CYTOGEOGRAPHY AND TAXONOMY
OF THE PORTULACA OLERACEA L. POLYPLOID COMPLEX

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ABSTRACT
Nine subspecies in the polyploid series of Portulaca oleracea L. have been studied including seven that are described here for the first time. Seed size and seed coat cell morphology were used as the main diagnostic characters. Distribution of diploid, tetraploid and hexaploid subspecies shows that one of the centres of diversity of the species is in Mexico. In Australia there is a high diversity of forms which differ from those in all the other parts of the world. The subspecies have rather distinct areas of distribution which may indicate their specialization to certain climatic and edaphic conditions. The New World diploid grows mainly as a halophyte in coastal areas. The other subspecies grow frequently as weeds. The New World diploid is restricted to low latitudes and altitudes, the tetraploids are found in the widest range of latitudes and altitudes and the hexaploids are found mainly in high latitudes and altitudes.

Portulaca oleracea L. is a cosmopolitan weed whose place of origin is doubtful. De Candolle (1883) stated that “Purslane is one of the kitchen garden plants most widely diffused throughout the world from earliest time and introduced to America”. He described its origin in Europe and Asia by a vague statement “that it is difficult not to admit that the plant is indigenous in that central region”. In reviewing the French version of De Candolle’s book, Gray and Trumbull (1883) pointed out that it was already in the New World when Columbus arrived in Cuba on October 28, 1492. However, Muensch (1955), Parker (1972), Gaines and Swan (1972) and Smith (1976) continue to quote De Candolle’s statement that P. oleracea is of Eurasian origin; Thellung (1912) wrote that it is of ancient naturalization in Europe (including France) and should not be considered as an adventive. Walters (1964) stated that “its native range (is) unknown”. In fact P. oleracea was found in Roman and Pre-Columbian archaeological sites on both

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sides of the Atlantic respectively (Knörrer, 1970; Chapman, Stewart & Yarnel, 1974; Byrne & McAndrews, 1975).

Four ploidy levels are reported in the literature for P. oleracea: diploid (2n = 18) from Timbuktu, Mali (West Africa) (Hagerup, 1932); tetraploid (2n = 36) from northern India (Khullar and Dutta, 1973) and hexaploid (2n = 54) from many localities in North America, Europe, Africa and northern India (Hagerup, 1932; Cooper, 1935; Steiner, 1944; Heiser and Whitaker, 1948; Mul- ligan, 1961; Walters, 1964; Bouharmont, 1965; Khullar and Dutta, 1973); pentaploid was reported by Sharma and Bhattacharyya (1956). Hence, P. oleracea seems to be a polyploid complex.

The aim of the present research was to study the relation between the cytotypes and morphological characters and geography. An attempt was made to evaluate the evolutionary significance and the distribution of the subspecies described.

MATERIAL AND METHODS

We studied the number of chromosomes in plants grown from seeds collected in Nicaragua, Guatemala, California, Hawaii and Israel (Table 1). For chromosome counts, root and shoot apices of seedlings were pretreated with colchicine or paradichlorobenzene. The former gave more contracted chromosomes and hence clearer plates. Fixation was made in 3:1 ethanol and acetic acid and followed by hydrolysis in concentrated HCl: absolute alcohol (1:1 v/v) for 8 min; aceto-carmine was used for staining.

Seeds were examined with a dissecting microscope under diffuse light, and with a scanning electron microscope (SEM). Figures 22 and 30 were taken with a Coats and Wel ters SEM after vacuum drying and sputter coating with a platinum/palladium electrode at the University of California, Berkeley. All the other plates were taken with a Cambridge Stereoscan S4-10 SEM after vacuum drying and gold covering, at the Hebrew University of Jerusalem. Photographs were taken at approximately 100 ×, 300 ×, and, in a few samples, at 1000 ×.

The mean sizes of seeds were calculated from the measurements of 20 to 50 seeds for each population. The mean weights of 100 seeds are based on seven determinations, each of 100 seeds. After studying the distribution and diagnostic value of seed size and sculpture in living populations, nearly 1200 herbarium specimens were studied (cf. listing in the acknowledgements). The determination of seed type was made by inspecting ca. 20 seeds in each specimen. An additional seven living populations were studied after the herbarium survey to confirm the previous findings. Cross checking of living and dried material was possible in 6 of the 9 subspecies.

THE POSITION OF PORTULACA OLERACEA IN THE GENUS

The most recent review of the genus Portulaca after that of von Poellnitz (1934) was published by Geesink (1969) concerning the Indo-Australian species. He placed P. oleracea in section Portulaca, subsection Portulaca together with P. lutea Solander ex Forst., which is a perennial, robust plant. He did not accept P. fosbergii Poelln. as a separate species, but considered it as synonymous with P. oleracea. We did not compare our material with that of P. fosbergii. The lumping
<table>
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<th>Locality</th>
<th>Habitat</th>
<th>No. of Chromosomes*</th>
<th>Seed length</th>
<th>Seed width**</th>
<th>Seed Weight***</th>
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<td>sodic soil</td>
<td>18</td>
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<td>6. Hawaii, Kauai</td>
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* Number of chromosome in somatic cells (in number 3 PMC had n = 18).
** 20–50 measurements were made for each population; standard deviations ranged from 0.03 to 0.06 mm.
*** Mean weight based on seven determinations each of 100 seeds.
approach of Geesink (1969) was not approved by Fosberg (1977). Fosberg (pers. comm.) found hybrids between P. oleracea and P. lutea in which unfortunately neither seed morphology nor cytology was studied.

TAXONOMIC TREATMENT IN THE POLYPLOID COMPLEX OF P. OLERACEA

The taxonomy of a polyploid complex is rather difficult when morphological differences between the components are slight. The subject has been reviewed by Löve (1951) and discussed by Davis and Heywood (1963). Several botanists have separated polyploid races at a specific level, for example Nannfeldt (1938). This view was also adopted by Davis and Heywood (1963). Conversely, races of Veronica prostrata L. which differ in their ploidy level were recognized as subspecies by Brandt (1961). Our cytotypes are large geographically distinct entities which differ in their ecology, distribution and seed coat characters; we decided to regard them as subspecies. The possibility of gene flow between taxa of the same ploidy level and between taxa of different levels is not known yet in P. oleracea. If, in future, experimental genetic studies are carried out, the taxonomic status of our taxa may change. Following the description of the taxa we shall discuss the complications involved in taxonomic ranking of our taxa.

