MECHANISMS FOR LONG-DISTANCE DISPERSAL

IN SOME AMPHITROPICALLY DISJUNCT PLANT SPECIES

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Presented to the Graduate Faculty of
the Claremont Graduate School in
partial fulfillment of the requirements
for the degree of Master of Arts.

We certify that we have read this document
and approve it as adequate in scope and
quality for the degree of Master of Arts:

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Date May 8, 1974

METHODS

In order to explore potential dispersal mechanisms of the plants in question, the morphology of each seed or fruit, as well as vegetative portions of the plant, was examined under a dissecting microscope. In many cases seed or fruit morphology suggested possible dispersal mechanisms which could be tested easily. For example: (1) Dropping a seed or plant fragment containing mature seeds into water to see if it would float. If so, would it float indefinitely (a month or more)? After letting it dry for a few weeks, would it germinate? (2) Moistening a mature seed to see if it would become gelatinous, and to see how firm a bond, if any, it would form with downy feathers, for example. (3) Bringing a prickly, hairy or wooly disseminule or plant fragment into contact with feathers from a bird's wing, to visualize the probability of it being caught there indefinitely. (4) Handling a minute seed to see if it would catch readily in downy feathers. Such tests are simple and so obvious as to be elementary, yet they reveal some fundamental capabilities which should not be overlooked in a discussion of long-distance dispersal. The results of such determinations of probable dispersal mechanisms appear below in a tabulation of 112 of the amphitropically disjunct taxa. Note that the term "disseminule" has been used in a broad sense. Dispersal of

a number of disjunct species may depend upon characteristics of their capsules or calyces, or other portions of the plant (e.g., bristly or viscid.) Because dehiscence is usually not completely instantaneous, some mature seeds may remain in a partially dehisced capsule; mature nutlets (Boraginaceae) may be found surrounded by the calyx; and a mature caryopsis (Poaceae) may be found still enclosed in the lemma. The truth of this observation is demonstrated by the retention of mature seeds on herbarium specimens.

This study was limited by the availability of North American specimens at Rancho Santa Ana Botanic Garden, and the relative scarcity of South American material. Consequently, conclusions as to dispersal mechanisms have been based primarily upon North American material.

Many of the species in question were seen in the field. Familiarity with the various habitats of the disjunct species lends perspective to a consideration of their dispersal capacity. Descriptions of habitats contributed by workers who have studied some of the plants thoroughly was also very helpful.

Field observations of the habits and habitats of shorebirds were especially informative and provided important background experience and knowledge.

An effort was also made to test for dispersal mechanisms which, although seemingly unlikely given the present-day distributions of some species, might well have

been probable mechanisms for dispersal during different climatic regimes when distributions were somewhat different than they are today. (See below, The Relation of Distribution and Habitat to Dispersal.) For example, fragments and seeds of some species which grow in warm desert habitats were tested for flotation in water. Some Baja California desert species do, in fact, reach the coast, and some other inland desert species once may have had a wider distribution which would have enabled their disseminules to reach the ocean; therefore, it is conceivable that oceanic drift or rafting might have played a part in their historic dispersal. Even coastally situated species which are densely hairy were tested for flotation. In these cases negative results were important in the elimination of oceanic drift as a probable dispersal mechanism for these plants, although loss of dispersability, including loss of floatability is possible (Carlquist, 1966b; 1966c; Wilson, 1970). The longest floating period for hairy or bristly plant fragments was six days, certainly not long enough for oceanic drift from North to South America or vice versa.

SOURCES AND ACKNOWLEDGMENTS

Information as to habitat and distribution of the plant disjuncts was obtained from Raven (1963a), Munz (1959, 1968), monographs and revisions of the various families and

seed or spore suspected of long-distance wind dispersal can even more likely be transported in the downy feathers of migrating birds which pass through their habitats. Given the vast numbers of birds migrating between North and South America each year, and their relatively direct flight to appropriate recipient areas, dispersal in bird feathers is actually a far more likely mechanism for these disjuncts than air flotation.

