

# Distribution of *Malacothrix* (Asteraceae) on the California Islands and the Origin of Endemic Insular Species

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## INTRODUCTION

*Malacothrix* DC. consists of approximately 20 species of annual and herbaceous perennial plants distributed in the western United States and Mexico, with disjunct populations of one species, *M. coulteri* Harv. and Gray, in Chile and Argentina. Ten taxa have been collected on the California Islands. Some of them are insular endemics and some also have a mainland distribution.

A study of the island *Malacothrix* was begun following a taxonomic revision of *M. clevelandii* Gray which resulted in the establishment of three new species, *M. stebbinsii*, *M. sonora*, and *M. similis* (Davis and Raven 1962). The latter species is a tetraploid with both mainland and insular distributions and it was speculated that other taxa of *Malacothrix* now endemic to the islands might have participated in its allopolyploid origin. In addition, there was disagreement in the literature concerning the taxonomic status and circumscription of most of the island endemics of *Malacothrix* (Williams 1957, Ferris 1960, Munz 1974). It seemed probable, therefore, that a thorough study of all of the insular *Malacothrix* would be a fruitful one and that a more stable taxonomy might result.

## CURRENTLY RECOGNIZED SPECIES ON THE ISLANDS

*Malacothrix clevelandii* Gray is an autogamous annual with a chromosome number of  $2n = 14$  and has been collected on Guadalupe of the Baja California Islands (see Thorne 1969 for a description of the island groups). It is also distributed on the mainland from northern Baja California to Tehama County in California. Closely related to *M. clevelandii*, and most certainly derived from it, is *M. similis* Davis and Raven, an autogamous annual. It is a tetraploid ( $2n = 28$ ) and has been collected on Todos Santos, Cedros, and Los Coronados of the Baja California Islands. It also occurs on the mainland in northwestern Baja California and perhaps in Ventura County, California. Specimens of *M. clevelandii* and *M. similis* from the islands fall within the range of variation found in populations of their respective species on the mainland and there is no evidence of adaptive radiation by either species on the islands. Dispersal over water is certainly the route by which *M. clevelandii* arrived on Guadalupe, but *M. similis* may have reached its island habitats via land connections to the mainland or by over-water dispersal.

*Malacothrix coulteri* var. *cognata* Jepson, an annual that is probably autogamous and diploid, has been collected on Santa Rosa and Santa Cruz of the Northern Channel Islands. It has been collected rarely on the mainland; there have been single collections recorded from Contra Costa, Kern, Los Angeles, and San Diego Counties in California. It differs from *M. c. coulteri*, which has a widespread mainland distribution, by its modally smaller achenes and by its dissected leaves. The two varieties are very similar in achene micromorphology (Fig. 1).

From the populations making up the white-flowered, self-incompatible, herbaceous perennial *Malacothrix*, which have a chromosome number of  $2n = 18$ , six species have been described: *M. arachnoidea* McGregor, *M. altissima* Greene, *M. commutata* T.&G., *M.*

