another slightly resembles *A. caudatus* L. in its bract structure. Toward the lower right corner of the same grid are two highly sterile plants which resemble *A. caudatus* more than *A. retroflexus* in tepal structure, but are closer to *A. retroflexus* in the other three characters.

In three of the population samples listed in Table 1 (Tucker *3277, 3278,* and *3279*) the same species were involved—*A. cruentus* L., *A. powellii,* and *A. retroflexus.* Since results of the analyses were quite similar in all three, only one (*3278*) is shown graphically (fig. 3).

It is evident from these graphs that the delta amaranth populations have variation patterns which are intelligible but extraordinarily complex. Instead of the monotonous repetition of character sets found in ordinary species sampling, these collections show reshuffling in a rich variety of individual combinations of several character sets. Characters of two species, *A. retroflexus* and *A. powellii,* recur in each field collection, while a third element alternates between characters of *A. hybridus* L., *A. cruentus,* and *A. caudatus.* Fortunately for the task of graphic representation, populations with more than three elements have not yet been encountered!

Discussion

Recent hybridization between the five species mentioned seems the best explanation of the genesis of these populations. There is a loose but definite tendency for characters in the intermediate individuals to associate in the same combinations that are constant in the extremes—the recognized species. This is evidence of recent gene recombination hindered by old linkages that were established during more effective breeding discontinuity. This discontinuity may have resulted primarily from the former geographic segregation of the species, discussed below. If so, spatial isolation has been reinforced by secondary sterility barriers. High sterility is common in raw hybrids between *Amaranthus* species. For example, Murray (1940, p. 416), in many experimental interspecific crosses, obtained almost sterile F_1's bearing only a few seeds to an entire inflorescence. Some of these crosses involved species in the delta complex—*A. caudatus, A. hybridus, A. powellii,* and *A. retroflexus.*[1]

Highly sterile plants, similar morphologically to certain of Murray's specimens, occur sporadically in the delta populations, but some apparent hybrids are not at all sterile. At first glance this recovery of fertility suggests amphidiploidy, but actually the hybrids must have regained fertility by some more subtle mechanism. Several progenies (from *Tucker 2314, 3278,* etc.) have been examined cytologically by Dr. Walter Plaut of the University of Wisconsin and Dr. W. F. Grant of McGill University and found to have the usual *Amaranthus* diploid number.

Another peculiarity which emerges in many individual delta amaranths is failure of the mature utricle to dehisce. Each of the field collections contains both dehiscent and indehiscent types; offspring of known "mother" plants usually but not always are like their mothers in this respect. Indehiscent utricles are an anomaly among all the species involved here. There are other sections of the genus in which indehiscence is the rule, but there is no trace of their other characteristics in these populations.

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[1] In referring to this work it is necessary to revise a few of the original species determinations (Sauer, 1953).

