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Pollination Biology and Taxonomy of *Dinemandra* and *Dinemagonum* (Malpighiaceae)

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ABSTRACT. *Dinemandra* and *Dinemagonum*, the only two genera of Malpighiaceae in Chile, have calyx glands borne on stalks rather than appressed to the surfaces of the calyx lobes as is typical of malpighs. It is proposed that this positioning of the glandular secretory surfaces (elaiophores) on the ends of stalks provides an intergland distance and surface area needed for the robust *Centris* bees that serve as pollinators. The structure of the stalked calyx glands and similarities in pollen provide evidence for the close relationships of the two genera despite their traditional placement in different tribes. However, the sister group of the two genera is impossible to determine at the present time. Extensive collections of both genera in the desertic regions of northern Chile where they are endemic has shown that each is monotypic. The previous recognition of several species in each genus resulted from few available specimens and a tendency, particularly in the case of *Dinemandra*, for plants from small isolated populations to have rather distinctive morphologies.

Of all of the countries in South America, Chile has the fewest taxa of Malpighiaceae, two genera, *Dinemandra* Adr. Juss. and *Dinemagonum* Adr. Juss., each with only one species. This low diversity undoubtedly stems in part from the fact that Chile lacks moist tropical and subtropical habitats, in which most malpighs are found. Moreover, the subtropical portion of Chile is xeric and separated from similar areas of Argentina (which could serve as sources of immigration) by the Andes. The Malpighiaceae are generally poorly represented in xeric regions such as those in northern Mexico, the southwestern United States, and northwestern Argentina. Nevertheless, what the malpighs of Chile lack in terms of diversity, they make up in novelty. Morphologically, the two genera are unusual within the family in their mutual possession of stalked calyx glands. Most of the members of the Malpighiaceae have two oval glands appressed to the dorsal side of all (five), or most of, the calyx lobes. These glands, known as elaiophores, secrete oils that are collected primarily (as judged by documented visits to malpigh flowers) by female bees of the genus *Centris* (Anthophoridae). For many malpighs, oils are the only floral rewards produced, and *Centris* species are therefore the primary or exclusive pollinators. *Centris* presumably uses the oils collected from these glands similarly to those collected from other oil-secreting species (Neff and Simpson 1981; Vogel 1974), to mix with soil to form part of the nest lining and/or in combination with pollen and nectar as part of the larval provisions. Only four genera of the Malpighiaceae are known to have stalked glands: *Dinemagonum*, *Dinemandra*, *Heladena* Adr. Juss., and *Henleophytum* Karsten. *Dinemandra* and *Dinemagonum* are distinctive in having gland stalks 1.4-2.5 mm long. In addition, the stalked glands are basally connate, forming pairs between glands on adjacent sepals. As might be expected, this strange positioning of the glands plays a role in the pollination biology.

Dinemandra and *Dinemagonum* also share the unique features of 8-colporate, reticulate pollen (Lowrie 1982). Nevertheless, Niedenzu (1928) placed the two genera in different tribes of his Pyramidotorae (=Gaudichaudioideae) because of their distinct fruit morphologies. Both have dry fruits that split into three winged segments, but the morphologies of the mericarps differ. *Dinemandra* has mericarps each of which has two large lateral wings on the dorsal surface. *Dinemagonum* has mericarps each with a single large median dorsal wing. These differences prompted Niedenzu (1928) to place *Dinemandra* in the Hiraeeae (=Hiptageae) subtribe Mascagniinae and *Dinemagonum* in the Banisterieae subtribe Banisteriinae. Despite their unusual morphology, few botanists have discussed the relationships or biology of the two genera. Works on the vegetation of northern Chile, such as those of Reiche (1907) and Johnston (1929), merely commented on their presence.

In this article I examine the unusual morphology of the flowers of *Dinemandra* and *Dinemagonum*, relate the floral morphology to the pollination system, assess the relationships of the genera to one another, and provide a systematic revision of both genera. The problems involved in trying to find their nearest relatives are also discussed.

MATERIALS AND METHODS

Pollination Ecology and Insect Behavior. Throughout the month of October 1983, field observations and photographs of floral visitors were made across the ranges of both genera. Because *Dinemandra* and *Dinemagonum* grow in the Atacama Desert region of northern Chile, where rainfall is sparse and erratic, it is often difficult to find populations in flower, and collections in herbaria are correspondingly rare. I was fortunate that in the fall of 1983, the aftereffects of the 1982–1983 El Niño were being felt and flowering throughout the region was excellent.

Flowers were fixed in FAA, later changed to 70% ethanol, for morphological and anatomical studies. Glands were plucked from other flowers, placed in chloroform in glass pharmaceutical vials, and sealed with a blowtorch for subsequent chemical analysis. Flowers were later removed from solution and the distance of the span across the posterior four glands and the maximum distance between glands across a flower were measured. Measurements were also made on sympatrically collected flowers of *Krameria cistoidea* Hook. and Arn. (Krameriaceae). The spans across the posterior four glands of *Dinemagonum* and *Dinemandra* were compared to each other and to the distance between the outer gland surfaces of *Krameria* using a GLM (General Linear Model) model of SAS (SAS 1982).

Floral and Fruit Morphology. Gland arrangements and gross morphology were viewed using scanning electron microscopy. The petals and sexual organs were removed from fluid-preserved flowers leaving the receptacle, sepals, and calyx glands intact. This material was dehydrated, critical-point dried, mounted on SEM stubs, coated with gold, and viewed with a Phillips 313 Scanning Electron Microscope. Anther morphology, stigma positions, and fruits were also assessed using SEM. Individual stamens, ovaries with intact styles, and schizocarps were similarly prepared. Pollen of mature buds was acetolyzed according to the methods of Erdtman (1960). Some of the acetolyzed grains were mounted in glycerin jelly for measurements and the rest were floated onto SEM stubs. Some grains were cut open by cutting across a stub with the edge of a microscope slide before coating. Stubs were coated with gold and viewed as above.

Anatomy. Fluid-preserved buds, open flowers, and initiating fruits were dehydrated, embedded in paraffin, sectioned transversely at 30 μm, and stained with safranin and fast green. Petals of *Dinemagonum* were rinsed, stained with osmium, and sectioned. Petals of *Dinemagonum* were also cleared and photographed in water.

RESULTS

Pollination Ecology and Insect Behavior (observations and data on pollination were provided by John Neff). Three species of anthophorid bees, *Centris chilensis*, *C. rhodophthalma*, and *C. bucholzi*, have been recorded visiting *Dinemandra* and *Dinemagonum* (fig. 1). Judging from its distribution and the morphology of its oil-collecting setae, *Centris escomeli* is also likely to be associated with *Dinemandra*. The other *Centris* of northern Chile are either non-oil-collecting, or are specialized for harvesting oils of *Calceolaria* L. (or similar) flowers. The *Centris* females involved are robust, medium-sized bees (11.5–14.5 mm long). Females of *C. rodophthalma* and *C. bucholzi* have setal-collecting structures typical of malpigh-visiting *Centris*, putatively the primitive arrangement for the genus (Neff and Simpson 1981). Females collect oils from the elaiophores of both mature buds and open flowers of *Dinemagonum*, but apparently only from open flowers of *Dinemandra*. No active pollen collection by female *Centris* was observed, but a small, pollen-collecting, undescribed, polylectic panurgine bee was abundant on *Dinemagonum* flowers at several localities. Male *Centris* patrol plants of *Dinemandra* and *Dinemagonum*, but because the flowers lack nectar, they do not visit them.

The behavior of *Centris* on *Dinemandra* and *Dinemagonum* is basically similar to that observed on most tropical malpighs. Female bees arrive, orient with their bodies along the axis of symmetry with the head at the flag (often referred to as the posterior) petal (figs. 2, 3). The bees grasp the flag with the mandibles and stroke

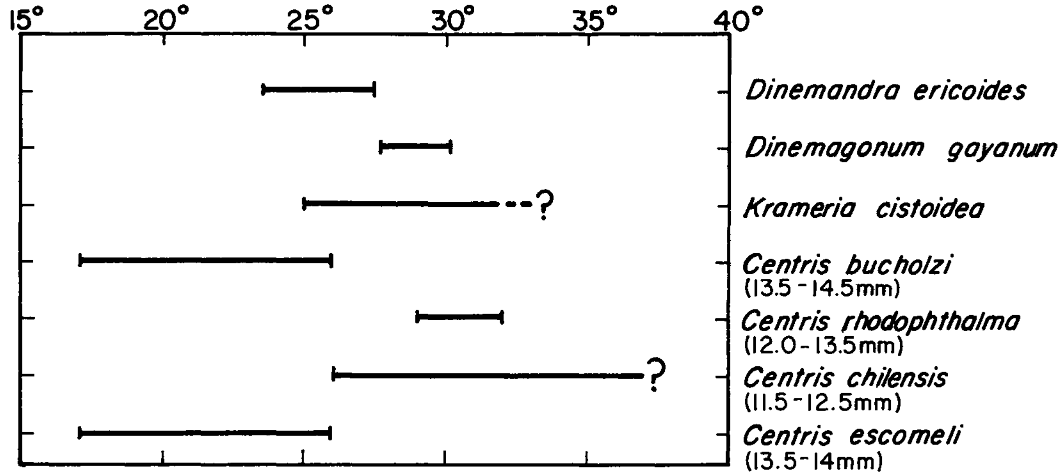


FIG. 1. Latitudinal distributions (in degrees south of the equator) of *Dinemandra ericoides. Dinemagonum gayanum, Krameria cistoidea,* and the *Centris* species that serve as their pollinators. *Centris escomeli* has never been collected on *Dinemandra* or *Dinemagonum,* but on the basis of its morphology is expected to be a visitor. The question marks indicate uncertainties about distributional limits. Floral host records from Wagenknecht (1973) and Neff (unpubl. data). Geographical distributions of bees from Moldenke (unpubl. data). The lengths of the bees (Neff, pers. comm.) are provided to show the robustness of the species involved. Lengths are proportional to mass. For reference, a honey bee is about 8-9 mm long.

the gland surfaces with both fore and mid basitarsi, thus rupturing the cuticle over the pockets of oil (figs. 3, 4). Each foreleg works one of the pair of glands flanking the flag petal; the midlegs work the pairs of anterior lateral glands. While visiting *Dinemagonum* and *Dinemandra, Centris* females use a primarily vertical stroke very similar to that employed while visiting *Krameria* (Simpson 1989; J. Neff, pers. obs.). Pollen is deposited on the thoracic venters of the bees as they work the flowers and is subsequently carried to the next flowers visited.