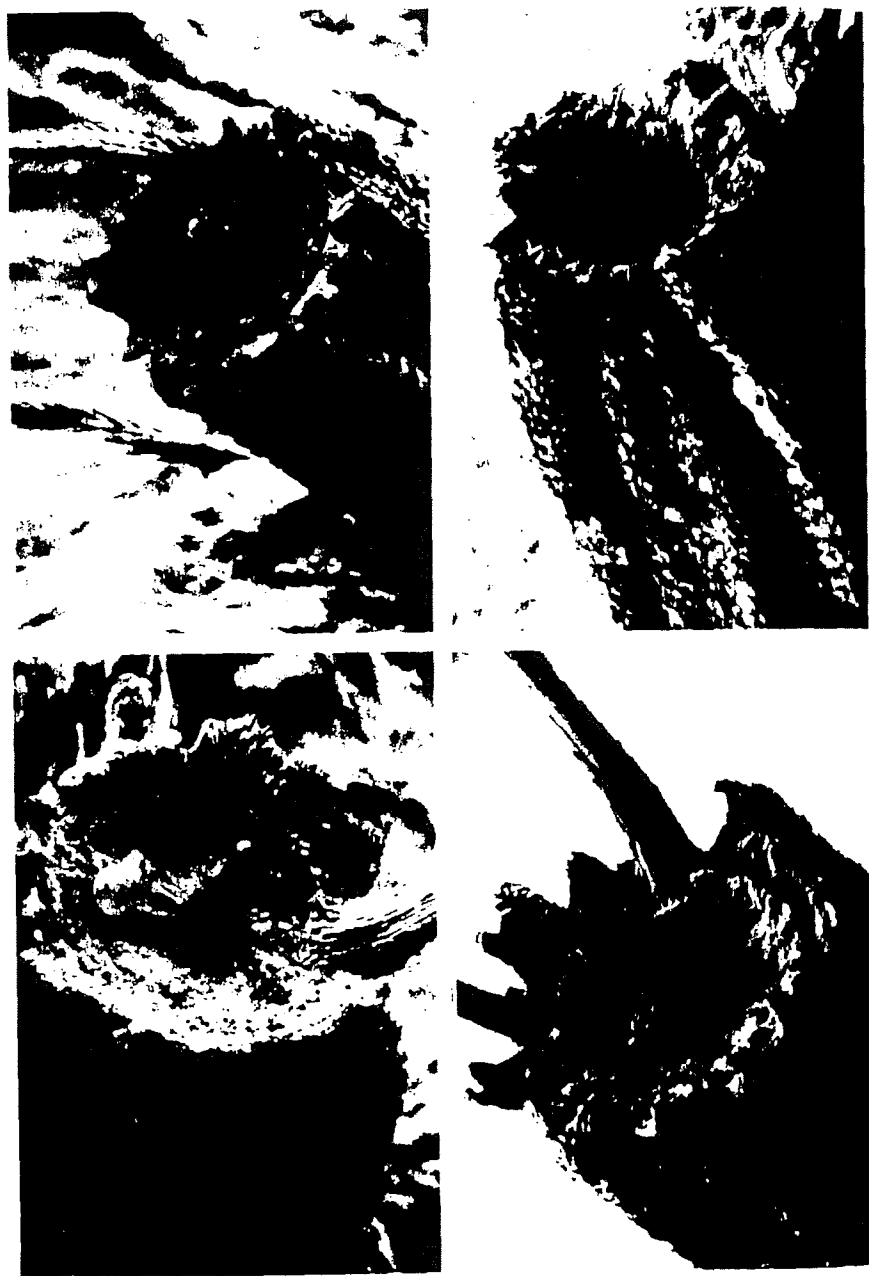


FIGURE 1. Scanning electron micrographs of the apical 0.3 mm of achenes of *M. insularis* (upper left); *M. squalida* (upper right); *M. coulteri* var. *cognata* (lower left); *M. coulteri* var. *coulteri* (lower right).

*saxatilis* (Nutt.) T.&G., *M. tenuifolia* (Nutt.) T.&G., and *M. implicata* Eastwood. The most recent treatments of *Malacothrix*, however, consider all of these as varieties of *M. saxatilis* (Williams 1957, Ferris 1960). Only two of the taxa have island distributions. *M. tenuifolia* has been collected on Santa Catalina Island and is distributed in mainland California as far north as Santa Barbara County, as far west as Riverside County, and as far south as San Diego County. *M. implicata* is restricted to the islands and has been collected on Anacapa, San Miguel, Santa Cruz, and Santa Rosa of the Northern Channel Islands, and on San Nicolas of the Southern Channel Islands. In the herbarium, *M. implicata* is easily distinguishable from all of the other perennial taxa but is closest to *M. tenuifolia* in overall morphology. *M. tenuifolia* is sometimes difficult to distinguish from *M. altissima*, *M. commutata*, and *M. saxatilis*. All four taxa occupy mainland habitats that are generally more xeric than the island habitats of *M. implicata* and, when all of the evidence is considered, it appears that *M. implicata* may be the most primitive of the group and that its island distribution is relictual.