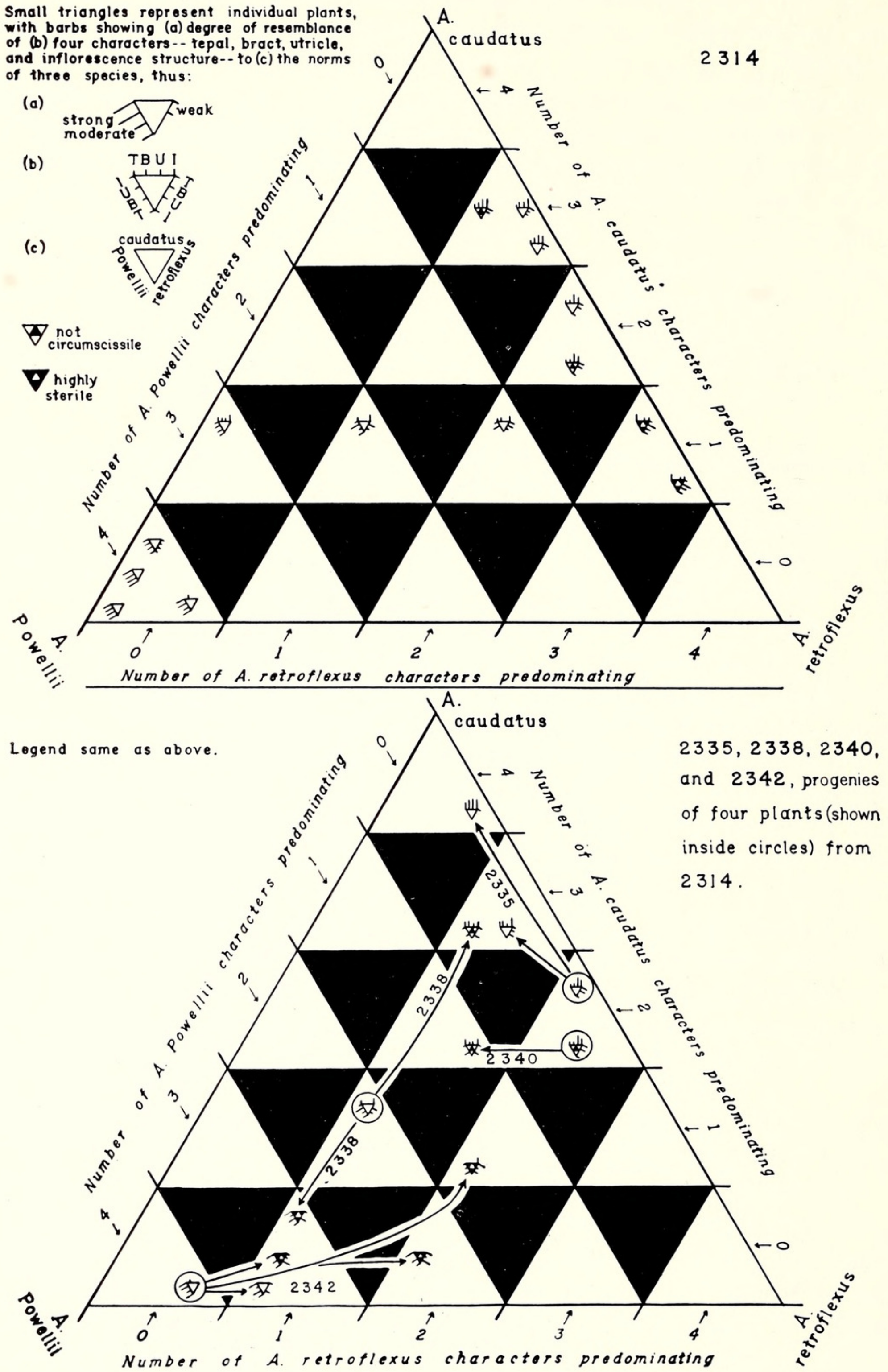
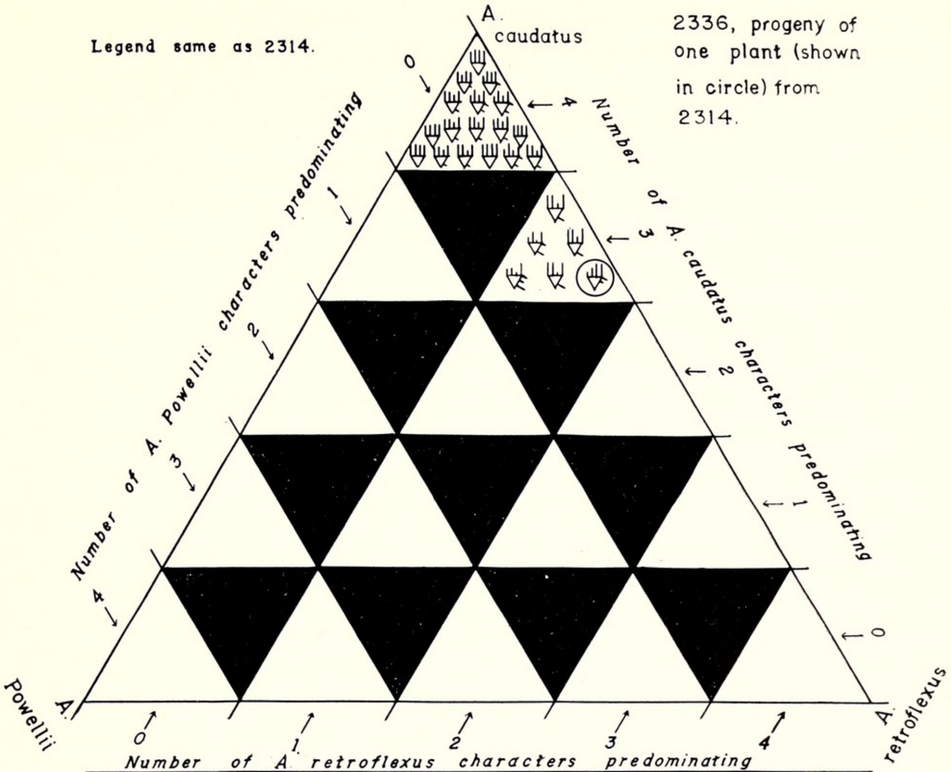


FIG. 1. Character combinations in a delta amaranth population sample, and in progenies of four of its members.