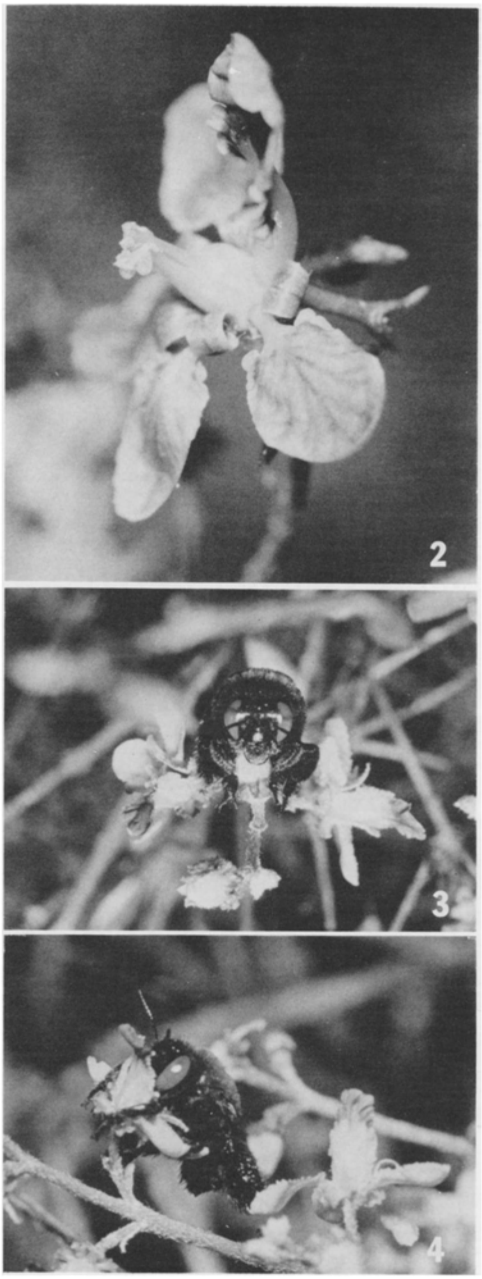
Chemical analyses performed by David Seigler (in prep.) showed that the oils secreted by the stalked glands contained primarily 3-acetoxy fatty acids, most of which have chain lengths of C_{16} and C_{18}. The most abundant compound has an NMR spectrum identical to that of the most common 3-acetoxy fatty acid found in *Krameria* species (Seigler et al. 1978). Also present in the oils were smaller amounts of glycerides, possibly diglycerides, similar to those described by Vogel (1974) as well as some unidentified polar compounds.

Measurements of the gland distances of *Dinemagonum* and *Dinemandra* and their comparisons with the measurements of *Krameria cistoidea* show that *Dinemagonum* does not differ significantly from *Krameria* but that the *Dinemandra* intergland distance is significantly smaller (table 1). Overlap, however, is extensive among all three species.

Floral and Fruit Morphology. The glands of both *Dinemandra* and *Dinemagonum* form pairs (figs. 5, 6, 9). Of interest is the fact that pair formation is between glands of adjacent calyx lobes, not between the two glands of a single sepal. There is basically no difference between the genera in morphology of gland position. The stalks either bifurcate at the tip, or expand apically into irregular, lobed shapes (figs. 5, 6, 9). The result of the apical expansion is an increase in the secretory area relative to the area of the cross-section of the stalk. The gland apices tend to be broad and lobed more often in *Dinemagonum* than in *Dinemandra.*

Both genera have three slender styles, one emerging from the ventral side of each carpel. The stigmas are inconspicuous and located at the tips and toward the interior side of each style (fig. 9). Some individuals of *Dinemandra* have one style, usually that on the opposite side of the flower from the flag petal, shorter than the other two.

Dinemandra and *Dinemagonum* flowers differ conspicuously in their stamen arrangement, filament shape and amount of connation, and number and position of fertile anthers (fig. 18,



FIGS. 2-4. Flower orientation and pollination. 2. A flower of *Dinemandra ericoides* (×6) showing the orientation of the flag petal and glands common to both *Dinemandra* and *Dinemagonum*. 3, 4. Flowers of *Dinemagonum gayanum* being visited by a female *Centris rhodophthalma* (×2.5 and 2, respectively). In figure 3, the flag petal is at the bottom under the bee. While normal orientation is with the flag petal uppermost, twisting of the branches, wind, and the weights of the bees can cause flowers to be in almost any position as was the case when this picture was taken. Photos by J. L. Neff.

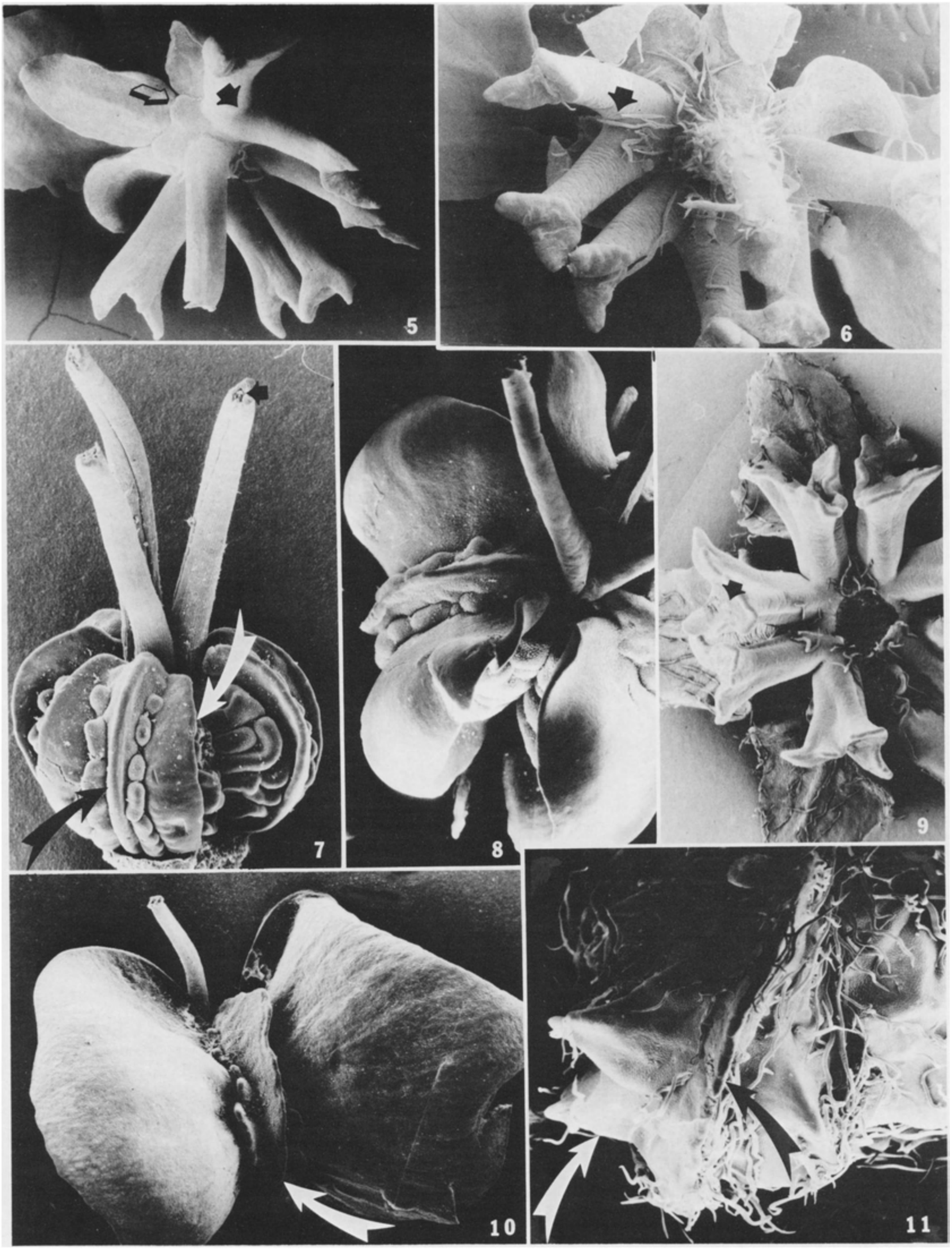
TABLE 1. Comparisons of intergland distances of *Dinemagonum*, *Dinemandra*, and *Krameria cistoidea*. Upper portion of the table, statistics for the three taxa. ^{b} and ^{c} indicate the results of the Duncan's multiple range test. The means with the same letters are statistically not different at the 0.01 level. Lower portion of the table, sum of squares table from GLM [General Linear Model, SAS (1982)] procedure.

Species	Mean	Standard dev.	*N*	Range
Dinemagonum	4.28 mm^b	0.607	59	3.2–5.4 mm
Krameria	4.07 mm^b	0.828	10	2.4–5.0 mm
Dinemandra	3.52 mm^c	0.723	98	1.4–5.8 mm

Source	d.f.	SS	Mean sq.	*F*	*P*
Model	2	21.83	10.92	22.92	<0.001
Error	164	78.10	0.48		
Corr. total	166	99.93			

20). The stamens of *Dinemagonum* are free and have slender filaments. Eight of the anthers are fertile with the two anthers opposite the sepals flanking the flag petal represented by pointed staminodes (fig. 18C). *Dinemandra* has stamens that are connate basally, forming a ring about 1 mm tall. The filaments are broad at the base and taper upward. The number of fertile anthers varies from two to four, although four is uncommon. The positions of the fertile stamens are somewhat variable (fig. 20C). Most commonly, only the two stamens opposite the anterior-lateral sepals are fertile. If three stamens are fertile, the third is that opposite the anterior sepal. In the rare cases where four stamens are fertile, one of the stamens opposite a posterior-lateral sepal is fertile. The staminodes are about one-half as long as the fertile stamens.