MORPHOLOGICAL AND SYSTEMATIC NOTES

Seed: Seed coat characters were used by von Poellnitz (1934) to divide the sections of Portulaca into subsections. Kowal (1961), who studied seed characters of the Portulacaceae, recognized two taxa in the P. oleracea complex. Relying on seed size, he regarded those 1–1.5 mm in diameter as belonging to P. sativa Haw. and those 0.6–1.0 mm to P. oleracea L. Both of these taxa were recognized by Thellung (1912), Walters (1964), Coode (1967) and others as subspecies of P. oleracea. Kowal (1961) found in each of these two taxa two units based on seed coat characters: “linea typica”, with tuberculate seeds, and “linea stellata” with stellulate seeds. He suggested that the two seed types could be found on one individual plant. This was not confirmed in our observations on several populations of other subspecies. Geesink (1969), who divided P. pilosa L. into eight subspecies, each with typical seed coat characters, overlooked the different sculpture and size types in P. oleracea and lumped the forms there into one taxon.

In this study the long and short diameters of the elliptic seed were measured as marked in Fig. 1. The mean length and width of seeds in populations which were studied cytologically are presented in Table 1. Another parameter used there is the weight of 100 seeds. Seed size and weight give a good correlation (Fig. 2). Therefore, measuring seed size in herbarium specimens was sufficient. In Fig. 2 the tetraploid and diploid populations form a group of points separate from that of the hexaploids. A test of the differences between 11 populations of tetraploids and six of hexaploids in mean values of seed length, width and weight, displayed
significant statistical differences ($p = 0.001$). Therefore we regarded populations with mean seed lengths greater than 0.85 mm to be hexaploids. Those populations with mean seed length less than 0.85 mm were regarded as tetraploids or diploids. So far our data on seed size distribution in diploid populations are insufficient. Most specimens of *Portulaca oleracea* we have seen from Europe have large seeds. Walters' (1964) record of *P. oleracea* in Europe as a hexaploid ($2n = 54$) is in agreement with our finding.

In this study we investigated the seed coat characters, particularly on the lateral faces of the seed. Except for one rare form, the sculpture of the periphery (5 in Fig. 1) differs from that of the lateral faces. Three main elements of structure can be seen in the seed coat: stellulae (3 in Fig. 1), papillae (4 in Fig. 1) and tubercles (which are larger structures than the papillae). The structures which are described here were observed with a light dissecting microscope ($\times 20$ to $\times 40$) and with SEM. For the convenience of the taxonomist who does not have access to SEM, we shall use mainly those characters which can be seen also with a light dissecting microscope. Differences in shape of the stellulae, which are epidermal cells of the seed coat, are the most useful diagnostic character; they vary in shape from blunt and irregular, with the central part of each cell more prominent than the arms
(Fig. 3), to those with very sinuous anticlinal walls forming well developed arms (3 in Fig. 1). The ratio of length to width of the arms varies from low (Fig. 4) to high (Fig. 29). Surfaces of stellulæ and papillae vary from very shiny through shiny to dull or matt. The papillæ, if developed, occur among the stellulæ, on their arms and obscure the shape of the stellulæ. The tubercles, if developed, occur above the central part of the stellula. In some cases (Figs. 18 & 26) the tubercles are so prominent compared with the stellulæ arms, that the latter appear as parallel lines in the “valleys” between the steep “mountain-like” tubercles.

The capsule is circumsessile. The campanulate capsule-оперкум falls when ripe together with the calyx, dried petals, stamens and styles (together called the “calyptra”). Most seeds are discharged gradually from the opened capsules. At the top of the capsule there is a nipple-like projection containing seeds which are retained in the calyptra (synapotspermic seeds, cf. van der Pijl, 1972). Conditions for dispersal and germination of these seeds are different from those of the regular seeds; for germination water has to penetrate not only the seed coat but the calyptra as well. The number of seeds in this nipple differs significantly between populations. The results of tests of significance of variations in this character are presented in Table II and are discussed in detail under each subspecies. The mean number of seeds in the fruit varies from 13 in a population of a hexaploid race, to 70 in a population of a tetraploid.

Stamens and styles vary in number from 15–25 in the chasmogamous flowers in the tropics to 5–7 in the cleistogamous flowers in temperate latitudes.

Petals can hardly serve as a diagnostic character as they may vary during the life of the same individual plant from small in the completely cleistogamous to larger in the partially cleistogamous and to largest in the chasmogamous flowers. Some populations, such as the one in Guatemala and the tetraploid and hexaploid in Berkeley, had only cleistogamous flowers.
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TABLE II
MEAN NUMBER OF SEEDS IN THE OPERCULUM OF FRUIT IN SEVERAL POPULATIONS OF Portulaca oleracea AND "t" TEST RESULTS OF SIGNIFICANCE OF THE DIFFERENCE BETWEEN THE POPULATIONS
Population numbers as in Table I: 1. subsp. nicaraguensis; 2-9. subsp. granulato-stellulata; 11. subsp. nitida; 13-16. subsp. papillato-stellulata; 17. subsp. oleracea
In brackets — degrees of freedom; * = p < 0.001, ** = p = 0.002-0.03; without an asterisk = not significant
Figs. 3–5. Scanning electron micrographs of seeds of *Portulaca oleracea* subsp. *nicaraguensis*, waxy seeds. From La Calera, Nicaragua (1 in Table I).

*Sepal* structure could not serve as a diagnostic character in differentiation of subspecific taxa for, being succulent, the sepals lose much of their basic morphology when dried.

*Leaves* and *habit* change considerably from population to population and also with environmental conditions. Under cold and drought stresses small leaves may develop. We could not evaluate the few varieties which were based on leaf characters and mentioned by von Poellnitz (1934) from Europe. The habit of the plant seems to vary according to light intensity. The prostrate plants in Nicaragua gave rise to ascending offspring in the greenhouse, probably due to a lower light intensity. There is no statistical difference in the size of stomata between the studied populations.
Pigmentation differences seem to provide good characters to differentiate subspecies when they grow sympatrically. The red pigments which tinge various parts of the plant above the root (including the hypocotyl) are betacyanins (Gibbs, 1974). Some subspecies have tinged calyx and leaf margins while others do not have it. The stems may be red in some subspecies and green in others. Pigmentation of the stems is linked with seed characters at least in five of the nine subspecies described below.

In this study subspecies were differentiated according to seed size and morphology of seed coat following von Poellnitz (1934), Kowal (1961) and Fosberg (1977). For a general description of *P. oleracea* see Fosberg (1977).