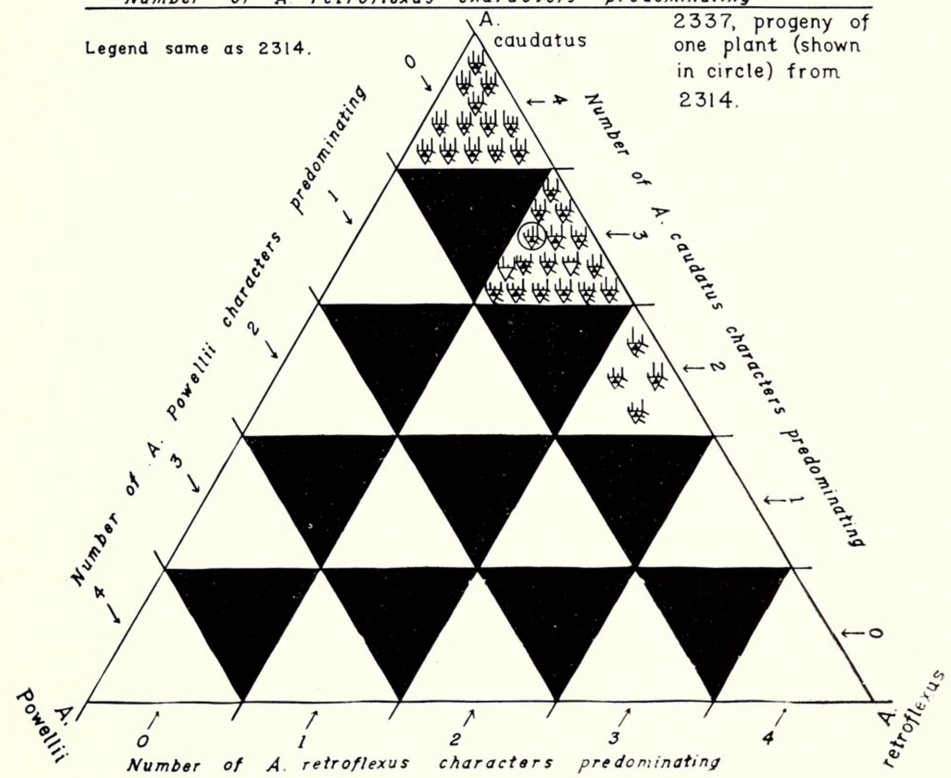
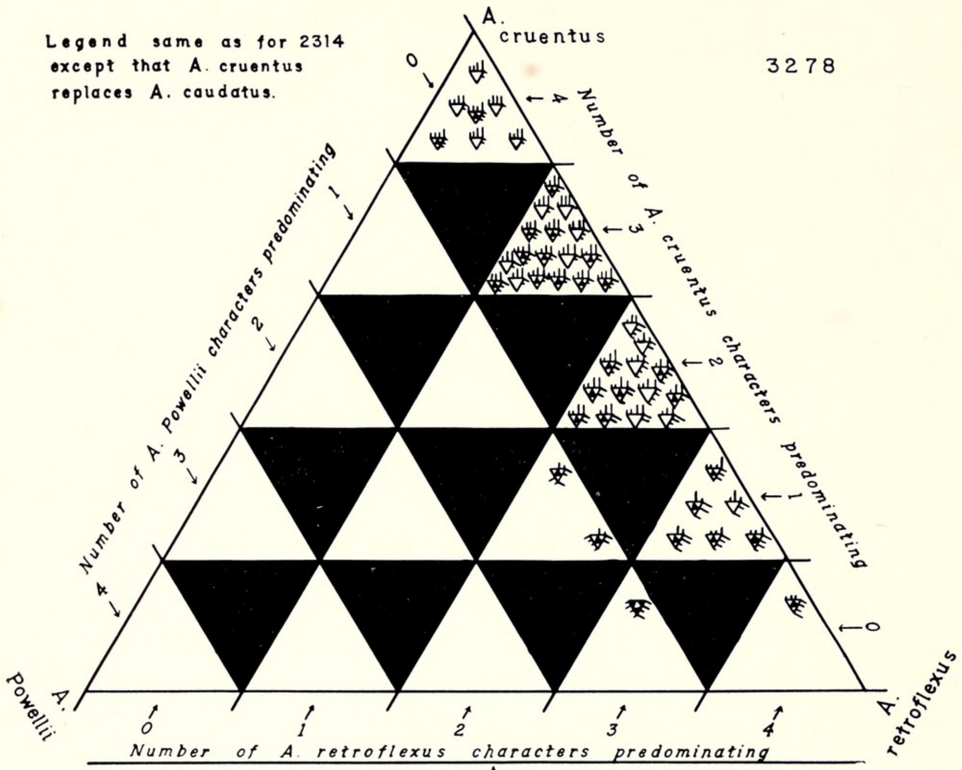


FIG. 2. Character combinations in progenies of delta amaranths.