The anthers of both genera possess swollen glandular areas on the dorsal surface of the connectives above the point of the filament attachment (figs. 12, 13). The size, color, and appearance of the glandular areas sometimes differ between the two genera. The glandular patches on *Dinemagonum* anthers are comparatively flat and cream-colored like the locules and connectives. The two to three (occasionally four) fertile anthers of *Dinemandra* generally have pronounced, bulbous glandular areas on the con-



FIGS. 5–11. Flowers and fruits of *Dinemagonum* and *Dinemandra*. 5. A flower of *Dinemandra* seen from below showing the basal connation of glands on adjacent sepals (black arrow), the abortive glands on the anterior sepal (open arrow), and the bifurcating apices of the stalks bearing the elaiophores (×10). 6. A similar view of a flower of *Dinemagonum* (×10). In this species, the abortive glands are more difficult to see. 7. An ovary of *Dinemandra* showing the three nude styles with minute, oblique stigmas (straight black arrow)

nectives. The glandular knobs are often red. In flowers with three fertile anthers, one of the anthers is generally smaller than the other two and has a lighter colored, less prominent gland.

Palynologically, *Dinemandra* and *Dinemagonum* are extremely similar (figs. 14–17). Pollen grains of both species are generally octocolporate (varying from hexacolporate to decacolporate), with reticulate sexines. The surface of the grain of *Dinemandra* is more pronouncedly sculptured than that of *Dinemagonum* (figs. 14, 16). In cross section, the sexine is seen to consist of short, thick collumellae (figs. 15, 17). The primary differences between the genera are in the overall shape of the grains and the thickness of the nexine. Grains of *Dinemagonum* are essentially globose while those of *Dinemandra* are oblate. The nexine of *Dinemagonum* (fig. 17) is thinner than that of *Dinemandra* (fig. 15).

Anatomy. The ovaries of both genera are tricarpellate with the dorsal sides of the ovary walls ridged. By the time a flower is ready to open, the ridging pattern of the ovary indicates the final morphology of the fruit (figs. 7, 8, 10, 11, 18C, 20C). As the fruit matures, these differences are accentuated. Basically, however, the fruits show an underlying similarity.

DISCUSSION

If *Dinemagonum* and *Dinemandra* were unrelated, as indicated by Niedenzu's treatment (1928), then we would have to assume that morphological similarities in non-fruit features are the results of convergence. However, the numbers of similarities and the kinds of similar features are so striking that they argue against the use of fruit wing morphology as the major character determining tribal placement. Furthermore, an analysis of the similar characters suggests that they are shared derived features. Among the shared characters are pollen aperture number and type, exine sculpturing, calyx gland position, and gland morphology.

Dinemandra and *Dinemagonum* have an octocolporate, reticulate pollen type that is found nowhere else in the Malpighiaceae (Lowrie 1982). A tricolporate reticulate pollen similar to that found in the modern Byrsonimoideae has been postulated to be primitive in the family by Lowrie (1982). He considered the 8-colporate pollen of *Dinemandra* and *Dinemagonum* to be derived from a byrsonimoid tricolporate type. Interesting in this regard is the recent report of a fossil malpigh from the mid-Eocene of Tennessee (Taylor and Crepet 1987). The flowers of this fossil contain pollen that is tricolporate and reticulate. All other early Tertiary malpigh pollen described to date is tricolporate suggesting that, as predicted by Lowrie, it is primitive in the family. *Dinemandra* and *Dinemagonum* can therefore be considered to share unique modifications of the primitive pollen type (3-colporate and reticulate). Both the increase in the number of colpi to eight and the shortening and thickening of the columellae constitute synapomorphies of *Dinemagonum* and *Dinemandra*.

Both *Dinemagonum* and *Dinemandra* have calyx glands borne on long stalks. *Henleophytum*, one of the other two genera with stalked glands, is monotypic and confined to Cuba. It is quite distinct from the two Chilean genera in its habit (scandent subshrubs), the possession of foliar glands (lacking in both *Dinemandra* and *Dinemagonum*), 10 fertile stamens, and setose schizocarps. Its eight calyx glands, each of which is borne on a thick stalk, are flared apically into slightly concave, peltate secretory areas. Adjacent glands are not connate basally. *Heladena*, the last of the four genera with stalked glands, is a genus of about six species native to Brazil

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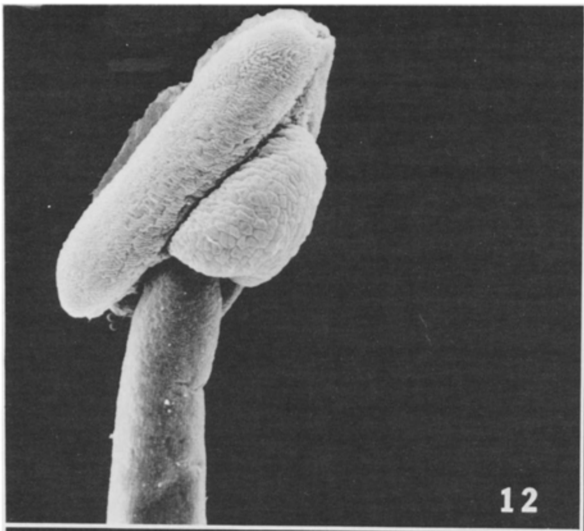
and the three ridges on the dorsal side of each mericarp (×20). The curved black arrow indicates the ridge that will be supressed in the fruit and the curved white arrow shows a ridge that will become one of the two expanded dorso-lateral wings. 8. A partially mature fruit of *Dinemandra* showing the expansion of the lateral ridges into wings (×14). 9. A basal view of a flower of *Dinemagonum* showing the tendency of some glands to have irregularly lobed, flared apices with a broad, concave secretory surface (black arrow) (×7). 10. A mature fruit of *Dinemandra* showing the occurrence in some fruits of a medial dorsal ridge (white arrow) that is expanded into a small wing (×11). 11. An ovary of *Dinemagonum* showing the three dorsal ridges of a carpel (×18). In this case, the central ridge (black arrow) will expand into a wing while the lateral ridges (one of which is indicated by the white arrow) will remain short with irregular teeth. Because of the trichomes on *Dinemagonum* ovaries and fruits, they are more difficult to photograph than those of *Dinemandra*.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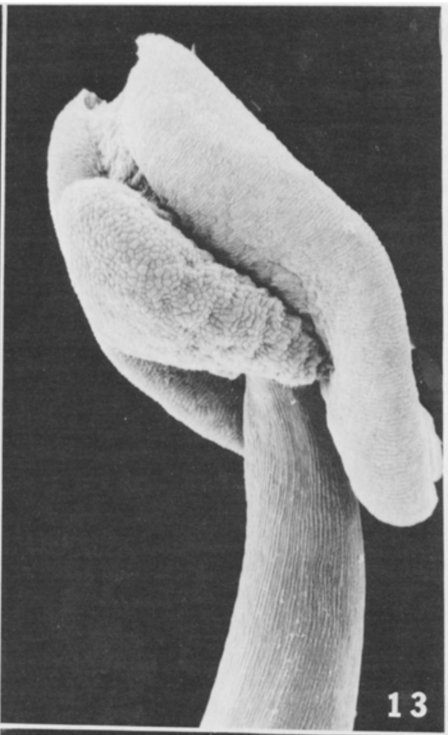
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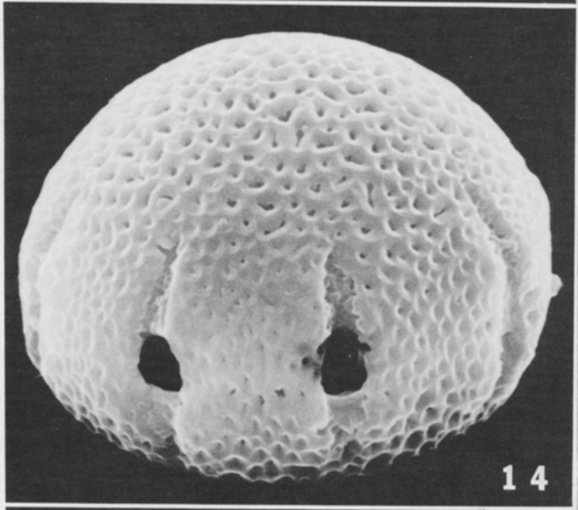
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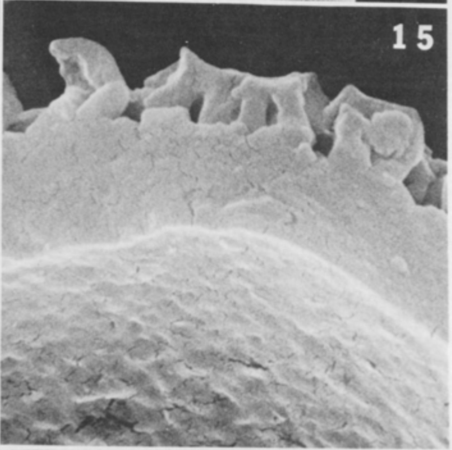
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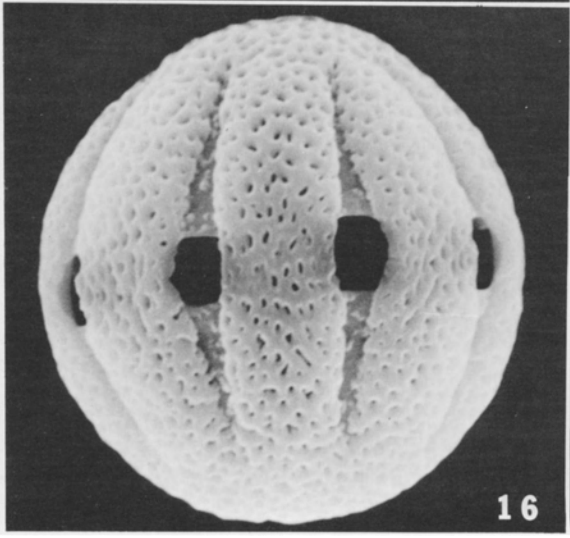
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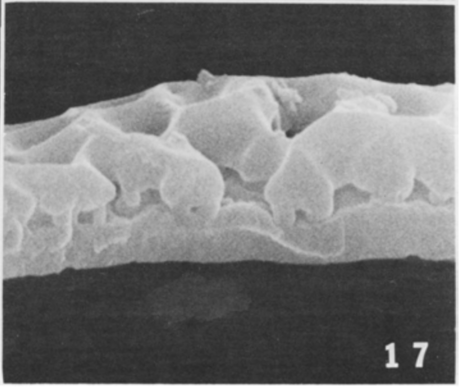
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and Argentina. Species of this genus usually have foliar glands, 10 fertile stamens, three flared stigmas, and fruits that are schizocarps. Flowers have eight sepal glands, each of which is borne on a short thin stalk. The bases of the glands are not connate and the apices are abruptly flared into peltate secretory surfaces. The character of stipitate glands thus seems to have arisen independently in *Henleophytum* and *Heladena* and does not indicate any phylogenetic relationship between them and either *Dinemandra* or *Dinemagonum.*

In contrast to the situation involving *Henleophytum* and *Heladena,* the similarities in the glands of *Dinemagonum* and *Dinemandra* argue for a close relationship. The lengths, orientations, and aspects of the secretory surfaces are similar. Both genera share, among those with stipitate-glands, the unique feature of the basal connation of adjacent glands. In fact, the glands are so similar that their structural features can be considered synapomorphies of the two genera.