**ARTIFICIAL KEY TO THE SUBSPECIES**

1. Seeds blueish, covered with wax; large blunt stellulae radially elongated; arms short (Figs. 3-5).
   1. subsp. *nicaraguensis*

1. Seeds not covered with wax.
2. Seed surface dull, at least some seeds have metallic sheen; white dots visible at magnification of ×100 to ×1000 (Figs. 22-25).
   6. subsp. *impolita*
3. Seed surface shiny to varying extents but not dull or with metallic sheen; no white dots visible.
4. Lateral faces of seeds with tubercles.
5. Seed coat with tubercles, without papillae; flat stellulae in center; surface prominently shiny in center (Figs. 9 & 10).
   2. subsp. *africana*

6. Seed coat with tubercles and papillae; flat stellulae in the center; surface not shiny.
7. Tubercle elliptic in outline in the 1–2 peripheral rows (Figs. 18 & 19).
6. subsp. *tuberculata*

8. Tubercles irregularly shaped throughout the lateral seed faces (Figs. 16 & 17).
3. subsp. *granulato-stellulata*

4. Lateral faces of seeds without tubercles.
7. Lateral faces of seeds with flat stellulae, surface prominently shiny (Figs. 20 & 21).
5. subsp. *nitida*

8. Lateral faces of seeds with papillae in addition to stellulae.
9. Seeds black with long-armed stellulae and papillae or papillae only; tops of the highest structure somewhat shiny (Figs. 1, 11-14).
3. subsp. *granulato-stellulata*
8. Seeds brown with very short-armed stellulae and papillae among them; tops of highest structures very shiny (Figs. 6-8).
1. subsp. *nicaraguensis*

3. Seed length more than 0.85 mm.
4. Seed coat with flat stellulae only; surface shiny (Figs. 28 & 29).
8. subsp. *stellata*
5. Seed coat with papillae or tubercles; surface not shiny.
6. Only large, regular tubercles observable on seed coat; sometimes also papillae present (Figs. 26 & 27).
7. subsp. *oleracea*
10. Stellulae and papillae observable on seed coat; sometimes large, irregular, elliptic or angular (but not circular) tubercles are found (Figs. 30 & 31).
9. subsp. *papillato-stellulata*

Cultivated taxa and several rare forms of seeds from one or two localities will be discussed after the listing of the nine common subspecies.
Figs. 6–8. Scanning electron micrographs of seeds of *Portulaca oleracea* subsp. *nicaraguensis* non-waxy seeds. From La Calera, Nicaragua (1 in Table I).

**ENUMERATION**


The type subspecies is a hexaploid and will be discussed later as we list the subspecies in an increasing level of ploidy.

1. **P. oleracea** L. subsp. *nicaraguensis* Danin & H.G. Baker subsp. nov. (Figs. 3–8).

A typo differt seminibus minoribus, 0.6–0.75 mm diam., glaucis vel nitido-brunneis, stellulorum marginibus paucis sinuatis.

TYPE: Nicaragua, La Calera, 5 km northeast of El Mercedes (Managua Airport), new roadside at the edge of swamp with sodic soil. Seed collected

Figures 3–5 — waxy seeds, and 6–8 — non-waxy seeds.

CHROMOSOME NUMBER: 2n = 18. Waxy and non-waxy seeds from populations from the type locality were used for chromosome countings. (Vouchers in UC.)


Seeds are usually covered with waxy material which gives them a blueish appearance. However, in some population, individuals without wax on their seeds may occur. Also, there are specimens such as that from Belize, mentioned above, where only half of the seed is covered with wax. The seed coat structure of the non-waxy seeds is similar to that of the waxy seeds; the blunt stellulae and the papillae which may develop among them have very shiny tops. In all the 100 herbarium specimens seen, there were at least several blueish seeds or seeds with blue spots. Plants developing from waxy or non-waxy seeds from Nicaragua gave rise to the same seed type as the parent. As the two seed types are found together in most cases and rare transitions between them occur, they were regarded as belonging to the same subspecies.

DISTRIBUTION (Fig. 15a): Mainly around the Gulf of Mexico, the Bahamas and West Indies. Partly overlaps with the area of P. oleracea subsp. granulato-stellulata (Figs. 15a & b) which has much larger area.

BIOLOGY: When raised in a greenhouse in Berkeley, all the flowers were chastemogamous with large prominent petals and set seeds by self-fertilization.

The mean number of seeds in the calyptra of this subspecies (4.13) is the highest in the species (Table II) and differs significantly from all the other subspecies.

2. P. oleracea L. subsp. africana Danin & H.G. Baker subsp. nov. (Figs. 9 & 10).

A typo different seminibus minoribus 0.6–0.75 mm diam., nitentibus testae cellulis centralibus planis peripheralibus unituberculatis.

TYPE: Sudan Francais (Mali): Timbuktu, dry sand, 14.VII.1927, Hagerup 262 (K, holotype).

CHROMOSOME NUMBER: 2n = 18 (Hagerup, 1932).

Of the two specimens of Hagerup's collection one was reported by him as a diploid whereas the other one was a hexaploid. By comparing the similarity between the specimen photographed in Hagerup's article and the specimen in the Herbarium of Kew, we concluded that the type of P. oleracea subsp. africana is
Hagerup's diploid. The second specimen, which is similar to Hagerup's hexaploid, did not have any seeds.


The diagnostic characters of the seed coat of subsp. *africana* are the prominently shiny faces and the testa cell morphology of the lateral faces. The two peripheral rows of cells have a tubercle at the centre of each, whereas the central ones are flat. No papillae are developed on the seed surfaces.

**Distribution:** see Fig. 28.


**Type:** Described from the Hawaiian Islands: Molokai (n.v.).

**Chromosome Number:** 2n = 36; populations from California: Berkeley and Stanford University; Guatemala: Antigua; Nicaragua: La Calera, 5 km northeast of Managua Airport; Nagarete, 35 km northwest of Managua; Malacatoya, 40 km east of Managua; Hawaii: Kauai (Fosberg 57447, US); Israel: ‘En Gedi (vouchers in UC).


**Seed Structure:** The diagnostic character which was used by von Poellnitz to differentiate this taxon was the shape of stellulae and papillae of the seed coat. In populations of this subspecies from La Calera and Nagarete in Nicaragua, seed coat characters vary from stellate with papillae at the ends of the arms (Figs. 11 & 12), through stellulae with papillae among them (Figs. 1, 13 & 14),

Figs. 9 & 10. Scanning electron micrographs of seeds of *Portulaca oleracea* subsp. *africana*; seed from the type specimen, Timbuktu, Mali, Hagerup 262 (K).

Figs. 11–14. Scanning electron micrographs of seeds of *Portulaca oleracea* subsp. *granulato-stellulata*; seeds from La Calera, Nicaragua (2 in Table 1).
Fig. 15. Distribution maps of subspecies of *Portulaca oleracea*

15a. ▲ subsp. *nicaraguensis*; □ subsp. *ittida*; ● subsp. *impollta*.
15c. ▲ subsp. *oleracea*; □ subsp. *stellata*; ● subsp. *papillato-stellulata*.