Birds

Cruden (1966) has grouped the 58 species and subspecies of birds which migrate from North America to temperate South America according to the plausibility of individuals of those taxa transporting seeds across the tropics in one step. He disqualifies a number of them as improbable candidates for a variety of good reasons: rare in California, rare in temperate South America, pelagic in one or the other or both hemispheres, etc. However, he has, in some cases, evaluated the possibilities too conservatively. In order to focus attention upon the most likely candidates among migratory birds, the following tables (I A & I B) have been devised. Breeding, migratory and wintering data pertain primarily to the western hemisphere and do not constitute exhaustive descriptions. Information regarding the food of these birds is principally from Bent's compilations of ornithological life histories (1921, 1927, 1929, 1949). Such data will serve to characterize the species in

question and to suggest the possibilities of avian transport of fruits and seeds.

The most likely bird agents for dispersal of the amphitropical disjuncts have been grouped in the tables below as "coastal" or "inland" birds. Although such a division is not at all clear-cut (many shorebirds are found migrating through both coastal and inland habitats) it is important to realize that many shorebirds frequent inland valleys, prairies, lakes, rivers and plains. This is especially important since many of the disjuncts are species of valley grassland, vernal pools, mudflats, plains, etc., of the interior. (See tables.)

The whimbrel may be an important agent in the dispersal of plants. This species is found foraging for insects near masses of drying seaweed which has been deposited on shore by the tides. On southern California beaches I have noticed that whimbrels usually are the shorebirds farthest from the tidal line. I have seen them foraging within inches of the base of a coastal bluff on which Amblyopappus and Carpobrotus were growing in profusion. I have no doubt that the whimbrel comes into direct contact with the western coastal disjunct plant species. Numerous reports that whimbrels and curlews eat fleshy berries and seeds, especially in the fall, serves to further support this conviction (Bent, 1929).

No ducks or geese are known to migrate between North

and South America and so are not considered here, although stragglers may occasionally appear in South America. Unlike his eastern counterpart, the western race of Swainson's thrush, Hylocichla ustulata ustulata, does not winter as far south as South America (Bob Stewart, personal communication) and so is not included in these tables. However, the eastern subspecies may well be a vector in the dispersal of some of the widespread North American and eastern North American disjuncts (Raven, 1963a: Appendices II C & II D). Although an insect-eater, the species also eats seeds and fruits. One stomach content study found 36% vegetative matter, including 50 varieties of fruits (Bent, 1949).

The numbers of shorebirds migrating between North and South America has undoubtedly fluctuated greatly through the years during which the plant disjunctions have occurred. However, current shorebird survey data (Jurek and Leach, 1971, 1972) indicate that in peak periods of fall or spring migration as many as 11,700 shorebirds have been observed on one day (in late April, 1970) at one location (Palo Alto Marsh, San Francisco Bay, California.) A year later approximately 8000 shorebirds (including turnstones, surfbirds, plovers, phalaropes, sandpipers, etc.) were seen there at one time. More frequently single day shorebird censuses reported 4000-5000 birds at a given location. Of course many of these birds do not migrate far enough south

to be considered putative bird vectors for the dispersal of the amphitropical disjuncts. However, the black-bellied plover, definitely a possible vector, has been observed in late winter and early spring (northern hemisphere) in numbers of 150 (Palo Alto Marsh, 1970), 200 (San Diego Bay Salt Ponds, 1970) and 320 (Upper Newport Bay, 1970) on peak days (Jurek and Leach, 1971). On one day in late February, 1971, 692 black-bellied plovers were observed at Anaheim Bay, California. Sanderlings, also possible vectors, were sighted in numbers of 300 (September, 1970) and 500 (early August, 1970) at two different locations (Jurek and Leach, 1972). It is difficult, if not impossible, to determine the number of individual birds or birds of a given species which fly from North to South America, or vice versa, in one (spring or fall) migration. However, judging from the large flocks which have been observed as cited above, one can easily imagine occasional introduction of several seeds of a given plant species from a different hemisphere by a large flock of migrating shorebirds.

External Transport by Birds

The types of disseminules transported by birds externally are as follows:

Spores. The transport of fungal spores in the feathers of birds is now well established. Pugh (1964, 1965a, 1965b, 1966) and others have documented the presence of fungal spores in the feathers of birds including migratory species, and the differences between the fungi present on birds with different feeding habits.

Klekowski (1972), Tryon (1970), Carlquist (1967) and others have noted the fact that fern spores can be wind dispersed great distances due to their minute size. Of course, any spore which can be wind dispersed can also be easily dispersed in the downy feathers of birds, with less direct exposure to the elements and with a more direct means of transport to an appropriate location for establishment. According to Klekowski and Baker (1966) ferns are capable of intragametophytic selfing and a single spore can start a colony.