If, as argued above, the stalked glands of *Dinemandra* and *Dinemagonum* are shared derived traits, the two genera must be descended from an ancestor that had stalked glands. Pushing the origin of stalked glands further back in time, however, still leaves the basic question of why stalked glands arose in the first place. If we consider the consequences of having flowers the current size of *Dinemagonum* and *Dinemandra* with glands appressed to the calyx surface, we can calculate that the distance between secretory surfaces on opposite sides of the flower would be about 2 mm. Moreover, the secretory area of each gland would be about 1.3 mm^2. The short distance between the glands would undoubtedly create a handling problem for robust *Centris.* Similarly, glands of 1.3 mm^2 would probably produce too little oil to maintain (in the absence of other oil-secreting species) robust *Centris.* For flowers the size of modern *Dinemandra* and *Dinemagonum,* bearing the glands on stalks simultaneously solves the problems of distance and gland size. By bearing the glands on stalks, flowers produce a distance between opposing secretory surfaces of up to 3.5–5 mm. The stalks also allow the apices of the glands to bifurcate or flare, thereby increasing the secretory area of the elaiophores by 50 to 130 percent. When all of the glands of a flower are considered, the secretory area could be as much as 18 times greater than that of a flower with non-stalked, non-apically expanded glands.

It is difficult to say whether the pre-stalked ancestor was large-flowered with selection favoring reduction in flower size while maintaining adequate inter-gland distance and gland surface area, or if it was small-flowered with selection for increasing the intergland distance and gland surface area. It seems most likely, because *Dinemandra* and *Dinemagonum* have flowers smaller than those of most malpighs, that flower size has been reduced, perhaps because of the advantage conferred by restricting transpirational loss in the desertic Atacama climate. The hypothesis of a reduction in size from a larger, stalkless ancestor is also supported by the pollinator relationships. All of the close relatives of the *Centris* associated with *Dinemandra* and *Dinemagonum* are also robust bees. A postulation of a small-flowered ancestor for this clade with stalkless glands would necessitate the presence of a small, now extinct *Centris.* Nothing in northern Chile indicates such a bee ever existed there. Some small members of the genus *Paratetrapedia* are of the right size, but they are absent from Chile. Nevertheless, final resolution of this issue must remain speculative until a clearer idea of the relationships of the genera has emerged.

Determination of the relationships of *Dinemandra* and *Dinemagonum* has, however, proved to be extremely difficult. As this study indicates, and as Anderson (1977) and Lowrie (1982) have pointed out, the fruit features traditionally deemed important as defining characters of in-

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FIGS. 12–17. Anthers and pollen. 12, 13. Anthers of *Dinemagonum* (×23) and *Dinemandra* (×52), respectively, showing the similarity in the glandular area of the connective. 14. A pollen grain of *Dinemandra* (×3225) showing the oblate form and four of the eight apertures. 15. Cross section of a pollen grain of *Dinemandra* showing the thick nexine (×10,044). 16. A pollen grain of *Dinemagonum* (×2861) illustrating the spherical shape. 17. Cross section of a grain of *Dinemagonum* (×11,979) showing the comparatively thin nexine.

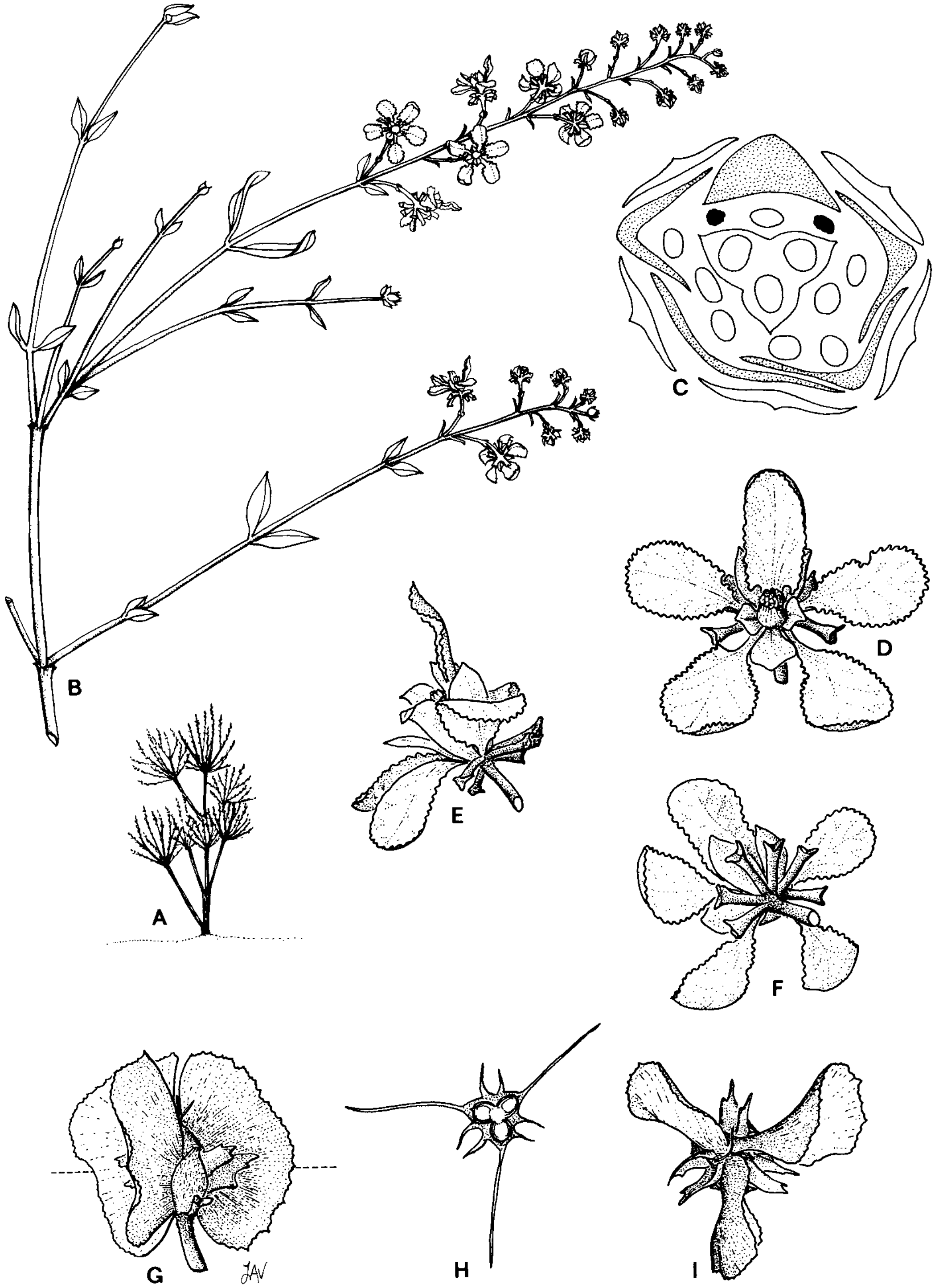

FIG. 18. *Dinemagonum gayanum.* A. Habit (×0.02). B. A branch (×1.6). C. Floral diagram showing the outline of the gynoecium in the bud and the positions of the fertile and sterile stamens. Petals are indicated by stippling. The largest petal (top) is the flag petal. Staminodia are black. D. Flower, apical view (×1.6). E. Flower, lateral view (×1.6). F. Flower basal view (×2). G. Fruit, lateral view (×1.6). H. Cross section of a fruit through the plane indicated in G (×1.6). I. Fruit, apical view (×1.6).

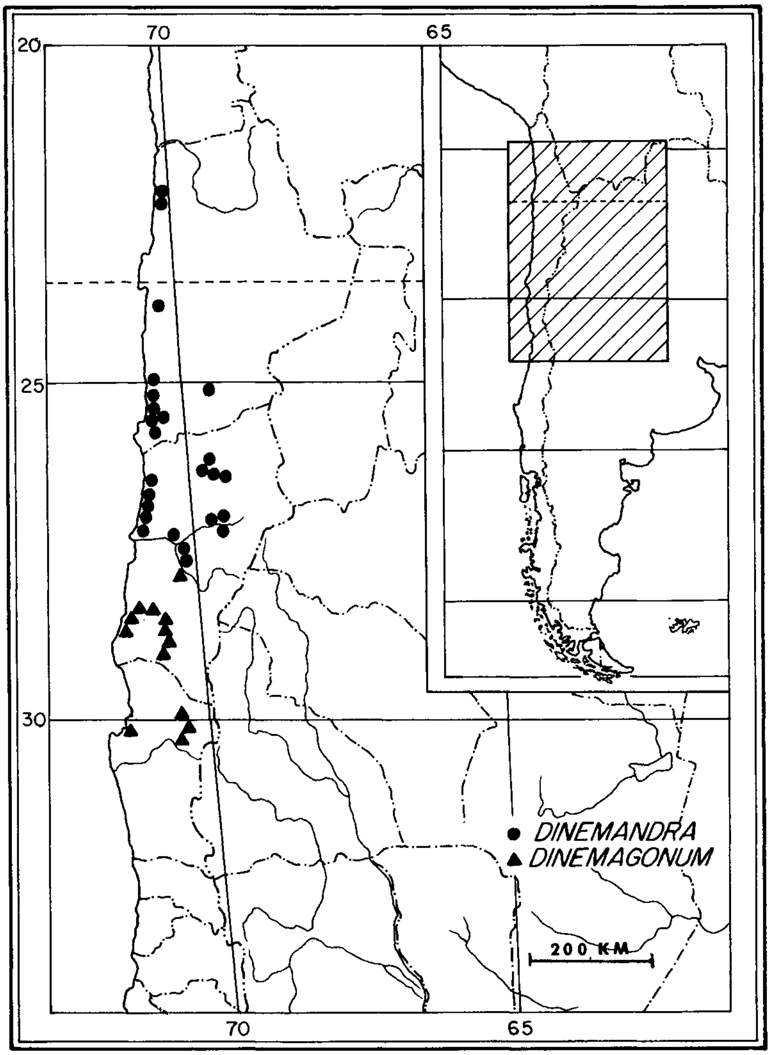

FIG. 19. Distribution of *Dinemagonum* and *Dinemandra* in Chile.

trafamilial groups in malpigh systematics are homoplasious and cannot be confidently used to determine relationships. Most floral characters, on the other hand, are so constant throughout the family that they provide few clues to relationships (Anderson 1979). *Dinemandra* and *Dinemagonum* do share the homologous floral character of specialized stalked glands, but features of the glands are unique to these two genera and, thus, give no indication about a sister group. Adrien de Jussieu (1843–1844) placed both genera together in the Hireae (Pleuropterygieae), and Baillon (1878) considered the genera related to one another, placing them in the equivalent group (his Hiraea series) with the comment that the two genera could be considered intermediate between the Hiraea and the Gaudichaudia Series.