The next two species, *M. insularis* Greene and *M. squalida* Greene, are obviously closely related and have been considered conspecific by some taxonomists (Williams 1957, Ferris 1960). Both are annuals and both are endemic to the California Islands. *M. insularis* has been collected at least four times on Los Coronados but there have been no recent collections. *M. squalida* has been collected on Santa Cruz Island (the type locality) and recently on Anacapa Island. On the basis of pollen size, both species are assumed to be polyploid and both are probably autogamous. Gray (1886) suggested that *M. insularis* was intermediate between *M. coulteri* and *M. incana*, an herbaceous perennial that will be discussed later. Evidence from my work supports a relationship of *M. insularis* and *M. squalida* to *M. coulteri*. The three species are similar in most aspects of leaf morphology, in their scarious-margined outer involucrel bracts, and in the presence of unbarbed receptacular bristles (many in *M. coulteri*, but fewer in *M. insularis* and *M. squalida*). Details of achene micromorphology also suggest that all three species are related but at the same time distinct (Fig. 1). The outer pappus of *M. insularis* and *M. squalida* is evenly dentate while that of *M. coulteri* is more dissected and ragged. As many as five long, persistent bristles are found as part of the outer pappus of *M. coulteri*, while *M. insularis* possesses only one bristle and *M. squalida* generally has none. In all three species the five most prominent ribs of the achene extend above the other, weaker, intermediate ribs at the apex, which is constricted only in *M. squalida*. The mean lengths of the achenes of the three taxa are: *M. coulteri*, 2.5 mm; *M. insularis*, 2.1 mm; and *M. squalida*, 1.7 mm.

The taxa that have been described to this point possess achenes with both an inner pappus and a well-developed outer pappus (as do all but one of the exclusively mainland species). The remaining insular taxa that will be considered in this paper have achenes that have only an inner pappus; they also share other characteristics that, in combination, distinguish them from most other species of *Malacothrix*. The formal taxa are: *M. incana* (Nutt.) T.&G., *M. foliosa* Gray, and *M. indecora* Greene.

*M. incana* is an herbaceous perennial that blooms at the end of its first year of growth. The single representative that I have grown in cultivation is self-compatible. *M. incana* has been collected on Santa Rosa, Santa Cruz, and San Miguel of the Northern Channel Islands, and on San Clemente of the Southern Channel Islands. The type collection is from "an island in the bay of San Diego" but, as far as I know, it has not been collected again from that region. On the mainland, its distribution is more to the north, and it is restricted to sand dune areas along the coast of California in the counties of San Luis Obispo and Santa Barbara.

*M. foliosa* is a self-incompatible annual that is endemic to the islands. It has been collected on Santa Barbara and San Clemente of the Southern Channel Islands, and on Los Coronados of the Baja California Islands.

The third species, *M. indecora*, is an annual island endemic that has been collected on San

Miguel and Santa Cruz (the type locality) of the Northern Channel Islands. Based on the size of the pollen, it is assumed to be a diploid and it is probably autogamous.

#### NEW TAXA AND THEIR RELATIONSHIPS

In the course of my studies of *M. incana*, *M. foliosa*, *M. indecora*, and specimens referred to the latter two species, living material has been obtained from the islands and representatives of various populations have been grown for the past several years in an environment room at the University of Louisville. In addition, conclusions regarding the distribution and taxonomy of the *foliosa*-related taxa have been influenced by a thorough study of herbarium specimens and by firsthand information regarding the appearance, relative blooming times, and habitats of some of the taxa as they occur on the islands (R. Philbrick and P. Raven, pers. comm.). I have concluded that there are at least three undescribed population groups on the islands that, although related closely to *M. foliosa* and *M. incana*, are sufficiently distinct to be given formal taxonomic status. A detailed taxonomic treatment of these taxa will be published elsewhere; the remainder of this paper will be confined to a brief description of the salient features within the groups.

The first entity is a self-incompatible annual from Santa Barbara Island which shall be referred to as Species A. The second, Species B, is an autogamous annual occurring on Anacapa Island. The third, Species C, is a self-compatible annual from San Nicolas Island. All three taxa share the following characteristics with *M. foliosa* and *M. incana*: (1) a chromosome number of  $2n = 14$  and chromosomes that are the smallest in *Malacothrix*; (2) achenes that have no outer pappus; (3) a bristleless receptacle; and (4) well-developed cauline leaves. Although the chromosome number of *M. indecora* is unknown, it shares the remainder of the characteristics with the others. On the basis of comparative studies of several sorts, I suggest the following: (1) that Species C from San Nicolas is closely related to, and has been derived rather recently from, *M. foliosa*; (2) that Species B from Anacapa has been derived from Species A; (3) that *M. indecora* is more closely related to Species A and B than to *M. foliosa* and Species C; and (4) that *M. incana* has been involved in the origin of Species A and perhaps Species B. Evidence on which these conclusions are based has come from comparative studies of flower color, leaf morphology, growth habit under uniform conditions, length of time from germination to flowering, and number of heads per plant.