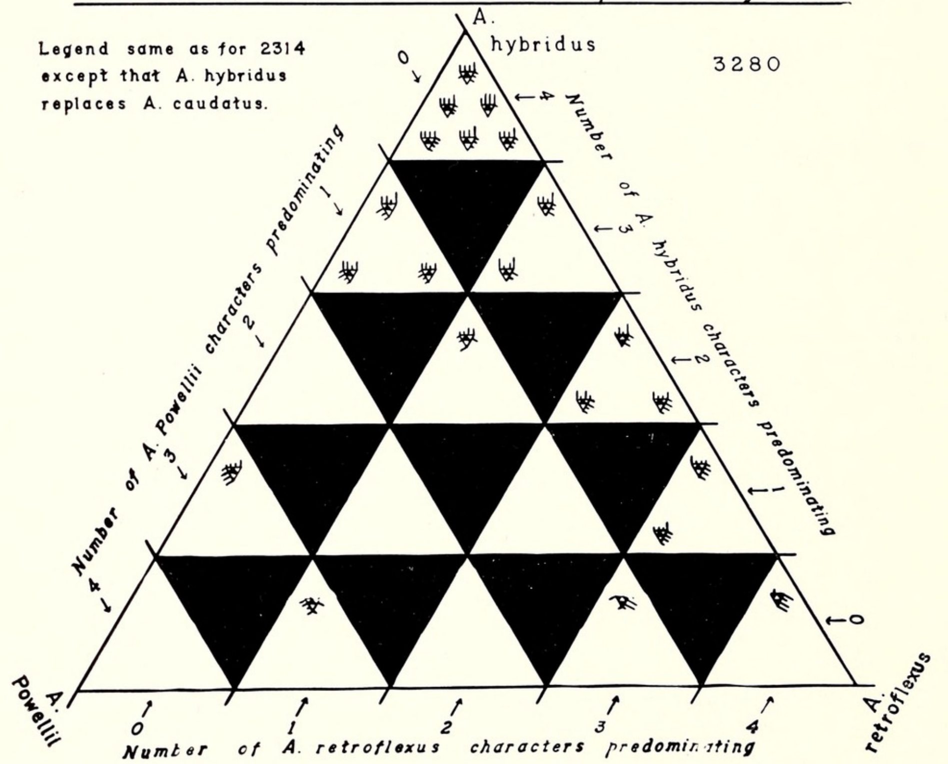


Fig. 3. Character combinations in delta amaranth population samples.

It seems likely that indehiscence in this group should not be regarded as a positive character traceable as a unit to distant ancestral species, but rather as simply a loss or breakdown of the mechanism controlling circumscission of the utricle in some hybrid genotypes. Thellung (1926) proposed the name *A. bouchoni* for similar plants which turned up as adventives in Europe, but he expressed uncertainty as to whether he was dealing with a new species or merely a form of ordinary *A. hybridus.* A heterogeneous lot of similar plants have been collected in many parts of the world. In the herbarium they mostly bear, perhaps properly, the name of some ordinary dehiscent species which they closely resemble.

Four of the five species which have joined forces in the delta area are natives of distant regions of America (Sauer, 1950). Only *A. powellii* appears to be native to the western United States. It is now mainly a weed of artificial habitats, but it is still found in what may have been its original habitat: naturally open sites along stream channels. It is conceivable that it was in the delta area in aboriginal times and has merely spread locally as the tule marshes were converted to modern farms.

The other species are probably late arrivals whose appearance in the delta country could hardly have antedated its opening to agricultural exploitation. The earliest attempt to reclaim any of this tule land for cultivation was evidently in the late 1850's (Hoag, 1872, p. 338), when a few farmers settled on Sherman Island, the southwestern extremity of present-day Sacramento County. The phenomenal productiveness of the fertile peat soil and California's Swampland Act of 1861 encouraged the reclamation of additional areas (Calif. Dept. Public Works, Div. Water Resources, 1931, p. 157). Results of early efforts were often temporary, however, and only about 15,000 acres had been reclaimed by 1870. During the next decade the area increased apace, and by 1880 a total of about 107,000 acres had been reclaimed. Reclamation continued at a fairly rapid pace to as late as 1920 (*op. cit.,* p. 158).