Partly developed stellulae (which look like irregular tubercles) (Figs. 16 & 17), to hapillae only. Because these forms intergrade, we included all the forms with small
black seeds with papillae and larger irregular elements of structure derived from stellulæae, in one subspecies.

An unusual seed structure is that of plants from several of the Galapagos Islands. The cells of the first peripheral row have irregular tubercles above their stellulæae. This was seen in plants from the following islands: Española, Albemarle, Chatham, Indefatigable, Charles, Garden and Santa Cruz. Seeds of plants from few of the other Galapagos Islands, such as Hood and Narborough, have the typical flat stellulæae and papillae. Further research is needed to reveal the relation of this peculiar form from the Galapagos Islands to the other forms of subsp. granulato-stellulata. Though this form resembles subsp. africana, the latter differs from it by the shiny surface and absence of papillae.

**Pigmentation:** When growing sympatrically with the hexaploid subsp. papillato-stellulata in Stanford University, the absence of red pigments from the sepals of subsp. granulato-stellulata served as an efficient diagnostic character, though the two subspecies have rather similar seed coat characters. Similarly, when the two tetraploids—subsp. granulato-stellulata and subsp. nitida inhabited together a roadside in Berkeley, the former had leaves with red margins, whereas the latter had green leaves with no pigmentation. Red margins of leaves were observed in 11 populations of subsp. granulato-stellulata from: Nicaragua, Hawaii, California, Israel and Nigeria (Hepper 1085 cited above).

**Distribution** (Fig. 15b): This is the most common subspecies of *P. oleracea*. It is found between the latitudes of 50°N and 40°S (as represented in the herbarium specimens which were available to us).
BIOLOGY: The variability among populations of this subspecies is rather high. The number of seeds in the calyptra shows a significant difference between 10 of the 15 possible pairs of our six populations (Table III). The least difference was found between the Guatemalan population and that of Berkeley.
Populations differ also in the extent of chasmogamy: in the population of La Calera, Nicaragua, the first flowers were cleistogamous and all the rest chasmogamous; the population of Nagarote, Nicaragua, had mostly cleistogamous and a few chasmogamous flowers; the two populations from Guatemala and Berkeley, mentioned above, are completely cleistogamous.

Although the variability in biology of the few populations that we raised together was very high, we found it impossible to split this widespread subspecies into more uniform units.

(Figs. 18 & 19)

A typo differt seminibus minoribus, 0.5–0.75 mm diam. sed testis similaribus tuberculato-papillatis.

**Type:** Peru: Dept. Loreto, Mishuyacu near Iquitos, alt. 100 m, IV.1940, Klug 1214 (US, holotype).

**Chromosome Number:** unknown.


This subspecies seems rather similar in seed coat characters to the hexaploid subsp. *oleracea*. However, it has small seeds (length 0.55–0.75 mm), a size that was found in several diploid and tetraploid subspecies. Seeds of subsp. *tuberculata* have tubercles which are circular to oblong-ovate in cross section. The anticlinal walls of the cells with tubercles are very undulating, with narrow arms forming dense parallel lines among the tubercles. These lines are prominent in the tangential direction. They differ from those of subsp. *granulato-stellulata* by the irregularity of tubercles in the latter (if they are present).

**Distribution:** see Fig. 15b.

Most specimens of *P. oleracea*, which were collected from the catchment of the Amazon River in Peru, Colombia and Brazil, are of this subspecies.

5. **Portulaca oleracea** L. subsp. **nitida** Danin & H.G. Baker subsp. nov.  
(Figs. 20 & 21)

Subspecies seminibus minoribus, 0.65–0.85 mm diam. nitentibus testae cellulis stellulatis.

**Type:** North Carolina, Henderson County, shallow soil on granite outcrop 29.VIII.1940, McVaugh 5418 (UC, holotype).

**Chromosome Number:** 2n = 36; populations from California: Berkeley (voucher UC) and from Israel: Hadera (voucher HUJ).

Fosberg (1977) believed this subspecies to be the typical Linnaean variety of *P. oleracea* when he determined specimens from Aldabra, in the Indian Ocean. It does not agree with the type subspecies of *Portulaca oleracea* as described later on.

The relation of subsp. nitida to var. delicatula Fosberg from Aldabra Island (holo US! iso MO!), needs further investigation. The latter, which is endemic to the restricted type locality, has very delicate stems and leaves which were not observed in any of the specimens of subsp. nitida. The ploidy level of var. delicatula should be determined as well.

SEED STRUCTURE: Seed structure in this subspecies is rather constant as regards the lateral faces. They have only compactly interdigitate flat stellulae and shiny surface. The stellulae vary from isodiametric to radially elongated. There are populations where tubercles are present at the seed periphery; other populations do not have these tubercles. Both forms are present in the type collection.

In Wilmington, Delaware, a population with tuberculate seeds (as in Fig. 20) had red leaf margin whereas a neighbouring population with no such tubercles had green leaves. Populations of both seed forms from Englewood, New Jersey, as well as New York City and from several localities in Israel did not show such pigmentation. We may conclude that no linkage exists between tuberculate seeds and leaf pigmentation in subsp. nitida.

DISTRIBUTION (Fig. 15a): This subspecies was represented in the herbarium specimens studied by us in North America north of 25°N and south of 50°N but not from the central part of the U.S. If subsp. nitida is really absent from the central states of the U.S. it seems rather a peculiar pattern of distribution. Recent invasions of subsp. nitida to Great Britain and to Israel are discussed later on.

6. Portulaca oleracea L. subsp. impolita Danin & H.G. Baker subsp. nov. (Figs. 22–25)

Subspecies seminibus stellulato-papillatis stellularum superficie impolita grisea plerumque nitore metallico praedita.

TYPE: Texas: Hartley Co., in sandy soil along Punta de Agua Creek, between Romero and Middle Water, 9.X.1964, Correll 30330 (UC, holotype; GH, isotype).

CHROMOSOME NUMBER: unknown; seed size varies from that of the tetraploid to that of the hexaploid.