In addition, scanning electron microscope studies have disclosed a number of useful aspects of achene micromorphology (Figs. 2 and 3). For example, the apex of the achene in Species C and *M. foliosa* has a flattened area within which the stumps of the inner pappus are situated. This characteristic is lacking in Species A, Species B, and *M. indecora*, which have, instead, a cup-shaped area at the achene apex which is deeper than that of the former two taxa. The achene of *M. incana* differs in several details from the achenes of the other taxa. The involucre of Species A, Species B, and *M. indecora* differ from those of Species C and *M. foliosa* (Fig. 4), and the involucre of *M. incana* is most similar to the A-B-*indecora* group. A close relationship among all the taxa is also suggested by the fact that fertile hybrids have been produced from the several possible pairs of *M. foliosa*, Species A, Species B, and Species C. In addition, fertile hybrids have been produced between *M. incana* and *M. foliosa*, and between *M. incana* and Species A. In general,  $F_1$  progeny have been self-compatible, even when both parents have been self-incompatible. When the perennial *M. incana* has been one of the parents, none of the  $F_1$  progeny has maintained the perennial habit. Intercrosses between  $F_1$  plants have produced some individuals with a perennial habit, and different levels of sterility have been found in the  $F_2$ . In nature, *M. foliosa* is isolated from Species B and Species C by its distribution, and from Species A and *M. incana* by differences in flowering time.

The present distribution of *M. foliosa* on three widely separated islands whose geologic pasts