Small sculptured seeds. Minute seeds (0.3 - 1 mm. long) which are angular, papillate, tuberculate, rugose, etc., may easily catch in feathers of birds and are much more likely to be dispersed between North and South America in this manner than by air flotation. Secretions from a bird's

body itself may sometimes also help seeds to adhere externally, especially to remote portions of the body such as top of legs, facial and anal areas. Similarly, small bits of mud and organic or other debris may also help provide adhesion for tiny disseminules that are not themselves viscid or prickly.

Small smooth seeds. Small seeds that are not sculptured may require the help of birds' bodily secretions or small bits of mud to help them adhere externally. Verified instances have been cited by Ridley (1930), McAtee (1947) and others, in which seeds have been found in mud on the feet and legs of shorebirds (BM). However, it has been demonstrated that mud and organic debris rarely remain on ducks suspended in air longer than 30 minutes and this suggests that in flight most debris would fall off in even less time (Schlicting, 1960). It is possible that seeds which are angular, pitted, papillate or otherwise sculptured, are more likely to stick in mud than smooth ones. However, the effectiveness of this occurrence as a means of long-distance dispersal is questionable. Carlquist (1967) attributes a small percentage of arrivals on oceanic islands to dispersal in mud on birds' feet, noting that this mode of dispersal is limited largely to marsh plants or land plants of very moist habitats. He also proposes that it may be most abundant on islands close to continents where flyways can be said to exist. Even on migration routes,

however, it should be considered a much more effective form of short distance dispersal than long distance dispersal. Even if mud does occasionally remain on shorebirds for a period of days, it still is probably not very significant in the distribution of North American plants to South America, or vice versa, a distance of approximately 5,000 miles.

Barbed, bristled and woolly fruits. Adhesion to the coats, fur and feathers of animals and birds by fruits and seeds with barbs, bristles, prickles, hooks and hairs, etc., is common (Ridley, 1930). There is abundant evidence that birds, including seabirds and shorebirds, play an important role in the transport of insular plants with this type of seed (Carlquist, 1967).

Mucilaginous seeds. Numerous species of plants are known to have fruits which become mucilaginous when wet (Ridley, 1930). Ridley explains (p. 622) that this feature is more pronounced in dry-land species than in ones which grow in damper spots. Whatever the adaptive significance of this character it accomodates dispersal by adhesion of disseminules externally to birds and animals, as the mucilage upon drying forms a bond to feathers, fur, etc. Seeds or fruits sticking onto birds in this fashion may remain in place for extended periods of time, becoming unglued only in very wet weather, when the portion of the animal's body which harbors the seed is submerged in water, during

preening or when feathers are shed, etc. Shorebirds are generally waders which feed on the margins of aquatic habitats, such as in tidal flats, estuaries, muddy shores, marshlands, etc. It is not difficult to imagine that an occasional seed in its mucilaginous state might stick to a wading or wandering shorebird and remain there indefinitely. Although waterfowl such as ducks may carry such seeds short distances, their frequent swimming and diving would make them less likely agents of dispersal over such long distances as between North and South American temperate regions, aside from the fact that they normally do not fly between the two regions.

Viscid herbage. Although not a character of the disseminule itself, the gumminess of herbage surrounding fruits of various disjunct species probably promotes dispersal by causing them to stick in the feathers of birds. Examples of this mechanism are Madia and Phacelia (see Table II B.)

Internal Transport by Birds

Numerous factors have bearing upon the plausibility of internal transport of disseminules by birds, including feeding habits of the probable vectors, viability of seeds recovered from birds, migration speeds and migratory behavior.

concomitant fact is that shorebirds on occasion devour berries and other vegetative food. If this pre-migration gorging is an instinctive activity which takes place even when the preferred food source is for any reason less abundant than usual, then this season is the most likely occasion for long-distance dispersal to take place.

AMPHITROPICALLY DISJUNCT PLANTS

Explanation of Tables II A and II B

Abbreviations relating to probable mechanisms for long-distance dispersal[1] of the "Western coastal disjuncts" (Table II A) and "Western temperate disjuncts" (Table II B).