Characters recently explored by Lowrie (1982) that show promise in helping to indicate generic relationships in the family are those of pollen grains. Pollen aperture type and exine sculpturing provide characters that appear to define monophyletic groups and provide some of the synapomorphies of *Dinemandra* and *Dinemagonum*. Lowrie (1982) placed both genera with *Lasiocarpus* Liebm. and *Ptilochaeta* Turcz. in his "Lasiocarpus" pollen group because of the common possession by the four genera of polycolporate, reticulate pollen grains. *Lasiocarpus* and *Ptilochaeta*, however, have pollen that is more similar to one another than to either *Di-*

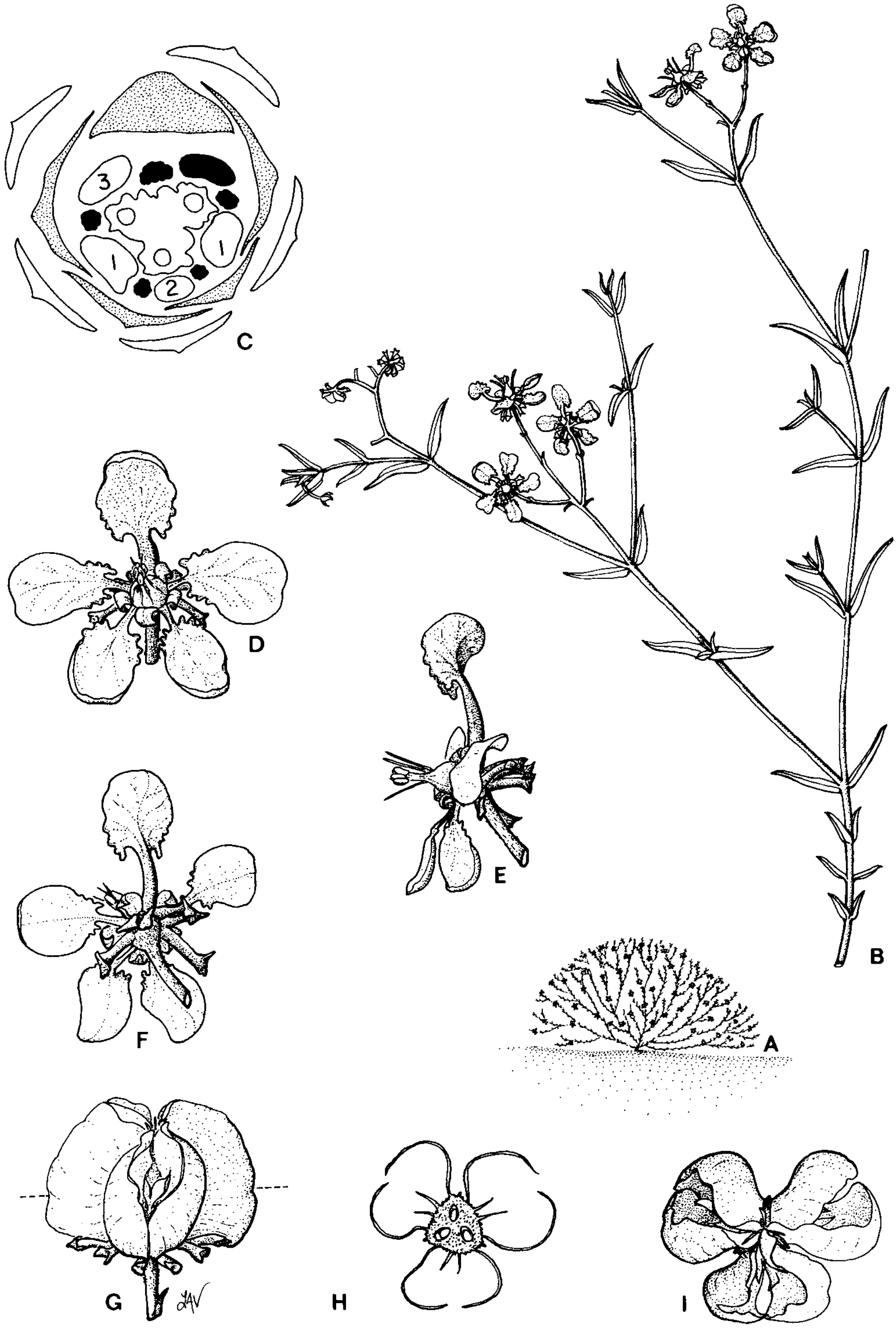

FIG. 20. *Dinemandra ericoides*. A. Habit (×0.04). B. A branch (×1.6). C. Floral diagram showing the shape of the gynoecium in bud and the positions of the fertile and sterile stamens. The diagram shows a view above the level at which the stamens and staminodia are connate. Petals are indicated by stippling. The largest petal

nemagonum or *Dinemandra.* The first of these genera consists of about four Mexican species and the second contains five tropical South American species, one of which occurs in Argentina. Lowrie suggested that the "Lasiocarpus" group might be the sister group of most of the wing-fruited Malpighiaceae, but, other than pollen characters, there is no evidence that *Lasiocarpus* and *Ptilochaeta* together constitute the sister clade of *Dinemandra* and *Dinemagonum* or, if so, if the entire assemblage is an offshoot of the lineage that led to the other winged members of the family.

It, therefore, appears that determination of the relationships of *Dinemandra* and *Dinemagonum,* as well as a solution to the problems of higher order classification within the Malpighiaceae as a whole, must await additional data from new sources. DNA restriction site data, now being gathered by William R. Anderson (pers. comm.) and Mark W. Chase may provide the information needed.

Given the close relationship of *Dinemandra* and *Dinemagonum,* their retention as distinct genera may appear somewhat arbitrary. I have retained them as separate genera in part because of historical reasons, and in part because the extent of their differences (e.g., the position of the sterile stamens) is as great as that between many currently recognized genera in the family.

SYSTEMATIC TREATMENT

Excluding my specimens, there are very few collections of *Dinemagonum* and *Dinemandra.* Material of the 12 large herbaria from which I borrowed specimens totaled only 100 sheets, many of which were duplicates. The localities of the representative specimens are given using the new Chilean system of Regions and Provinces whether or not the specimen cited used these political divisions. Unless otherwise stated, all types are designated herein. Specimens cited are arranged geographically from north to south.

ARTIFICIAL KEY TO THE GENERA

1. Stiff, upright subshrubs, with woody basal stems; young stems green, white-sericeous, robust, often congested; leaves generally lanceolate, attenuate at the base; inflorescences of terminal pseudoracemes; petals yellow with the flag (posterior) petal entirely yellow or with variable amounts of red on the blade, the remaining petals completely yellow; stamens 10 with slender filaments distinct to the base, two reduced to pointed staminodia, eight with fertile anthers; fruiting mericarps each with a prominent medial dorsal wing, occasionally with lateral ridges; Regions III [Atacama] and IV [Coquimbo] from 27.8°S to 30.10°S latitude .... 1. *Dinemagonum*
1. Mounded subshrubs woody only at the very base; young stems glabrous and reddish, or white-villous, delicate in appearance, not congested; leaves generally oblanceolate, abruptly cuneate at the base; inflorescences of terminal and axillary few to several-flowered panicles; petals yellow with all of the petals bearing red markings; stamens 10, connate basally forming a ring, with six to eight reduced to short staminodia and two to four with fertile anthers; fruiting mericarps each with two expanded dorso-lateral wings and a median dorsal ridge; Regions II [Antofagasta] and III [Atacama] from 23.6°S to 27.5°S latitude .... 2. *Dinemandra*

1. *DINEMAGONUM* Adr. Juss., Arch. Mus. Hist. Nat. 3:585. 1844.—TYPE SPECIES: *D. bridgesianum* Adr. Juss. (=*D. gayanum* Adr. Juss.). Name from the Greek meaning two filaments sterile.

A monotypic genus (fig. 18). A combined generic-specific description follows the synonymy of *Dinemagonum gayanum.*

DINEMAGONUM GAYANUM Adr. Juss., Arch. Mus. Hist. Nat. 3:585. 1844 (also Monogr. Mal-

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(top) is the flag petal. Staminodia are indicated in black. The numbers indicate the most common arrangements of fertile stamens. The two stamens labeled 1 are almost always fertile. The stamen labeled 2 will be fertile if there are three fertile stamens, although sometimes this stamen and only one of the anterior-lateral stamens will be fertile. If there are four fertile stamens, one of the posterior-lateral stamens (number 3) will be fertile. D. Flower, apical view (×1.6). E. Flower, lateral view (×1.6). F. Flower basal view (×1.6). G. Fruit, lateral view (×1.6). H. Cross section of a fruit through the plane indicated in G (×1.6). I. Fruit, apical view (×1.6).

pigh. 331. 1844).—TYPE: Chile, [Region IV, Coquimbo], *Gay 277* (lectotype: P-JU, sprig on the upper right [IDC Microfiche of the Jussieu Herbarium 871, Catal. #11742!]). The label on the specimen in the Jussieu Herbarium has two localities, "Cerros d'Arquerros a 1630 mts. de hauteur" and "Rividavia a 1930 mts. de hauteur." On the sheet are five sprigs. The combination of the label data and the fact that there are separate entities mounted on the sheet indicate that the collection is a mixed one.