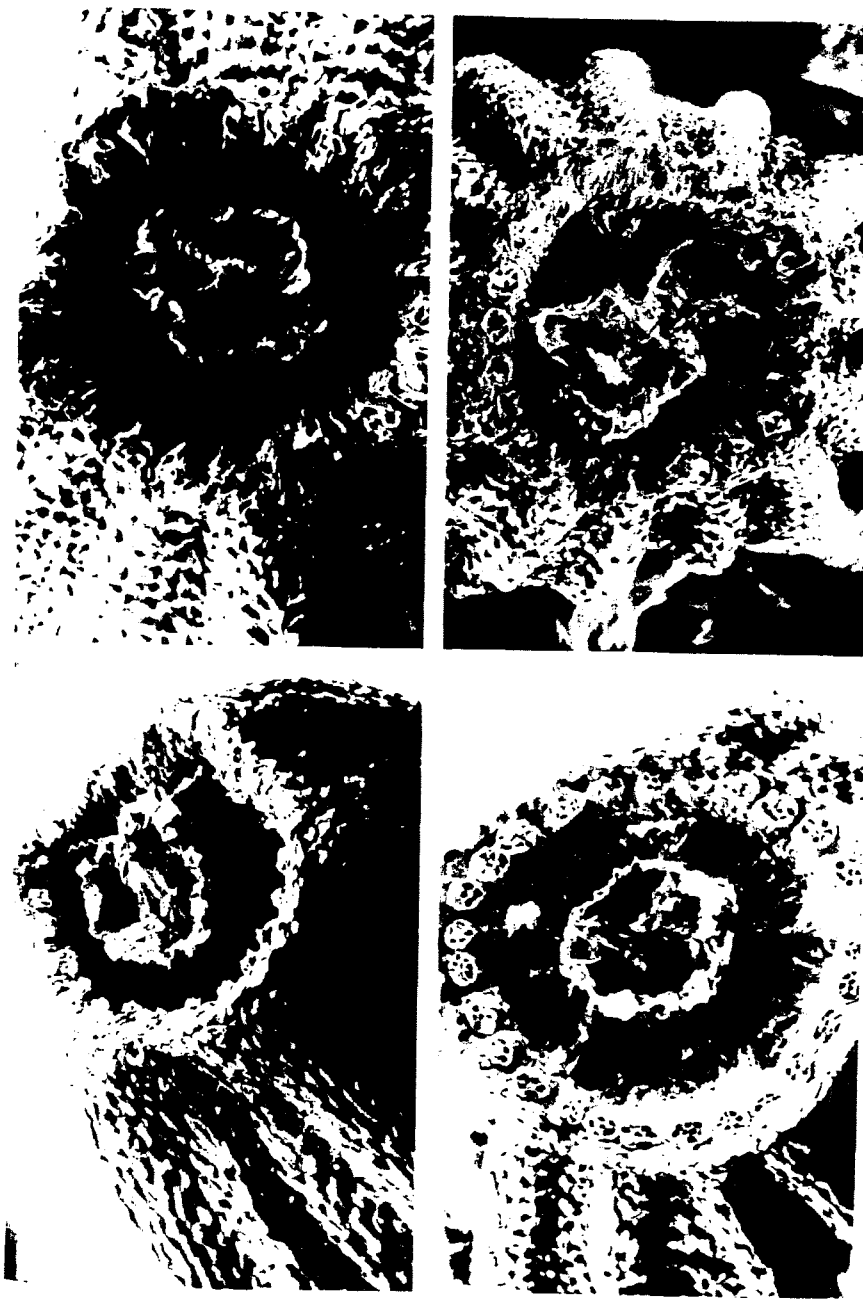


FIGURE 2. Scanning electron micrographs showing a polar view of the achenes of Species B (upper left); *M. foliosa* (upper right); Species A (lower left); Species C (lower right).