B = Birds -- minute (0.3--1 mm.) disseminules probably transported in the feathers of birds (in the manner of spores)

BB = Birds -- disseminules attached to feathers by means of barbs, bristles, awns, etc., and carried externally

BV = Birds -- disseminules and/or fragments attached to feathers by viscid substance from plant or disseminule

BI = Birds -- disseminules with tough seed coats ingested by birds (either intentionally as food or inadvertently while foraging) and transported, probably in the gizzard

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[1] similar to those used in Carlquist, 1967

BM = Birds -- disseminules embedded in mud on remote portions of their bodies, e.g., top of legs, head, anal region

DF = Oceanic drift of seeds able to float in sea water

A = Air flotation of minute disseminules

Mechanisms of dispersal which may operate successfully over short distances have not been included for plants listed in Tables II A and II B if they are considered ineffective for dispersal over long distances (e.g., ca. 5000 miles.)

If South American representatives are different species, subspecies or varieties from their North American counterparts, they are listed below the North American species in brackets. Their South American distributions in the far right column are then also given in brackets. Of course, as these plants continue to be studied and monographed, changes in their taxonomic status will undoubtedly be made.

The descriptions under Vegetative Communities in the tables below are meant to represent (1) the general vegetative type or community in which the species in question is found, and (2) any known habitat information which may directly relate to the probability of long-distance dispersal. Communities (some abbreviated) are as follows (see Munz, 1959):

Coastal Strand (dunes, sandy flats near the ocean, etc.)

Coastal Prairie

Coastal Salt Marsh

Freshwater Marsh

Coastal Scrub (=Coastal Sage Scrub)

Desert Scrub (=Creosote Bush Scrub or Shadscale Scrub)

Sgbrush Scrub (=Sagebrush Scrub)

Desert Wdld (=Northern Juniper Woodland, Pinyon-Juniper Woodland, Joshua Tree Woodland)

Valley Grassld (=Valley Grassland)

Woodld-Savanna (=Woodland-Savanna: Northern Oak Woodland, Southern Oak Woodland, Foothill Woodland)

Chap (=Chaparral)

ConiferForest (=Coniferous Forest)

MontConiferForest (=Montane Coniferous Forest)

MixEvergrnForest (=Mixed Evergreen Forest)

Alpine Fell-field

vernal pools ("hog wallows," see Whitney, 1948, and Twisselmann, 1967)

Other notations regarding habitat may appear in parentheses. The notation "nr aquatic hab" means that the species is sometimes found near aquatic habitats which may support migratory waterfowl.

North American distributions may include abbreviations such as the following:

CoRanges (=Coast Ranges)

CenVall (=Central Valley of California)

wSierraNevada (=west slope of Sierra Nevada)

transmontCalif (=transmontane California) (see Munz, 1959, for description)

cismontCalif (=cismontane California) (see Munz, 1959)

interior mts, sCalif (=interior mountains of southern California (San Diego and Riverside Counties; e.g., San Jacinto Mts., Santa Rosa Mts., Laguna Mts., etc.)

Channel Is (=Channel Islands off the coast of California, one or more)

BajaCalif (=Baja California)

Other abbreviations include:

BritColumbia (=British Columbia, Canada)

vall (=valley)

Co (=County in California)

n (=north), s (=south), e (=east), w (=west)

South American distributions are given in terms of the country and sometimes also the provinces (after the colon.)

For synonyms, references to literature of each species, some information on self-compatibility, polyploidy, etc., refer to Raven (1963a) Appendices II a and II B. Literature is footnoted in the tables below only when newer names have been used. Distributional information given below for both North and South America is primarily from Raven (1963a) but also from other literature and herbarium observations and is presented here for convenience.

eastern United States where the genus is more abundant.

Boraginaceae

In this family of plants which are typically hispid-hairy throughout (stem, leaves, inflorescence) and which fragment readily, dispersal of plant fragments (including calyces with mature seeds enclosed) in the feathers of birds is likely (BB) (FIGS. 5, 6, 7). Even the nutlets of three species (Lappula, Pectocarya) are distinctly prickly.

Brassicaceae through Elatinaceae

Lepidium nitidum (Brassicaceae) has seeds which swell with mucilage when moistened (BV) (FIGS. 17, 18) and adhere firmly to feathers when dry. Seeds from herbarium specimens labeled Thlaspi fendleri var. idahoense as well as several other species of Thlaspi also appeared to have this trait after soaking in water for 15 to 20 minutes. However, Holmgren (1971) has designated T. parviflorum A. Nels. as the species most closely related to the South American species (see Table II B), so material known to be T. parviflorum, as well as the South American species, should actually be tested to be sure that the disjunct taxa can definitely be considered BV (viscid).