Dinemagonum bridgesianum Adr. Juss., Arch. Mus. Hist. Nat. 3:585. 1844 (also Monogr. Malpigh. 333. 1844).—*Dinemagonum* (as *Dimagonum*) *gayanum* var. *bridgesianum* (Adr. Juss.) Reiche, Anales Univ. Chile 93:564. 1896 (also Fl. Chile 1:272. 1896).—TYPE: Chile, [Region IV] Coquimbo, near Coquimbo, Mar 1842, *Bridges 1294* (holotype: G-DEL; isotypes: BM! (2), K!, P! [IDC Microfiche of the Jussieu Herbarium 871, Catal. #11743], [Field Museum neg. #24277 of isolectotype at G, BM!, G!, K!, P!]).

Dinemagonum albicaule Philippi, Anales Univ. Chile 18:44. 1861 (also in Linnaea 33:32. 1864).—*Dinemagonum* (as *Dimagonum*) *gayanum* var. *albicaule* (Philippi) Reiche, Anales Univ. Chile 93:564. 1896 (also Fl. Chile 1: 272. 1896).—TYPE: Chile, [Region III, Atacama], Vallenar, Sep, *Volckmann s.n.*, (presumably destroyed in World War II at Berlin).—NEOTYPE: Chile, [Region III, Atacama], Vallenar, *Philippi s.n.* (BM, right side!).

Dinemagonum maculigerum Philippi, Anales Univ. Chile. 82:725. 1893.—TYPE: Chile, [Region III], Atacama, Huasco, 1885, *Philippi 1926a* (lectotype: SGO 040727!; isolectotype: BM, upper plant!, [Photos of SGO 040727 at BM!, GH!]). Two specimens, SGO 040727 and SGO 051488, were listed as types by C. Muñoz P. (1960). Because only the former has a Philippi collection number, it is designated here as the lectotype.

Dinemagonum bridgesianum f. *glanduloso-bracteolata* Niedenzu, Pflanzenr. IV. 141(1)[Heft 93]:462. 1928.—TYPE: Chile, [Region III, Atacama], Huasco, *Philippi s.n.* (presumably destroyed during World War II).—NEOTYPE: Chile, [Region III, Atacama], Huasco, *Philippi s.n.* (SGO 0511480!).

Dinemagonum bridgesianum var. *parvifolium* Niedenzu, Pflanzenr. IV. 141(1)[Heft 93]: 462. 1928.—TYPE: Chile, [RegionIII], Atacama, Vallenar [Alta de Carmen], Nov 1923, 800 m, *Werdermann 157* (lectotype: K!; isolectotypes: BM!, G!, GH!, UC!, [Field Mus. neg. #24228 of isolectotype at G!]). The specimen on which Niedenzu based his description was presumably at B but destroyed during World War II. The specimen at K is designated here as the lectotype.

Subshrubs to shrubs 10 cm to 1.5 m tall; branches dichotomous, often fastigiate; old stems gray-white, covered with a fissured wax layer; young stems green, appearing white because of the dense vestiture of appressed trichomes. Leaves opposite, eglandular, lacking stipules, variable in abundance, sometimes numerous on young growth, at other times almost restricted to the flowering apices of the stems, lanceolate, acute to obtuse at the apex, attenuate at the base, occasionally forming a short petiole ca. 1 mm long, entire, sometimes slightly revolute when dry, decreasing in size distally with the lowermost 6–18 mm long and 2.5–6 mm wide, vestitured with variable densities of trichomes, bright green, often with a conspicuous median vein on the lower surface. Inflorescences of terminal pseudoracemes with densely setose rachises; individual flowers borne on pedicels subtended by a leafy bract; bracts decreasing in size distally, lanceolate, entire, acute apically, sessile, with variable amounts of T-shaped trichomes; peduncle and pedicel separated by a pair of minute, ovate, marginally scarious, setose bracteoles, 1–2 mm long and ca. 1 mm wide. Flowers bilaterally symmetrical; sepals 5 with lobes distinct, 3–6 mm long, 1–3 mm wide, ovate, entire, acute, with the sepals flanking the flag (posterior) petal each bearing 2 stipitate glands, each anterior-lateral pair of sepals with 1 stipitate gland and 1 suppressed gland, and the anterior sepal (opposite the flag petal) eglandular; glands of adjacent sepals united basally but those of the same sepal separated by 0.33–0.66 mm leading to the production of 3 pairs of glands from adjacent sepals; glands yellow, red, or brown, with stalks 1.4–2.5 mm long, sometimes vestitured along the shaft, bifurcating or flaring apically into a broad, oval to irregularly lobed concave glandular area up to 2 mm long; petals 5, clawed; posterior (flag) petal 7–9 mm long with the blade 5–6.5 mm long and 4.5–6 mm wide, oblong in outline, dentate with many of the teeth primarily those at the base of the blade, inflated and appearing glandular, yellow with the blade partially or completely red; lateral petals clawed, 7–8 mm long with oblong blades 5–6 mm long and 4.5–5 mm wide, extremely denticulate, often with the teeth swollen and glandular, yellow; stamens 10, 2 opposite the sepals flanking the flag petal reduced to staminodia, 8 remaining fertile, ca. 3 mm long; anthers dorsifixed, ca. 1 mm long with the connective bearing a protruding yellow glandular area ca. 0.5 mm long; pollen ovoid to spherical, 34–36 μm in equatorial diameter, reticulate; ovary trilobed due to connation of 3 carpels, irregularly shaped with the dorsal surface of each carpel bearing 3 irregular ridges, densely villous; styles 3, nude, each 2.5–3.5 mm long, tipped with an oblique minute stigma; ovule 1 per carpel, borne parietally, extremely concavely curved so as to form a tight "U" shape. Fruit composed of 3 mericarps that separate at maturity; each mericarp with a body ca. 3 mm long and 2 mm wide, rugose dorsally, bearing a single large median wing and often 2 dorsolateral ridges sometimes with prominent teeth to 2 mm long; wing semicircular, serrate, 10–11 mm long and 5–7 mm wide at maturity, red; seed 1 per mericarp, concavely curved with a smooth, yellow-white seed coat, lacking endosperm; embryo green, with unequal cotyledons. Chromosome number unknown.

Distribution. Rocky slopes in the shrub desert of Chile in Regions III [Atacama] and IV [Coquimbo] from 27.8° to 30.10°S at elevations from sea level to about 1100 m (fig. 19). Flowering can occur from August to November depending on rainfall, but is usually confined to October.

Common names. "pingo blanco," fide *Geisse s.n.* (GH).

When Adrien de Jussieu (1843–1844) described *Dinemagonum,* he suggested that there were two species that differed primarily in the number of inflated, glandular teeth on the margins of the petal blades. *Dinemagonum gayanum* was reported as having inflated glandular teeth only along the basal margins of the petal blades whereas *D. bridgesianum* was noted to have blades with edges that were completely glandular-ciliate. Reiche (1986a, 1986b) combined the two species, indicating that he found that the number of inflated teeth of the petals to be extremely variable. He did, however, maintain *bridgesianum* as a variety of *D. gayanum.* In addition, he placed a species described by Philippi, *D. albicaule,* into *D. gayanum* as a third variety. This variety was reported to differ from the other two in being particularly densely vestitured with long silky trichomes and to have flag petals with basal blade margins glandularly toothed and the remaining margins fringed. However, as mentioned above, the amount of serration and/or the degree of glandularity of the teeth is extremely variable even within populations and cannot be used as a character to separate taxa, even infraspecific taxa.

Reiche also recognized a second species of *Dinemagonum, D. maculigerum,* described by Philippi from Huasco on the coast west of Vallenar. This species was described as having a red "moon" on the posterior petal in contrast to the presumably entirely yellow posterior petal of *D. gayanum.* John Neff and I have collected *Dinemagonum* from Paiguano in northern Coquimbo to Huasco, Atacama, and in all cases the posterior petal had some red marking. The amount of red varies from a stripe across the blade to an entirely red blade. There is no clinal pattern in the amount of red on the flag petal. It is noteworthy that Niedenzu described a form of *D. bridgesianum, D. bridgesianum* f. *glanduloso-bracteolata,* from a Philippi specimen also from Huasco. We found that the population of this species at Huasco was the most variable of any sampled. However, characters varied on a plant-to-plant basis leading to a polymorphic population in which no discrete species or infraspecific taxa could be defined. This same lack of constancy of characters prompted Marticorena (1962) to suspect that there was only one species in the genus.

Representative specimens examined. CHILE. **Region III** [Atacama]: Prov. Huasco, 88.5 km N of La Serena on Rt 5, 8 Oct 1983, *Simpson 83-10-8-2* (MICH, MO, NY, TEX); 125.9 km N of La Serena at Cuesta Pajonales, 8 Oct 1983, *Simpson 83-10-8-4* (MICH, NY, TEX, US); 179 km N of La Serena, S of Vallenar, 8 Oct 1983, *Simpson 83-10-8-5* (F, MICH, TEX); 5 mi N of Freirina between Freirina and Astillas, 250 m, 9 Oct 1983, *Simpson 83-10-9-3* (MICH, MO, TEX); ca. 3 km S of the turn to Vallenar on Pan American Hwy (Rt 5), 500 m, 9 Oct 1983, *Simpson 83-10-9-4a* (TEX); km 646, 15 km S of the turn to Vallenar, 640 m, 23 Oct 1983, *Simpson 83-10-23-2* (CONC, MICH, MO, TEX, US); km 664, 6.5 km S of the turn to Vallenar, 22 Oct 1983, *Simpson 83-*

10-22-1 (MICH, TEX); 4.5 km S of the turn to Vallenar, 22 Oct 1983, *Simpson 83-10-22-2* (CONC, F, MICH, MO, TEX); Vallenar, Oct 1927, *Claude-Joseph 5111* (US); Huasco, a little W of the main town, 10 m, 9 Oct 1983, *Simpson 83-10-9-1, 83-10-9-2* (MICH, MO, TEX); 4 km S of the turn to Domekyo on Rt 5, 940 m, 23 Oct 1983, *Simpson 83-10-23-3* (F, MICH, TEX); ca. 3 km SW of Huasco, 25 m, 27 Oct 1938, *Worth & Morrison 16239* (UC); coast between Copiapó and Vallenar, 200 m, 15 Oct 1983, *Rodríguez 9* (K); prov. Copiapó, vic. of Chañarcillo, *Geisse s.n.* (GH). **Region IV** [Coquimbo]: 1839, *Gay s.n.* (G, [Field Museum neg. #24229 at G, GH, MICH, US]); 1938, *Gay s.n.* (P); prov. Elqui, between Paiguano and Monte Grande, 27 km N of Paiguano, 7 Oct 1983, *Simpson 83-10-7-6* (TEX); on the rd. from Rividavia to Paiguano, 850 m, 4 Oct 1948, *Ricardi 8470* (SGO); between Paiguano and Monte Grande, 6.5 km N of Paiguano, 7 Oct 1983, *Simpson 83-10-7-7* (MICH, MO, NY, TEX); 4 km beyond Vicuña on the road to Huertado, 750 m, 7 Oct 1983, *Simpson 83-10-7-9* (MICH, TEX); rd. from Vicuña to Hurtado, 740 m, 24 Oct 1983, *Simpson 83-10-24-1* (CONC, MICH, MO, NY, TEX); 1000 m, 13 Oct 1940, *Looser 4250* (GH); Monte Grande 18 km S of Rividavia 2 km W of village, 1000 m, 10 Aug 1940, *Wagenknecht 18537* (G, GH, UC); Valley of Río Claro between Rividavia and Paiguano, gritty clay, 900 m, Nov 1935, *West 3894* (GH, UC); ca 4 km from Rividavia on rd. to Paiguano, 860, 4 Nov 1938, *Worth & Morrison 16375* (UC); Cuesta El Almendro, 18 km on the rd. to Hurtado, 1100 m, 10 Oct 1939, *Wagenknecht 18463* (UC).