In this subspecies, the seed sculpture is similar to that of subsp. granulatostellulata, but the stellulae have more regularly arranged arms. The seed surface appears matt and greyish, especially at the surface of the stellulae. This is due to small white spots which are observable at magnifications of more than $\times 100$ (Figs. 24 & 25). A unique character of this subspecies is the perforation along the sutures between the epidermal cells, especially at the tips of the stellulae rays (Figs. 24 & 25). In each population there are at least some seeds with a metallic sheen. Seed characters vary considerably in the herbarium specimens of this subspecies and may represent segregation or a hybrid swarm: the specimens from the New York Mountains, California, and from Magdalena Bay, Baja California, have small seeds as well as large ones; stellulae vary from isodiametric to radially elongated, from convex to pyramidal and tuberculate (Figs. 2, 24 & 25). Some seeds resemble much those of Portulaca pilosa ssp. pilosa “race” pilosa as described by Geesink (1969).

DISTRIBUTION (Fig. 15a): subsp. impolita has, so far as is known, a narrow range of distribution as compared to the other subspecies. Except for sandy habitats where it was collected, it is hard to figure any similarity in other environmental conditions between Baja California and high elevations of the central and southern United States.

7. Portulaca oleracea L. subsp. oleracea

Linnaeus’s diagnosis (phrase-name) “Portulaca foliis cuneiformibus, floribus sessilibus” in the Species Plantarum 1: 445 (1753) is not one specially drafted for that work. It was taken from Adrian van Royen’s Flora Leydenensis Prodromus 473 (1740) which was prepared with Linnaeus’ help during his stay in Holland. That diagnosis is, however, only a slightly abbreviated version of his earlier diagnosis Portulaca foliis cuneiformibus verticillatis sessilibus, floribus sessilibus in the Hortus Cliffortianus 207 (1738), i.e. with no information added. Hence the lectotype should be chosen from the Hortus Siccus Cliffortianus material in the British Museum (Natural History!).

CHROMOSOME NUMBER: $2n = 54$; populations from California: Berkeley (voucher in UC) and Israel: Jerusalem (seeds in HUJ).

Figs. 26–27. Scanning electron micrographs of seeds of *Portulaca oleracea* subsp. *oleracea*; seeds from She‘ar Yashuv, Israel, 16.VII.1978, Danin (HUJ).

Figs. 28–29. Scanning electron micrographs of seeds of *Portulaca oleracea* subsp. *stellata*; seeds from Coer D’Alene Lake, Idaho, Lelberg 1545 (UC).


**Distribution (Fig. 15c):** It is the most common subspecies in Europe and Asia growing mainly as a weed and in disturbed habitats, in summer (Zohary, 1973). It is not represented as frequently in the material we have seen from North America.
8. Portulaca oleracea L. subsp. stellata Danin & Baker subsp. nov.  
(Figs. 28 & 29).

A typo differt testis nitentibus cellulis stellulates (non tuberculates).  
TYPE: Idaho: Coer D'Alene Lake, 640 m, Leiberg 1545 (UC holotype; GH,  
MO, NY, US isotype).  
CHROMOSOME NUMBER: 2n = 54; Mulligan (1961) counted a population from  
Ottawa (Voucher Mulligan 1250! DAO).

SELECTED SPECIMENS (34 examined): Canada: British Columbia, Landley Fraser Valley,  
16.VIII.1939, Eastham (UC); Southern Ontario, Byrne & McAndrew (1975) photo! New York:  
Marquesas Islands: Tahuata Island Schaefer 5478 (US).

Kowal (1961) considered this subspecies as a “line” in subsp. oleracea, but it seems  
to have a different distribution from that of subsp. oleracea, and should be  
regarded as a separate subspecies. Kowal noted that seeds of subsp. oleracea and  
subsp. stellata can be found on the same plant. From our observation of herbarium  
material, living populations and raising of other subspecies, we cannot agree with  
his conclusion. Schimper collected the two subspecies in Sinai. He had a mixed  
collection on a herbarium sheet deposited in the Dudley Herbarium (DS), but had  
only subsp. oleracea on the other sheets. Sympatric growth of two or more sub-  
species is rather common in populations of Portulaca oleracea (see below under  
Discussion of the Taxonomic Rank).

Figs. 30-31. Scanning electron micrographs of seeds of Portulaca oleracea subsp. papillato-  
stellulata; seeds from Palm Springs, California (14 in Table I).
Seeds of subsp. *stellata* are as shiny as those of subsp. *nitida* and may or may not have tubercles at the periphery.

**Distribution** (Fig. 15c): Only one specimen from South America agrees with this subspecies; together with the material from the Marquesas Islands (Schafer 5478) they both seem to be recent introductions. In North America it is more common north of 45°N latitude. In Europe it is not as commonly represented in herbaria as subsp. *oleracea*. 
Byrne and McAndrews (1975) assumed that *Portulaca oleracea* “came into the area” of Ontario with Amerindian agriculture. The micrograph presented by them depicts subsp. *stellata*. Although it is clear from their paper that the plant appeared in the area discussed by them as a result of human activity, *P. oleracea* subsp. *stellata* need not have been brought by man to the area; its distribution seems to fit the ecological conditions which prevail there.


A typo differt seminibus papillatis stellulatis.


**CHROMOSOME NUMBER:** 2n = 54; populations from the following localities in California: Palm Springs, Berkeley, San Francisco and Stanford University (vouchers in UC).


Seed coat characters of this subspecies resemble those of subsp. *granulato-stellulata*. Seeds of the type population differ from the latter only in their size (Figs. 31 & 32), but those from Berkeley have many more and narrower arms (Figs. 33 & 34). As in subsp. *granulato-stellulata*, the number of stellulae and papillae vary in populations of subsp. *papillato-stellulata*. If some seeds are shorter than 0.85 mm, in the same populations always more than 20% of seeds are longer than 0.90 mm. In such populations red pigmentation of the calyx may also be of help in determination of the subspecies. All the five populations of this subspecies, in which we counted the chromosomes, had red pigmentation in the calyx and leaf margin.

**DISTRIBUTION** (Fig. 15c): This subspecies is essentially of New World distribution mainly in northern and central America. It occurs regularly as far south as Mexico and Guatemala at high elevations. It is rare in other parts of the world. A similar area of distribution in America is that of the tetraploid subsp. *granulato-stellulata*. Several herbarium specimens from Guatemala and Mexico give the impression that the hexaploid subspecies replaces the tetraploid one at high elevations. Such an assumption should be tested in the field, because very few specimens are represented in herbaria.

**FORMS WITH RESTRICTED DISTRIBUTION**

Two herbarium specimens from Mexico show unique seed sculptures. They are worthy of further investigation:

1) A suspected hybrid of *P. oleracea* subsp. *nicaraguensis* and *P. pilosa* subsp.
piosa. Collected in Mexico: Yucatan: 35 km from Progreso to Mérida, Lundell & Lundell 8206 (US). The seed coat is provided with pyramidal tubercles projecting from the stellulæ (Figs. 34 & 35). Waxy and non-waxy, small seeds with this sculpture are found in this specimen. Similar pyramidal tubercles characterize seeds of P. piosa subsp. piosa race piola described by Geesink (1969). As this specimen shares seed coat characters of P. oleracea subsp. nicaraguensis and P. pilosa, we suspect it to be a hybrid between them.