Campanulaceae through Elatinaceae

As noted above, the extremely minute seeds of the disjunct members of Campanulaceae, Caryophyllaceae,

TABLE I A.--Pacific coastal migratory birds which are possible vectors for amphitropically disjunct plants.

	Breeds	Migrates	Winters	Habitat[1]	Food
Whimbrel *Numenius phaeopus*	Arctic coasts to Yukon delta	coast; valleys of California	cCalifornia to sSA	shore; tideflats marshes; prairies	insects, crustaceans, etc.; (*Empetrum*, *Vaccinium* berries)
Surfbird *Aphriza virgata*	s-c Alaska (high mts.)	coast	se Alaska coast to sSA	rocky coasts; beaches; mudflats	marine life, etc; (2% seeds in 8 stomachs examined)
Ruddy turnstone *Arenaria interpres*	Arctic coast to Yukon delta	coast (sparse inland)	SFrancisco to SA	rocks; beaches; mudflats; lake shores (inland)	marine life, insects, etc.; (*Scaevola* berries, *Draba alpina* seeds, algae)
Knot *Calidris canutus*	Arctic	coast (skips Oregon mostly)	sCalif to SA	tidal flats; shores	marine life, etc.; (*Carex*, *Luzula* seeds)
Sanderling *Crocethia alba*	Arctic	coast; some GBasin, GPlains	sBritColumb to SA	outer beaches; tideflats; lake shores	marine life, etc.; (sometimes a few seeds)
Semipalmated plover *Charadrius semipalmatus*	Alaska, to Mackenzie Terr.	coastal; some GBasin, GPlains	SFrancisco to SA	shore; tideflats	marine life, etc.
Common tern *Sterna hirundo hirundo*	c Mackenzie to Montana	coast; British Columbia south	SA to Sts. of Magellan	oceans; bays; beaches	small fish, shrimp, etc.; aquatic insects
Arctic tern *Sterna paradisaea*	Arctic, Aleutians to n BritColumbia	along and off coasts	subantarctic seas	open ocean; coast	(see common tern)
Elegant tern *Thalasseus elegans*	islands off Baja California	(wanders n to SFrancisco)	cCalif to Peru, Chile	coast	fish
Royal tern *Thalasseus maximus maximus*	Baja California & Mexican coasts	(wanders n to SFrancisco)	cCalif to Peru	coast (roams inland, winter)	small fish, shrimp, etc.

SOURCES: Cruden, 1966; Peterson, 1941; Bent, 1921, 1927, 1929.

NOTES: Distributional data is incomplete, referring only to that which relates to the amphitropical plant disjunction. Abbreviations: GPlains = Great Plains (U.S.); GBasin = Great Basin (U.S.); SFrancisco = San Francisco Bay (California); SA = South America.

[1]refers to migratory, not breeding, habitat.

TABLE I B.--Inland migratory birds which are possible vectors of dispersal for amphitropically disjunct plants.

	Breeds	Migrates	Winters	Habitat	Food
Pectoral sandpiper *Erolia melanotos*	Arctic coast to s Alaska; e-c Mackenzie	GPlains, Rocky Mts.; (scarce on coast, fall)	s SA	prairie pools; marshy shores; tidal marshes; grassy meadows	insects, amphipods; (occasionally a few seeds, algae)
Black-bellied plover *Squatarola squatarola*	Arctic coast to s Alaska	GBasin, GPlains, Mississippi Valley	s BC to large valleys of Calif; c Brazil, Peru	mudflats; marshes; shores; prairie lakes; (resort to meadows, fields)	marine worms, small mollusks, crustaceans, insects, larvae; (some seeds and berries)
Lesser yellowlegs *Totanus flavipes*	n-c Alaska to nw Mackenzie, BC, Alberta, Saskatchewan	western U.S., especially GPlains	Gulf states to Argentina	marshes (coasts); short-grass marsh, mudflats, shallow ponds (inland)	insects, larvae, small crustaceans
Greater yellowlegs *Totanus melanoleucus*	c Alaska to c BC, c Alberta,	throughout western U.S.	s coastal BC, s Nevada, e New Mexico, s to SA	open marshes; mudflats; streams; ponds; (occ. damp grassy meadows)	insects, larvae, minnows; (one report of *Empetrum nigrum* berries)
Solitary sandpiper *Tringa solitaria cinnamomea*	c Alaska to n BC, c Alberta, c Saskatchewan	western U.S.	Gulf of Mexico to Argentina	streams; wooded swamps; small ponds; rainpools; fresh marshes	aquatic insects, larvae, worms, etc.
Baird's sandpiper *Erolia bairdii*	Arctic coasts to w Alaska	coast; inland on plains (& probably high mountains)	Andes	rainpools; pond margins; mudflats; shores	insects
Wilson's phalarope *Steganopus tricolor*	w Canada to s-c Calif, Nevada, Utah, Colorado, Nebraska	throughout western U.S.	s SA	shallow lakes; marshes; pools; shores; mudflats; salt marshes	insects, larvae, etc.; (some seeds of various aquatic plants)