Other amaranth species have been found among the vegetable remains in old adobe bricks from the California mission period (Hendry and Bellue, 1925), and one of our species, *A. retroflexus,* was reported from 18th century bricks of Tumacacori Mission in Arizona (Hendry, 1931, p. 117). Other early reports of *A. retroflexus* and *A. hybridus* can be found in California botanical literature, but in the absence of contrary evidence from actual specimens such records may show nothing but taxonomic confusion. Early botanists were slow to recognize the western *A. powellii* as distinct from superficially similar eastern species, and in older herbarium determinations *A. powellii* usually masquerades as *A. retroflexus* or *A. hybridus.* In the 1890's *A. retroflexus, A. cruentus,* and *A. caudatus* begin to join *A. powellii* in the herbarium record from California; *A. hybridus* appears after 1900.

The backgrounds of these immigrants are diverse. *Amaranthus hybridus* probably originated in tropical America; it is now the commonest weed amaranth there and in the southeastern United States. Contrary to oft-repeated statements in taxonomic manuals, *A. retroflexus* is unknown in the tropics; it is a conspicuously successful weed in eastern Canada and the eastern United States, where it probably originated. Although centered much farther north, its range widely overlaps that of *A. hybridus*. *Amaranthus cruentus* and *A. caudatus* are cultigens, developed as grain crops by ancient Indian peoples of Central America and the Andes, respectively. *Amaranthus cruentus* was apparently derived from *A. hybridus, A. caudatus* from *A. quitensis* H.B.K., a species not known to be present in California. Both of these old Indian crop species have been widely distributed as ornamentals, often by commercial seed houses.

The introduction of these weedy and ornamental amaranths into California is in no way remarkable—all of them have immigrated into many parts of the world in modern times. Nor is the mere fact of hybridization between these species especially noteworthy. Two things do, however, impress us as being quite remarkable: firstly, the fact that the introduced ornamentals have not begotten just a few ephemeral escapes and abortive hybrids as is the rule elsewhere, but rather have made a spectacular contribution to successful weed populations. Secondly, despite their evident success in the delta country, these ornamentals and their hybrids have not spread beyond the area, but seem to be rather closely confined to it.

The two facts are in all probability closely interrelated. As with so many of man's vegetable creations, in the case of the two cultigens, *A. caudatus* and *A. cruentus,* selection has most likely been for rapid growth, large size, and high yield, *given* cultivation, *given* fertile soil, and *given* a moisture supply through the growing season. Whatever drought resistance their ancestors may have had, whatever ability to flourish under adverse soil conditions—most of this may well have been lost long since. As with the cultigen species, so with their hybrids in the delta region. Given a light and highly fertile organic soil,[2] a constant moisture supply, due to a high water table, and a long, warm growing season, these hybrids, by virtue of their more robust stature and often prodigious fecundity, can out-compete—as field weeds—their ruderal parents, *A. hybridus, A. powellii,* and *A. retroflexus.* However, the very circumstance of their ornamental parents' having evolved as cultigens is the undoing of the hybrids under conditions much less than optimal, keeping them from successfully invading areas that lack the highly organic soil, abundant moisture, and other favorable conditions which prevail in the delta.

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[2] After four years of experimental work on improving asparagus yields, G. C. Hanna (1939) had found no fertilizer which would improve yields on Ryer Island soils!

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THE GENUS ERYSIMUM (CRUCIFERAE) IN NORTH AMERICA NORTH OF MEXICO—A KEY TO THE SPECIES AND VARIETIES

GEORGE B. ROSSBACH

This key to twenty-three species and eight varieties of *Erysimum* is a result of detailed analysis of the specimens in various American herbaria plus collections of the writer from areas throughout most of the range of these taxa in the United States. Many morphological interrelationships exist among the various taxa, these usually manifesting themselves as local geographical forms which presumably have a genetical-ecological basis. Some of these forms are of sufficient magnitude to be treated as varietal entities. In a careful attempt to express much of this variability in the key, it frequently has been necessary to rely for identification upon a combination of many characteristics, to refer to exceptions and make cross-references, and to key three taxa twice. However, with understanding of the diagnostic characteristics and realization of the close relationships, the great majority of plants can be relegated to reasonably definite taxa. In order to present a survey of geographical distribution, a summary of the range of each taxon is added to the key.

Although the genus is native south through Mexico into Guatemala, taxa presumably limited to these countries are omitted due to insufficient representation. Thus at least two probably acceptable Mexican species,