Seeds black, large (0.89 × 0.81 ± 0.1 mm), with large tubercles at the centre of each stellula. This sculpture is similar to that of P. lanceolata Engelm. The latter has cream-coloured seeds with a metallic sheen. Some seeds of this suspected hybrid have shiny yellowish spots and a metallic sheen as well.

Most specimens that we have seen from different parts of Australia and New Zealand do not agree with our description of the subspecies from other parts of the world. Therefore we do not think that our account can be applied to Australia and New Zealand.

CULTIVATED TAXA

P. oleracea L. subsp. sativa (Haw.) Celak., Prodr. Fl. Böhm. 484 (1875).

The main diagnostic character by which subsp. sativa differs from the wild types is seed size. Specimens of P. oleracea subsp. sativa derived from commercial distributor Vilmorin-Andrieux & Cie., Paris 41086 and 41006 (BH) has seeds 1.2 mm long (± 0.07 mm) and 1.1 mm wide (± 0.07 mm). Seed sculpture is similar to that of subsp. oleracea. We therefore assume that the selection of the cultivar P. oleracea subsp. sativa took place in the Old World where subsp. oleracea is common and not in the New World where it is less frequent.

DISCUSSION OF THE TAXONOMIC RANK

We assume that autogamy and in many cases cleistogamy, together with different ploidy types, may provide a sufficient barrier between the populations of P. oleracea and enables them to grow sympatrially. Thus, there is a diploid and hexaploid at Timbuktu (von Hagerup, 1932), and a tetraploid together with a hexaploid in northern India (Khullar and Dutta, 1973), in Palo Alto and in Berkeley, California and in Jerusalem, Israel. Mixed populations of subsp. nitida and subsp. granulato-stellulata occur in several localities in California and in Israel. We do not know yet how effective are the genetic barriers between these taxa but a study of this problem was beyond the scope of the present research.

Following the dictum that polyploids which differ sharply in morphology and in chromosome number should be recognized as separate species (cf. Davis and
Heywood, 1963), we could divide the complex of nine taxa described above differently. The presumptive barriers between ploidy types suggest that three species could be recognized: "a diploid, a tetraploid and a hexaploid". These taxa could be subdivided into subspecies according to seed sculpture.

A second way of classifying the complex into species could rely on the similarity of seed coat characters and into subspecies according to seed size and ploidy type. With this procedure, P. oleracea will include only taxa with tuberculate seeds and subdivided into: subsp. oleracea (6×), subsp. sativa (6×) and subsp. tuberculata (2× or 4×). The species with stellate shiny seed coat may include subsp. stellata (8×), subsp. nitida (4×) and subsp. africana (2×). A third species with stellate-papillate-sculptured seeds may include subsp. nicaraguensis (2×), subsp. granulato-stellulata (4×), subsp. papillato-stellulata (6×) and subsp. impolita (6×?).

Altogether, we think that the close similarity of the vegetative and floral parts of taxa in the P. oleracea complex and the lack of information on the breeding system make this splitting into different species unpractical.

ECOLOGY

The distribution of P. oleracea throughout natural and man-induced habitats may be understood by studying its demands for germination and establishment and by the adaptation of the adult plant to environmental conditions.

Germinability

Some of the germination problems of P. oleracea were studied by Gutterman (1974) and by Zimmerman (1976, 1977). Neither of them was aware of the subspecific differentiation of the species. We have carried out some preliminary germination experiments concerning the establishment of the plant in temperate and tropical conditions and the transportation of seeds by sea water.

Seeds of subsp. nicaraguensis and subsp. granulato-stellulata were collected in Nicaragua and Guatemala (populations 1, 3, 4, 5, 6 in Table 1) at the beginning of October 1977; seeds of subsp. papillato-stellulata, in Berkeley, California (population 13) on October 30, 1977 and in Palm Springs, California (population 14) on December 22, 1977. The first experiments with germination were made in November 1977 in petri dishes with filter paper or on coarse sand moistened with distilled water. Optimal condition: white light and 40°C were supplied to the germinating seeds (cf. Gutterman, 1974). After 1–2 days, 80–100% of the seeds from Nicaragua and Guatemala germinated. No germination occurred in the seeds from California. Seeds of the seven populations mentioned above were sown on December 13, 1977 in 30 × 50 cm beds with coarse sand. Those from Nicaragua and Guatemala germinated during two days and those from California did not germinate for a few weeks. The beds were provided with water regularly but the first seedlings from "Berkeley" seeds appeared only on February 2, 1978;
more seeds germinated in mid-March and a third wave of germination took place at the end of April. At that time the seeds from Palm Springs germinated after 1–2 days in the petri dishes. At the end of May 1978, seeds which were produced by the plants that germinated in February, themselves germinated in the pots to which they were transferred.

At least two waves of germination were observed in subsp. nitida at Longwood Gardens, Pennsylvania and Englewood, New Jersey at the end of June 1978. The plants of the first wave began to produce seeds while new seedlings appeared among them. Gutterman (1974) found that the seeds germinate better if the parent plant had short day conditions during the last 8 days of seed ripening. The delay in germination occurred in “Berkeley” seeds which ripened in October when day length was 11–11 1/2 h, whereas those which germinated under the parent plants in May had a day of 14–14 1/2 h when ripening. Day length in Nicaragua and Guatemala when the seeds were ripening was approximately 12 h and the germination behaviour was totally different from that of “Berkeley” seeds with 11–11 1/2 h of day length.

We may conclude from our observations that either the photo-periodic response of subsp. papillato-stellulata differs from that of the subsp. oleracea and subsp. nitida with which Gutterman worked (identity determined by us in 1978), or that some other environmental factors play a role. The germinability of seeds in populations of subsp. granulato-stellulata is certainly different from that of the Californian subsp. papillato-stellulata. The delay in germination of the latter may represent adaptations to the cooler and more unpredictable winter weather of California. The seeds will not germinate in an unfavourable season when sudden frost can occur. This property was named by Zimmerman (1977) “overwintering proficiency”. The “waves” of “intermittent germination” (Salisbury, 1961) have an advantage in regions with unpredictable weather. Several mechanisms of the evolution of heterogeneity in germinability of seed population and their value in desert conditions were studied by Gutterman (1972). It is worth mentioning that the seeds from Nicaragua and Guatemala which were evolved in a more predictable climate did not display any “waves” of germination.