SOURCES: See Table I A.

NOTES: See Table I A. Additional abbreviations: BC = British Columbia; occ. = occasionally.

TABLE II B. (cont'd)
WESTERN TEMPERATE DISJUNCTS (cont'd)

Name	Disseminule Morphology	Probable Dispersal Mechanism	North American Vegetative Community	North American Distribution	South American Distribution
ASTERACEAE (cont'd)					
Psilocarphus brevissimus Nutt.	achene 1-2 mm. long, surrounded by saccate woolly bract	BB BM	vernal pools ValleyGrassland Woodld-Savanna	CoRanges, CenVall; to nBajaCalif Washington Montana, Utah	cChile to sArgentina
Soliva sessilis R. & P. S. daucifolia Nutt. regarded synonymous /S. valdiviana Phil./	achene-body ca. 2-3 mm. long, obcompressed, winged, pointed with a hardened persistent style of similar length, and 2 incurved teeth. (FIG. 1)	BB	Coastal Prairie CoSageScrub (moist places, mudflats)	CoRanges cismontCalif (S. daucifolia in CoRanges)	/cChile: Valdivia & Llanquihue/
Soliva pterosperma (Juss.) Less.	(see S. sessilis)	BB	vernal pools Woodld-Savanna	wSierraNevada; to sOregon	Argentina
Thelesperma megapotamicum (Spreng.) O. Kuntze	achene-body ca. 7 mm. long; pappus bristly	BB	Plains Grassland (calcareous or alkaline ground)	Wyoming, Nebraska to nArizona, Texas & adjacent Mexico	Uruguay; ne & c Argentina to Rio Negro
BORAGINACEAE					
Amsinckia menziesii (Lehm.) Nels. & Macbr. /complex of SA forms, some conspecific/	nutlet 2.5-3.5 mm. long, tuberculate, in persistent bristly calyx	BB	ValleyGrassland Woodld-Savanna (nr aquatic hab)	CoRanges, CenVall wSierraNevada ChanIds; to Washington Idaho, Utah	/nEcuador to sChile; eArentina from Rio Negro to Santa Cruz/
Amsinckia tessellata Gray /some SA plants similar to a 3rd NA species, A. intermedia Fisch. & May/	nutlet 3-3.5 mm. long, rugose, in hispid calyx	BB	ValleyGrassland Woodld-Savanna SgbrushScrub DesertWoodld etc.	CoRanges, CenVall Desert eSierraNevada; to BajaCalif eWashington Nevada, Arizona	/Chile: Santiago Argentina: Chubut/

TABLE II B. (cont'd)
WESTERN TEMPERATE DISJUNCTS (cont'd)