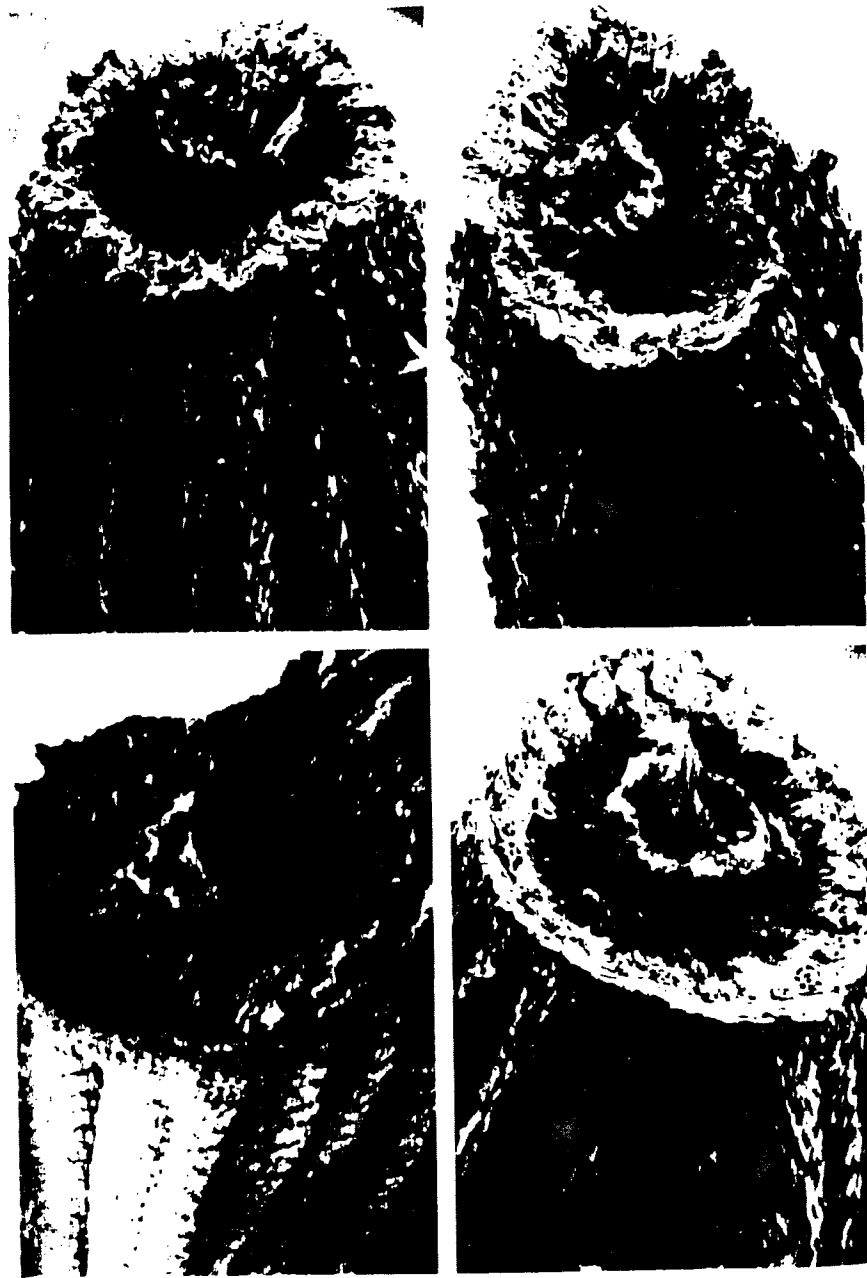


FIGURE 3. Scanning electron micrographs of the apical 0.3 mm of the achenes of Species B (upper left); *M. indecora* (upper right); *M. incana* (lower left); Species C (lower right). The magnification of *M. incana* is half that of the others.

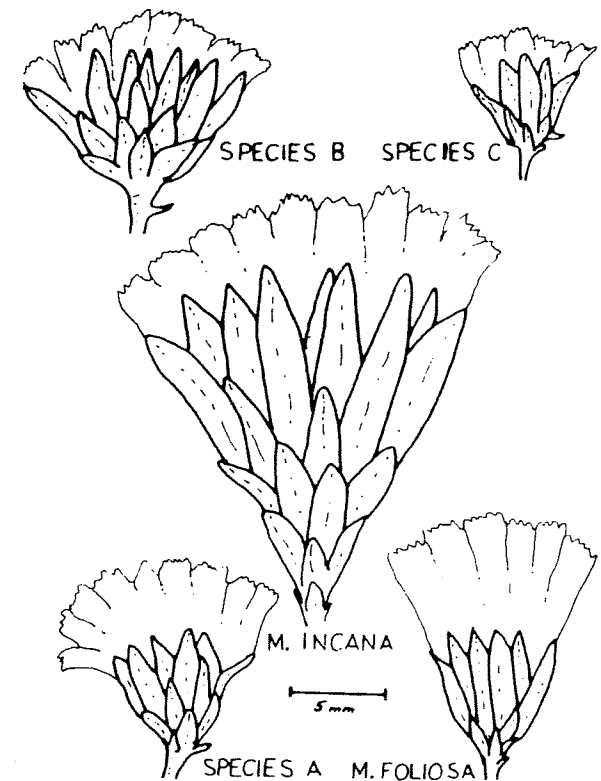


FIGURE 4. Camera lucida drawings of typical pressed flower heads of *Malacothrix*.

are apparently different suggests that it was once a mainland species and that its present island distribution is relictual. The restricted distributions of Species B and Species C and their probable derivative origin from the self-incompatible taxa suggest that they are autochthonous endemics.

#### SUMMARY

With the exception of four of the eight Baja California Islands, at least one representative of *Malacothrix* is found on all of the California Islands. Six taxa occur on the Northern Channel Islands, six occur on the Southern Channel Islands, and four are found on the Baja California Islands. Two taxa, *M. implicata* and *M. incana*, are found on the major islands of the Northern Channel Islands and on different single islands of the Southern Channel Islands. *M. foliosa* has been collected from two of the Southern Channel Islands and one of the Baja California Islands. So far as the insular distribution of *Malacothrix* is concerned, Los Coronados appear to be the most important of the Baja California Islands, with three species occurring there.

Of the thirteen taxa now documented on the islands, five are known to be self-compatible and four others are assumed to be on the basis of floral morphology. Of the four self-incompatible taxa, two are perennials and two are annuals.

Nine of the thirteen taxa are either strictly insular or primarily insular: *M. foliosa*, *M. implicata*, *M. incana*, *M. indecora*, *M. insularis*, *M. squalida*, Species A, Species B, and

Species C. The distributions of *M. tenuifolia*, *M. similis*, *M. clevelandii*, and *M. coulteri* var. *cognata* are primarily on the mainland. Where taxa have both an island distribution and a mainland distribution, the latter is now well to the north of the former.

The pattern of variation in insular endemics related to *M. foliosa*, *M. indecora*, and *M. incana* is a complex one but some progress has been made by the recognition of three reasonably coherent formal groups. Hybridization may have played a role in the origin of these new taxa, and a shift from self-incompatibility to self-compatibility has accompanied the origin of at least two of them.

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