Transportation of the seeds in the sea was discussed by Ridley (1930) and by Geesink (1969). The latter criticized the former in assuming that the transport by sea is impossible because the seeds do not float. In our preliminary investigations, ca. 300 seeds of populations 1, 3, 5, 6 and 13 (Table I) were floated for three weeks on sterilized sea water, half diluted sea water and distilled water. This was in order to compare the transportation in the sea, in brackish water of river deltas and in rivers with fresh water. After each week, 75 seeds were transferred from the solutions to petri dishes with coarse sand saturated with distilled water in room temperature and continuous white light. The results are presented in Table III. All the seeds which were floated on distilled water germinated while
TABLE III
PERCENTAGE OF GERMINATION OF *Portulaca oleracea* SEEDS WHEN TRANSFERRED TO SAND WITH DISTILLED WATER AFTER FLOATING FOR 1-3 WEEKS ON HALF STRENGTH SEA WATER AND 1-31 WEEKS ON FULL STRENGTH SEA WATER

<table>
<thead>
<tr>
<th>Weeks of floating</th>
<th>Half Strength Sea Water</th>
<th>Full Strength Sea Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1st</td>
<td>2nd</td>
</tr>
<tr>
<td>Population &amp; subspecies**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. La Calera, subsp. <em>nicaraguensis</em></td>
<td>97.3*</td>
<td>—</td>
</tr>
<tr>
<td>2. La Calera, subsp. <em>granulato-stellulata</em></td>
<td>40.0*</td>
<td>—</td>
</tr>
<tr>
<td>4. Nagarote, subsp. <em>granulato-stellulata</em></td>
<td>13.3</td>
<td>12.0</td>
</tr>
<tr>
<td>5. Guatemala, subsp. <em>granulato-stellulata</em></td>
<td>29.3</td>
<td>29.3</td>
</tr>
<tr>
<td>13. Berkeley, subsp. <em>papillato-stellulata</em></td>
<td>80.0</td>
<td>76.7</td>
</tr>
</tbody>
</table>

* No seeds left.  ** Numbers of populations as in Table I.
floating during the first 2–3 days. In half strength sea water more than half of the seeds germinated while floating, the rest of the seeds showed various percentage of germinability when transferred to sand with distilled water. No seeds germinated while floating on full strength sea water but seeds from all populations retained germinability. We cannot explain the lower germinability after floating in half strength as compared with full strength sea water in population 5. Seeds of *P. oleracea* subsp. *nicaraguensis*, which grows mainly in coastal areas, retain the highest percentage of germination after floating on sea water. Subspecies *nicaraguensis* and subsp. *granulato-stellulata* retained germinability on full strength sea water for 4, 8, 13 and 18 weeks. Unfortunately we did not float enough seeds and we had to terminate the experiment after 31 weeks.

We therefore support the assumption of Ridley (1930) that transportation of *P. oleracea* may be by sea when seeds are carried out into the ocean by detritus or pumice. This agrees with the findings of Keren and Evenari (1974) in *Pancratium maritimum*. It may certainly be an important factor in the dispersal of subsp. *nicaraguensis* which was collected in many small and large islands, keys, bars and atolls. The two other subspecies displayed lower germinability after floating on sea water. However, subsp. *granulato-stellulata* from Guatemala (5 in Table III) showed in the first 18 weeks higher germinability than the population from Nagarote. The differences in response of the subspecies and populations of the same subspecies to floating on sea water may reflect ecotypic differentiation and adaptation of the subspecies to salinity.

**Habitats**

*Portulaca oleracea* is found in many different habitats and, although each variety may display adaptation to a certain set of environmental conditions, there are some basic properties that most of them share. Germination takes place under high temperature and in light. The adult plant with a C₄ photosynthetic pathway (Black, 1973; Laetsch, 1974) withstands, but also demands, high temperatures and high light intensities. It degenerates when shaded and is killed by frost. At least some varieties are resistant to spray with sodium chloride (Dearborn, 1950). These conditions which are essential for the plant development are fulfilled in such natural habitats as coastal bluffs and beaches, slightly saline soils at the margin of salt marshes, sodic savannas, shores of lakes with fresh or brackish water, river banks and inundated river terraces. Specimens of *P. oleracea* have been collected in each of these habitats. Such habitats supply moisture in the season when temperatures are high enough and the vegetation is open and light is available. These kinds of “open” habitats, which could be primary habitats for weeds (Baker, 1974), occur frequently in the tropics and in temperate countries.

One particular habitat was studied by us in the Sebaco Valley, 100 km north of Managua, Nicaragua. *P. oleracea* subsp. *granulato-stellulata* inhabited the herb
layer of a seasonally dry savanna on deep heavy soil (vertisol = grumusol) in alkaline patches. Here Na\textsuperscript{+} accounted for more than 15\% of the cation exchange capacity of the soil. The proportion of sodium in the ash of the plants was significantly correlated with that of the sodium in the cation exchange capacity (Fig. 36). It is in these patches that the plant can avoid competition with taller grasses which shade the soil outside these patches. Here *P. oleracea* withstands three types of environmental stress throughout the year: in the dry season the soil desiccates, but the succulent plants continue to survive using the water which is stored in the leaves and stems. It has the ability to accumulate sodium and to withstand the high quantities of sodium in the soil which may be toxic to its competitors. It is also resistant to the temporary waterlogging of the sodic soil after rain.

The most common habitats of subsp. *nicaraguensis* are coastal areas of the Gulf of Mexico, the West Indies, and inland salty or sodic soils in Nicaragua, eastern Guatemala, eastern Honduras and southern Florida. It may also grow in the same areas in man-created disturbed habitats, such as roadsides and gardens. Its occurrence in salty habitats is reflected in its resistance to the sea water influence described above.

The main habitats where subsp. *tuberculata* was collected are river banks where new soil, with no competitors, is open for colonization.

Apart from habitats disturbed by man, subsp. *nitida* was collected in North America at the edges of swamps, lake shores and river banks. All these habitats could serve as primary habitats for this subspecies.

*Portulaca oleracea* subsp. *impolita* was collected mainly in sandy habitats at high elevations. In this respect it differs from all the other subspecies, but too little habitat information was given by the labels of the herbarium specimens to draw final conclusions.

Man-created habitats supply the same essential demands for seedling establishment in irrigated fields of the tropics or among summer crops and gardens in
temperate countries, roadsides where winter vegetation has been removed, and
gaps between flagstones of sidewalks. It became a widespread weed having most
of the characters of the “ideal weed” (Baker, 1974). These characters of P. oleracea
were studied and discussed by Zimmerman (1976). The fact that disturbed habitats
where the plant grows today are much more common than the primary habitats
led to its being regarded by many authors as being always a weed (De Candolle,
1883; Black, 1973; Smith, 1976).