Name	Disseminule Morphology	Probable Dispersal Mechanism	North American Vegetative Community	North American Distribution	South American Distribution
BORAGINACEAE (cont'd)					
Coldenia nuttallii Hook.	nutlets ca. 1 mm. long, smooth; plant and calyx hispid	BB	SgbrushScrub DesertScrub DesertWoodld	Desert eSierraNevada; to Washington Utah, wWyoming	Argentina: San Juan Mendoza
Cryptantha circumscissa (H. & A.) I.M. Johnst.	nutlets ca. 1.5 mm. long, angled; fruiting calyx circumscissle; plant hispid to strigose	BB	DesertScrub to Lodgepole Forest	Desert eSierraNevada; to Utah, Colorado, Arizona	Argentina: Neuquen
Cryptantha minima Rydb. [C. mendocina I.M. Johnst.]	nutlets ca. 1 mm. long; calyx hispid, deciduous w/ fruit; plant hirsute, fragments easily. (FIGS. 5,6)	BB	Plains Grassland Pinyon & Yellow Pine Belts	Saskatchewan thru Montana, Dakotas, to eColorado, Kansas New Mexico, Texas	Argentina: wMendoza Andean foothills
Lappula redowski (Nornem.) Greene (also var. cupulata (Gray) M.E. Jones)	nutlets 2.5 mm. long, tuberculate, with barbed prickles	BB	SgbrushScrub DesertWoodld ConiferForest	Deserts, eSierraNev & San Bernardino Mts; to Dakotas, Texas, Washington, adj. Canada (var. cupulata: GBasin)	Argentina: Santa Cruz, Chubut, Rio Negro, Mendoza (var. cupulata: Argen: Santa Cruz)
Pectocarya linearis DC. var. ferocula I.M. Johnst.	nutlets homomorphous, 4, divaricate, each 3 mm. long, (disseminule therefore ca. 5 mm. long) w/ bristle-tipped teeth	BB	Valley Grassland Savanna-Woodld CoSageScrub Chaparral (nr aquatic hab)	CoRanges, CenVall, wSierraNevada (c-s Calif), ChanIs; to BajaCalif	Argentina: Mendoza s to Patagonia; (c Chile)
Pectocarya pusilla (A. DC.0 Gray	nutlets homomorphous, 2 mm. long, 1-4, divergent in pairs (disseminule therefore ca. 4 mm. long), with hooked hairs	BB	Savanna-Woodld Chaparral (wooded or open)	CoRanges, CenVall (c Calif); to Washington	c Chile (rare)

TABLE II B. (cont'd)
WESTERN TEMPERATE DISJUNCTS (cont'd)

Name	Disseminule Morphology	Probable Dispersal Mechanism	North American Vegetative Community	North American Distribution	South American Distribution
BORAGINACEAE (cont'd)					
Plagiobothrys fulvus (H. & A.) I.M. Johnst. var. campestris (Greene) I.M. Johnst. [var. fulvus]	nutlets 2.5-3 mm. long, rugose; plant with shaggy hairs	BB	ValleyGrassland Woodld-Savanna	CoRanges wSierraNevada (cCalif); to sOregon	[cChile]
Plagiobothrys greenei (A. Gray) I.M. Johnst. [P. gracilis (R. & P.) I.M. Johnst.]	nutlets 2.5-3 mm. long, with subulate appendages with barbed tips; plant with sharp, stiff hairs (FIG. 7)	BB	ValleyGrassland Woodld-Savanna (nr aquatic hab) vernal pools	nCoRanges, CenVall wSierraNevada (cCalif); to sOregon	[Chile: Coquimbo to Concepcion]
Plagiobothrys myosotoides (Lehm.) Brand	nutlets 1.5 mm. long, ridged; plant with stiff hairs	BB	Chaparral (rare)	Mt. Hamilton Range (n Calif) Black Mt. (Fresno Co.)	sPeru to cChile
Plagiobothrys scouleri (H. & A.) I.M. Johnst.	nutlets 1-2 mm. long, rugose, with or w/out distally branched bristles; calyx and plant with sharp stiff hairs	BB	in wet sandy or gravelly soil; meadows	Humboldt Co., Calif; to Nevada, Idaho, Oregon, BritColumbia	sChile
BRASSICACEAE			BRASSICACEAE		
Lepidium nitidum Nutt.	seed ca. 2 mm. long, mucilaginous when wet (FIGS. 17, 18)	BV	ValleyGrassland Woodld-Savanna CoSageScrub (nr aquatic hab)	CoRanges, CenVall wSierraNevada ChanIds; to nBajaCalif sWashington	Chile: Aconcaqua to Valparaiso
Thlaspi parviflorum[5] Nels. T. mexicanum Standl. [T. magellanicum Lamarck]	seed ca. 1 mm. long, mucilaginous when wet	BV	often w/sagebrush moist to dry meadows, dry grassy slopes or limestone cliffs (ca. 4000-9000')	cIdaho to wWyoming & s-c Montana (T. mexicanum: high mts. of Mexico)	[SA]

[5]See Holmgren, 1971.