2. *Dinemandra* Adr. Juss., Ann. Sci. Nat. Bot. Sér. 2, 13:255. 1840.—Type species: *Dinemandra ericoides* Adr. Juss. Hutchinson (1967) listed Endlicher's *Genera plantarum* (p. 1059) as the place of publication of this genus. According to Stafleu and Cowan (1976, p. 750 and 1979, p. 476), Vol. 13 of the Ann. Sci. Nat. Bot. Sér. 2 and the *Genera Plantarum* were both issued in April of 1840. I consider the Annales the original place of publication.

A monotypic genus (fig. 20). The combined generic and specific description follows the synonymy of *D. ericoides*. Name from the Greek meaning two filaments male.

Dinemandra sect. *Trinemandra* Niedenzu, Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4:24. 1912.

Dinemandra sect. *Eudinemandra* (=*Dinemandra*) Niedenzu, Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4:25. 1912.

Dinemandra ericoides Adr. Juss., Ann. Sci. Nat. Bot. Sér. 2, 13:255. 1840.—Type: Chile, [Region II] Antofagasta, [Prov. Tocopilla], Cobija, 1839, *Gaudichaud s.n.* (lectotype: P-JU, lower right [IDC Microfiche of the Jussieu Herbarium 871, Catal. #11740!]; isolectotypes: G!, P!, [Field Museum neg. #24267 of isolectotype at G at GH!, MICH!]).

Dinemandra glaberrima Adr. Juss., Arch. Mus. Hist. Nat. 3:583. 1844 (also Monogr. Malpigh. 329. 1844).—Type: Chile, [Region III], Atacama, Copiapó, base of the cordillera near Potero Grande, Dec, *Gay s.n.* (lectotype: P-JU [IDC Microfiche of the Jussieu Herbarium 871, Catal. #117741!]; isolectotype: P!, [Field Museum neg. #35619 of isolectotype at P at GH!, MICH!, UC!]).

Dinemandra strigosa Philippi, Fl. Atacam. 12(50). 1860.—Type: Chile, [Region II], Antofagasta, beach near Paposa, Dec 1885, *Philippi 249* (lectotype: SGO 040736!).

Dinemandra ramosissima Philippi, Fl. Atacam. 12(51). 1860.—Type: Chile, [Region III], Atacama, Caldera, Dec 1853, *Philippi 248* (lectotype: SGO 040732! [photo of lectotype at GH!]).

Dinemandra subaptera Philippi, Fl. Atacam. 12(52). 1860.—Type: Chile, [Region III], Atacama, between Agua Dulce and Chañaral, Jan 1854, *without collector or number* (lectotype, chosen by C. Muñoz P. 1960: SGO 051499!).

Dinemandra glauca Baillon, Hist. Pl. 5:440. 1874. nom. nud. This name, used as a label for the flowers in figures 443–448 of Baillon's work, was never validly published. Niedenzu (1928, p. 236) listed it at the end of his treatment calling it "a species known only from a figure."

Dinemandra ericoides var. *triandra* Niedenzu, Feddes Repert. Spec. Nov. Regni Veg. 26: 345. 1929.—Type: Chile, [Region II], Antofagasta, Taltal, *Werdermann 1449* or *Wedermann 1563*. Both of these specimens were presumably lost during World War II and I have not been able to locate duplicates of either.—Neotype: Chile, Region II, [Antofagasta], Quebrada Taltal, 1 km S of Breas, 600 m, 2 Feb 1952, *Hutchison 415* (US!; isoneotypes: SGO!, UC!).

Mounded subshrubs to 50 cm tall, branching dichotomously, occasionally alternately; old stems gray, striate or fissured, or red-brown and striate; young stems green, glabrous, or densely hispid. Leaves usually opposite, eglandular, lacking stipules, sessile, lanceolate, variable in size and density, either small, numerous, and very congested on the stems, 3.5–7.0 mm long, 1.2–2 mm wide with internodes of 1 mm, or large, 9–20 mm long, 3–5 mm wide with internodes of 1–2 cm, sometimes with small leaves at the bases of the branches and larger, more widely spaced leaves above, revolute, sometimes so strongly so as to make the leaves appear linear, acute at the apex, when paired usually cordate at the base and forming a sheath around the stem, if solitary, often cuneate at the base, usually with trichomes at the point of attachment on the abaxial side, dark to bright green above, generally light green with a prominent red, tan, or beige midvein below, coriaceous, glabrous to densely vestitured. Inflorescences of compound, sometimes dichotomously branched, panicles; rachises glabrous or vestitured; individual flowers borne on pedicels subtended by a minute pair of ovate, acute bracteoles, 0.5–2 mm long, 0.5–1.0 mm wide; peduncles equal to or longer than the pedicel of a given flowering stalk, 2.0–7.0 mm long; pedicels 2.0–4.0 mm long, sometimes brown. Flowers bilaterally symmetrical; sepals 5, distinct, 2.0–3.5 mm long, 1.0–1.5 mm wide, ovate, entire, acute at the apex, marginally scarious, with the sepals flanking the flag petal each bearing 2 stipitate glands, the anterior-lateral sepals each bearing one stipitate gland and one suppressed gland, the anterior sepal eglandular; glands formed into 3 pairs by the basal connation of glands on adjacent sepals; individual glands red with stalks ca. 2 mm long and 0.25 mm in diameter, expanded apically into glandular, concave, forked, or irregularly lobed secretory areas up to 2 mm across the widest portion; petals 5, clawed; flag (posterior) petal 5.0–7.0 mm long with a blade 3.0–4.0 mm long, 2.5–4.0 mm wide, orbicular to rectangular in outline, abruptly cuneate at the base, with margins undulate above, more dentate below with the teeth inflated for about 1 mm on either side of the claw, yellow with a medial red spot; lateral petals clawed, 5–6 mm long with orbicular blades 4–5 mm long, 3–4 mm wide with simple undulate margins, or occasionally with glandular swellings at the tips of the teeth on the lower portions of the blades, yellow, often with red streaks; stamens 10, 6–8 staminoidia 1.0–2.0 mm long, opposite all of the petals, usually both of the posterior-lateral sepals and often opposite the anterior sepal, 2–4 fertile, 2.0–3.5 mm long, opposite the 2 anterior-lateral sepals, sometimes also the anterior sepal, occasionally also 1 posterior-lateral sepal; filaments of both the staminodia and fertile stamens tapering apically from a broad base, connate basally for 0.5–1.0 mm forming a ring; anthers dorsifixed, bearing a red or brown globose gland of variable size on the connective, variable in size, if 2 anthers are fertile, the glands are generally of the same size, if 3 or 4 anthers are fertile, often with 1 or 2 of the glands smaller than the others; pollen oblate, 36–46 μm in equatorial diameter, reticulate; ovary 3-carpellate with each carpel glabrous and bearing a medial and 2 lateral vertical ridges separated by horizontal rugose striations; styles 3, nude, 2.0–3.0 mm long, often with 1 of the 3 about 0.5 mm shorter than the other 2, each bearing a small subterminal stigma; ovule 1 per carpel, attached near the top of the inner wall, descending and then recurved into a "U" shape. Fruit composed of 3 mericarps separating at maturity; each mericarp wedge-shaped with the body of the mericarp 2.0–3.0 mm tall, 1.0–2.0 mm wide, bearing 2 large lateral wings each recurved in a direction away from the dorsal center of the mericarp with each wing about 6 mm in the vertical dimension, 4 mm in the horizontal dimension, and a median ridge often expanded into triangular projections of various sizes, knobby and villous between the wings and the dorsal ridge, rugose and villous between the wings and the edge of the mericarp, beige, red, or light brown with red markings; seed 1 per mericarp, concavely curved with a smooth to slightly rugose, yellow-white seed coat. Chromosome number unknown.

Distribution. Spottily distributed in gravel and sandy arid areas below the fog belt (sensu Johnston 1929) in the Atacama Desert, primarily in dry drainage basins and outwash areas near the ocean in the Chilean Regions II [Antofagasta] and III [Atacama] from 22.2°S to 27.5°S latitude at elevations from sea level to 2600 m (fig. 19). Flowering and fruiting from September to December.

Common names. "té bravo," "colorado," fide *Gigoux s.n.* (GH).

Compared to *Dinemagonum, Dinemandra* shows considerable interpopulational variation. Populations have been described as species on the basis of the number of fertile anthers and the density of trichomes on the leaves. According to the original descriptions by de Jussieu, *D. ericoides* was vestitured, had linear-ovate leaves, racemose inflorescences, and flowers with two fertile anthers. *Dinemandra glaberrima* was distinguished by its glabrous foliage, dichotomously branched inflorescences, and three fertile anthers. Philippi later described three additional species of *Dinemandra* that he distinguished from one another primarily on the basis of vestiture and the branching patterns of the inflorescences. *Dinemandra strigosa* was reported to have strigose herbage and strongly dichotomously branched inflorescences. *Dinemandra ramosissima* was purported to be glabrous and to have dichotomously branched panicles. The last of Philippi's species, *D. subaptera,* was described as being glabrous, few-flowered with axillary and terminal panicles, and to have fruits with narrow fruit wings compared to the other species of the genus.