To conclude, the diploid subspecies nicaraguensis grow in the narrowest range
of habitats, with mainly saline or alkaline soils. The other subspecies grow in a
wider range of habitats, with specialization of some subspecies to open habitats
near rivers and lakes with fresh or brackish water. The weedy properties enabled
the plant to expand into habitats disturbed by man.

PHYLOGENY

Morphological Relationships

The only morphological character by which we can attempt to elucidate phylo-
genetic relationships of the subspecies is the sculpture of their seed coat. All our
conclusions should be tested in the future by cytogenetic and electrophoretic
means.

The first line of assumed derivation is from the non-waxy form of subsp.
nicaraguensis (2×), which sometimes have stellulae with short but prominent
arms and papillae among them, to the tetraploid subsp. granulato-stellulata and
the hexaploid subsp. papillato-stellulata. The number of arms per stellula is
higher and the seeds are larger in the hexaploid than in the tetraploid. There are
no new structural elements in the polyploids as compared with the diploid. All
the other subspecies are plants of the New World.

The tuberculate seed coat of subsp. tuberculata (which in terms of its seed size,
could be a tetraploid or diploid) resembles that of hexaploid subsp. oleracea.
The present-day distribution patterns, as derived from the available collections,
show a disjunction between the two subspecies.

Populations of P. oleracea subsp. impolita share seed coat characters with subsp.
granulato-stellulata. The occurrence of dull faces and pyramidal tubercles in some
seeds of several populations of subsp. impolita leads us to suggest that it might
have been derived from hybridization of subsp. granulato-stellulata and P. pilosa
subsp. pilosa (sensu Geesink, 1969). The occurrence of large seeds in populations
of subsp. impolita may indicate that it is a hexaploid.

The seeds of the tetraploid subsp. nitida, with no tubercles at the periphery,
resemble those of the closely related perennial species Portulaca lutea Solander ex
Seeman (see Plate I, 10 in Geesink, 1969). These two also resemble each other in
the morphology of their vegetative parts. Dr. F.R. Fosberg (pers. comm.) found
hybrid swarm between populations of P. oleracea and P. lutea on islands in the
Pacific Ocean. This might perhaps give some support to the above assumption. The hexaploid subsp. *stellata* resembles subsp. *nitida* in the sculpture of the shiny seeds. Seeds of the poorly collected diploid *P. oleracea* subsp. *africana* have a shiny surface as in subsp. *nitida* and subsp. *stellata*. Further investigations are needed to reveal the phylogenetic relations within this group.

**Distribution of the Subspecies**

Of the three ploidy types of *P. oleracea*, the New World diploid has the smallest area of distribution. It was found mainly as a moderate halophyte under warm subtropical conditions. This agrees with the findings in *Crepis* (Babcock and Stebbins, 1938) and in the wheat group (Zohary, 1965) that the diploid taxa often have a narrower range of distribution than their related polyploids. Our knowledge of the Old World diploid is too poor to draw any conclusion. The tetraploid subspecies occur in a much wider range of latitudes and habitats throughout the world. The hexaploids occur mainly north of the Tropic of Cancer and a high elevations in Mexico and Guatemala. We have seen only one hexaploid specimen from the American continent south of Guatemala, from Argentina. North of latitude 45°N, in North America and Europe, it is mainly the hexaploid subspecies which are found.

Eight subspecies of the three ploidy types are present in the New World but we have seen only two hexaploid subspecies and a few specimens of a tetraploid subspecies which were collected in Europe. This fact may serve as a strong argument against the hypothesis of De Candolle (1883), and many others who followed him, that *P. oleracea* was introduced from Europe to America. The main Eurasian type is subsp. *oleracea* which is relatively rare in the New World. The present day distribution of this subspecies in the Old World could be a result of establishment of even a single seed which arrived there some thousands of years ago. The occurrence of seeds of *P. oleracea* from the Roman period (1st to 4th century) in Neuss, Germany (51°12’N/6°42’E) was reported by Knörzer (1970). From seed sizes reported by Knörzer it is evident that it was a hexaploid subspecies, but seed sculpture was not drawn clearly enough to make determination of the subspecies possible.

An older record of *P. oleracea* from North America was presented by Chapman et al. (1974) who found it in an archaeological site in Kentucky carbon dated to the first millenium B.C. They reported it also from southern Louisiana from 500 A.D. Byrne and McAndrews (1975) found the hexaploid subsp. *stellata* in southern Ontario, Canada, from the 13th century. Chapman et al. (1974) evaluated their findings to indicate an early prehistoric introduction or indigenous development of *P. oleracea* as a crop plant in the New World. Their latter hypothesis fits better with our findings.

The invasion of new subspecies in particular regions can be demonstrated by
the material from Britain and Israel. The earlier material represented in the British Isles collections of the British Museum, Royal Botanic Garden Edinburgh and Royal Botanic Gardens Kew is subsp. oleracea, subsp. stellata and subsp. granulato-stellulata. On the other hand, a specimen of subsp. nitida (McCallum Webster 9410) represents a recent introduction to England. It was possibly introduced with wool shoddy between 1969 and 1972 together with weed species which were studied by Ryves (1974).

The introduction of subsp. nitida and subsp. granulato-stellulata to Israel seems to be recent too. All the seven specimens from Israel which are deposited in the Herbarium of the Hebrew University, Jerusalem (HUJ) and those from the same region such as Myers & Dinsmore 4200 (K), Myers & Dinsmore 8200 (E) are P. oleracea subsp. oleracea. The illustration of P. oleracea in Zohary (1941) is also of subsp. oleracea. The collections mentioned above were made between 1912 and 1945. The first record of subsp. nitida that we could check was that of Gutterman (1974). The seeds were collected in Jerusalem on 19.VII.1967 (HUJ). During the summer of 1978, subsp. nitida was very common throughout the country. Of the 46 populations studied in Israel, 25 were of subsp. nitida, 16 of subsp. oleracea and 5 of subsp. granulato-stellulata. This may indicate the rate of invasion of a new subspecies which presumably came from North America.

In our study we found that long distance dispersal by sea and the “weedy” properties of P. oleracea could play a considerable role in its present day distribution. This makes the attempts to arrive at any conclusions regarding the origin of P. oleracea rather difficult. The highest number of subspecies (6) and local forms (2) occurs in Mexico. The presence of all the three ploidy types there may suggest that this is at least the center of diversity of Portulaca oleracea.

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