Dinemandra ericoides was not treated in either Gay (1847) or Reiche (1896a, 1986b) because it was considered to be a Peruvian species (Antofagasta was at that time part of Perú), but Reiche recognized two of Philippi's species as well as *D. glaberrima* of de Jussieu. He, like Philippi, considered the presence or absence of trichomes to be a sufficient character for species delimitation and separated *D. strigosa* from the other species in his treatment on the basis of its possession of white trichomes. He also maintained that *D. glaberrima* consisted of very ramified plants with dichotomously branched inflorescences while plants of *D. ramosissima* were comparatively open with 5–7-flowered inflorescences. Reiche considered *D. subaptera* of Philippi to be a doubtful species because it had been described from a specimen with immature fruit. Consequently the small size of the fruit wing used by Philippi as a major character of the species was considered an artifact of incomplete development.

Niedenzu (1912) erected two sections for the species of *Dinemandra* circumscribed by de Jussieu and Philippi. The first of his sections, *Trinemandra,* was characterized as having three fertile anthers with the median one lacking a gland on the connective. He included two glabrous species, *D. ramosissima* and *D. glaberrima,* in this section. The first of these species, occurring in Atacama, was described as having racemes with 3–7 flowers and semicircular lateral wings on the fruits measuring 4 mm wide. The second species, from the Valley of Copiapó, supposedly had two-flowered inflorescences and suborbicular wings 4.5 mm wide. The second section, *Dinemandra* (=*Eudinemandra* of Niedenzu), contained glabrous or vestitured species with two fertile stamens. *Dinemandra subaptera,* the only glabrous member of the section, was described as having racemes with four flowers and samaras with the long axis greater than the latitudinal axis. The two vestitured species, *D. ericoides* and *D. strigosa,* were both listed as having racemes with 4–6 flowers but to differ in their leaf shape and in the thickness of the trichome walls and lumen. The former had lanceolate leaves that appeared ericoid-like because of the extremely revolute margins, and trichomes with walls 6 μm thick. In contrast, *Dinemandra strigosa* was said to have ovate leaves and trichome walls 18 μm in thickness. Niedenzu's later description (1929) of a variety of *D. ericoides* (a species which he placed earlier in the section of *Dinemandra* with two fertile anthers), *D. ericoides* var. *triandra,* with three fertile stamens was never explained.

Given the limited amount of material available to Niedenzu, it is not surprising that he decided to recognize all of the species previously described. However, one year after Niedenzu's work appeared in *Das Pflanzenreich* (1928), Johnston (1929) published the results of his extensive field observations in the deserts of northern Chile. From his first-hand experience, he decided that there were only two species, *D. ericoides* and *D. glaberrima.* He placed *D. strigosa* in *D. ericoides* and concluded that both *D. ramosissima* and *D. subaptera* fell within the range of *D. glaberrima.* The characters he gave that distinguished the two species he recognized were the extensive appressed villous vestiture of *D. ericoides* relative to *D. glaberrima,* its comparatively less shrubby habit, its tendency to have two rather than three fertile anthers, and its more northerly distribution.

My collections from a transect through the entire range of the genus show that many of the characters used by Niedenzu, as suggested by Johnston (1929), are inconsistent and vary within populations. However, I have found that the characters used by Johnston also vary. If one takes a collection from near Antofagasta and compares it to plants from Chañaral, they do appear strikingly different. Plants from comparatively foggy moist areas such as Paposa (Antofagasta) are small with twisted stems and have leaves congested along the branches. Individual leaves are dark green and almost linear in outline because of the strongly revolute margins. Moreover, these plants tend to be quite villous. At the opposite extreme are plants from Caldera that are open with comparatively widely spaced leaves, straight branches, large leaves with only the distal margins revolute, and glabrous stems and leaves. However, there are various combinations and intermediate situations. One common habit not reported by earlier workers is medium-sized plants (30 cm) with congested, needle-like leaves at the bases of the stems and larger, lanceolate leaves in the middle of the branches. Such plants are generally glabrous, but trichomes regularly occur in the inner axils of the leaves and often around the bases of the calyces.

The stature of the plants (small and dense or comparatively large and open) appears to be related to the habitat. Small, vestitured plants are generally found at comparatively high elevations, often in areas with appreciable amounts of fog. More open plants tend to occur in sunnier, presumably warmer areas. Few plants consistently have dichotomously branched inflorescences. Often, the lower portions of the panicles will be dichotomously branched whereas the upper portions branch in various ways. Individual plants occur with panicles that contain two to five flowers. The leaves on a given plant likewise can be alternate (usually at the bases of the branches) and opposite with connate, clasping bases. The number of fertile anthers does not correspond to the amount of vestiture of a plant, the openness of the habit, or the degree to which a dichotomous arrangement of leaves and peduncles is maintained in the plant. Different flowers within a plant can have two or three (or even four) fertile anthers and flowers with two large anthers and one considerably smaller are found in many populations. Given this amount of variability, it is impossible to find characters that would unequivocally define more than one species of this genus.

Representative specimens examined. CHILE. **Region II** [Antofagasta]: Prov. Tocopilla, Tocopilla, *Jaffuel 2506* (GH); prov. Antofagasta, vic. Antofagasta, 31 Oct 1914, *Rose & Rose 19412* (BM, US); base of hills SE of La Chimba, 19 Oct 1925, *Johnston 3647* (GH); Quebrada de Chimba behind Antofagasto, 400 m, 16 Oct 1983, *Simpson 83-10-16-2* (MICH, TEX); Cerro Cerisso, rd. to airport SE of Antofagasta, 100 m, 27 Feb 1939, *Beetle 26186* (UC); Paposa between Paposa and Poman, 600 m, 15 Oct 1983, *Rodríguez 4* (K); Quebrada de Paposa, 200 m, 13 Jan 1971, *Lourteig 2559* (P); vic. of Paposa, Quebrada de Gaunillo, 700 m, 87 Dec 1925, *Johnston 5572* (GH); vic. Aguada de Cardon, gravel, 26 m, 4 Dec 1925, *Johnston 528* (GH); Punta Buitre, 4 Dec 1925, *Johnston 5240* (GH); hills S of Taltal, 50 m, 25 Feb 1939, *Beetle 26173* (GH, UC); Quebrada de San Ramón, N of Taltal, 26 Nov 1925, *Johnston 6297* (GH); 17 km N of Taltal on the Cuesta de Paposa, sea level, 15 Oct 1983, *Simpson 83-10-15-1* (MICH, MO, TEX); Quebrada de Taltal, 25 Nov 1925 (GH); ca. 10 km E of Taltal, Quebrada, 250 m, 13 Oct 1938, *Worth & Morrison 15826* (GH, UC); ca. 10 km E of Taltal, 250 m, Jun 1941, *Johnston 15826* (G); 7 km S of Taltal, 550 m, 14 Oct 1983, *Simpson 83-10-14-4* (MICH, MO, TEX); 5–6 km S of Taltal, 650 m, 14 Oct 1983, *Simpson 83-10-14-7* (MICH, TEX); 8 km S of Taltal, 650 m, 14 Oct 1983, *Simpson 83-10-14-5* (CONC, MO, TEX); 1 km S of Breas, 650 m, 14 Oct 1983, *Simpson 83-10-14-1* (TEX); at the turn from the N part of the "Y" from Taltal onto the Pan American Hwy, 16 Oct 1983, *Simpson 83-10-16-1* (MICH, MO, TEX); 37 km N of Taltal between Taltal and Paposa, sea level, 15 Oct 1983, *Simpson 83-10-15-3* (TEX); Quebrada de Doña Inges Chica, 1886, *Gigoux* (GH). **Region III** [Atacama]: Prov. Chañaral, vic. Puerto de Chañaral, hills of El Barquito, 28–29 Oct 1925, *Johnston 4781* (GH); 18 km S of Chañaral in disturbed areas, 12 Oct 1983, *Simpson 83-10-12-7* (MICH, TEX, US); 145 km N of Copiapó, 12 Oct 1983, *Simpson 83-10-12-6* (MICH, MO, TEX); 23.4 km before the turn to El Salvador, 1370 m, 13 Oct 1983, *Simpson 83-19-13-1* (CONC, MICH, MO, NY, TEX); before Llanta on the road from the turn to Potrerillos, 13 Oct 1983, *Simpson 83-10-13-4* (MICH, MO, TEX); vic. Potrerillos, 2100 m, 22 Oct 1925, *Johnston 3668* (GH); prov. Copiapó, Obispito on beach, 12 Oct 1983, *Simpson 83-10-12-4* (MICH, NY, TEX); Camino al Salar de Maricungam, near Puquios, 1200 m, 31 Jan 1963, *Ricardi et al. 525* (B); vic. Copiapó, gravel in hills N of town, 600 m, 17 Nov 1925, *Johnston 5019* (GH); vic. of Copiapó, Quebrada de Chanchoquin, Oct 1885, *Gigoux* (GH); above Pastillo, 2600 m, 3–4 Nov 1925, *Johnston 4858* (GH); Caldera, on small point of land N of town, 22

Nov 1925, *Johnston 5051* (GH); Tierra Amarilla, 750 m, Oct 1924, *Werdermann 414* (B, BM, CAS, G, GH, K, MUN, UC, US); Caldera, Quebrada León, Oct 1924, *Werdermann 435* (B, BM, CAS, G, GH, K, MUN, UC, US); 2 km ESE of Caldera on the road to Copiapó, 20 Oct 1983, *Simpson 83-10-20-3* (CONC, F, MICH, MO, NY, TEX); 46.2 km from the center of Copiapó on the Pan American Hwy toward Puquios, 21 Oct 1983, *Simpson 83-10-21-1* (F, MICH, MO, NY, TEX); Obispito along Rt 5, km 916 from Santiago, 3 m, 20 Oct 1983, *Simpson 83-10-20-1* (CONC, MICH, MO, NY, TEX); road from Paipote to La Puerta near km post 40, 11 Oct 1983, *Simpson 83-10-11-3* (CONC, MICH, MO, NY, TEX); 51.4 km from the center of Copiapó on the Pan American Hwy toward Puquios, 1020 m, 21 Oct 1983, *Simpson 83-10-21-2* (MICH, TEX).

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