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AN UNUSUAL KIND OF DISTYLY IN QUINCHAMALIUM CHILENSE (SANTALACEAE) ON VOLCÁN CASABLANCA, SOUTHERN CHILE¹

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ABSTRACT

IN MATURE FLOWERS of the southern Andean parasitic herb, *Quinchamalium chilense* (Santalaceae), the stigmas and anthers are closer together in the pin morph than in the thrum morph. While the stigmas and anthers of the two morphs are in reciprocal positions as the flowers open, such reciprocity is lost as the result of post-anthesis allometric growth of the styles and stamens. Experimental pollinations reveal that both morphs of *Q. chilense* are self-compatible. Natural fruit set is higher on the pin morph. The latter is also statistically under-represented in natural populations with respect to a 1:1 ratio for pins and thrums. Pin flowers produce larger numbers of pollen grains than thrum flowers and pollen of pin flowers is smaller in size than that of thrum flowers. Higher fruit set on the pin morph is consistent with some tendency towards subdioecious breeding behavior, although an expected excess of geitonogamous pollinations on the pin morph might also be contributing to the difference in fruit set on the two morphs. The unusual floral morphology of *Q. chilense* could have evolved as a result of selection for larger flowers by certain pollinator groups less likely to effect geitonogamous pollination. Alternatively, extended development of post-anthesis flowers might be a reflection of selection for an array of flower sizes on individual inflorescences, producing a target effect for pollinator attraction. The evolution of such inflorescence morphology would have been facilitated by the fact that a trend in the direction of subdioecious breeding behavior accrues the same outcrossing advantages as strict distyly. Precise information on periods of stigma receptivity is required to further our understanding of the floral morphology of *Q. chilense*.

HETEROSTYLOUS SPECIES are composed of two (distylous) or three (tristylous) morphs that differ in style and stamen length or in anther position if stamen length is uniform. In some species, features such as pollen size and quantity, exine characteristics, stigma morphology, and corolla size also differ between the morphs. Heterostyly is associated with genetic self-incompatibility in many of the 24 families for which it has been reported, many of which are phylogenetically unrelated (Ganders, 1979). *Quinchamalium* (Santalaceae) is a small genus of root parasites distributed along the South American Andes from Peru to Chile and Ar-

gentina, reaching sea level in Chile. Distyly has been reported in *Arjona* (Skottsberg, 1940), a close relative of *Quinchamalium*, but the question as to whether distyly occurs in the second genus has never been satisfactorily resolved. Philippi (1857) described 10 new species of *Quinchamalium* for Chile, which were later questioned by Dawson (1944) because of the minor vegetative differences separating them. Some of Philippi's species have the style included in the perianth tube with the stigma below the anther level, others have the style protruding beyond the mouth of the perianth tube with the stigma above the anther level, while in a few, there is little difference in the levels attained by the stigmas and anthers, suggesting that long-styled and short-styled plants may have been described as separate species on some occasions. Johri and Agarwal (1965) described the floral morphology, microgametogenesis and embryo development of *Quinchamalium* in great detail, based on material they assigned to *Q. chilense*. There is no reference to variation in style length. Kuijt (1969) gives details of the floral morphology of *Quinchamalium* using material identified as *Q. ma-*

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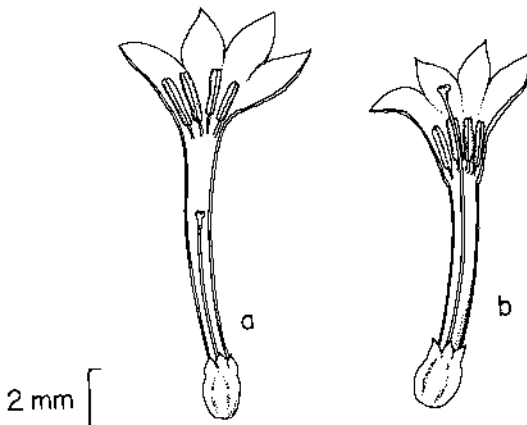


Fig. 1. Schematic drawings of mature thrum a) and pin b) flowers of *Quinchamalium chilense* (Santalaceae). One perianth lobe and stamen has been eliminated in each case.

jus. The stamens appear to be included in the perianth tube and the style exerted. However, heterostyly is not alluded to. Dawson (1944) in her treatment of Argentinian Santalaceae notes under the heading "Heterostilia," that "la longitud del estilo varía mucho según he observado en *Quinchamalium* y *Arjona*." However, there is no reference to separate long- and short-styled plants in her description of *Q. chilense*, the only species she recognized for Argentina.

In a survey of breeding systems being conducted on the flora of Volcán Casablanca in southern Chile, populations of *Quinchamalium* that are provisionally referred to *Q. chilense* (until the taxonomy of the group is clarified) have been discovered that are without doubt heterostylous. The heterostyly is of an unusual kind as the stigmas and anthers of the morphs are not in truly reciprocal positions in the mature flowers. In this paper we characterize and describe the development of the two floral types from the bud to open flower stage. Additionally, data are presented on morph frequencies and on their compatibility relationships.

MATERIALS AND METHODS—The plants studied are located between 1,100–1,200 m elevation in the andean (alpine) zone of Volcán Casablanca, Antillanca Valley, X Región, Chile (40°S, 72°W). Floral measurements of 50 open flowers per morph were made on preserved material collected in the field. Average pollen grain production per flower for 5 plants of each morph was determined by counting samples with a haemocytometer. Anthers were fixed in Carnoy's III and later crushed in a 3:1 mixture

of lactic acid:glycerine with a few drops of methylene blue added. The resultant pollen suspensions were agitated on a shaker for 10 min before the grains were counted. The long and short axes of 20 pollen grains of each morph were measured. Growth curves of thrum (short-styled) and pin (long-styled) flowers were constructed from measurements made on the complete range of stages from buds to open mature flowers than may be found on individual inflorescences. As the perianths are long-persistent on the fruits in *Quinchamalium*, another series of measurements (20–25 per morph) were made for the fruiting stage. These last two kinds of measurements were made on dried specimens softened in boiling water with added detergent. Morph ratios were determined by examining the floral morphology of all individuals present in three sampling areas each of 100 m × 100 m located between 1,100–1,200 m on Volcán Casablanca. Self-incompatibility was tested for by making intra- and intermorph cross-pollinations and intra-morph self-pollinations on flowers previously covered in the bud stage with light wt paper bags and emasculated in the case of cross-pollination. All crosses for a single plant of a given type were made on the same inflorescence. Inflorescences of both morphs were bagged and observed for spontaneous selfing. Non-bagged plants were observed for fruit set under natural pollinating conditions. Pin plants were hand-selfed initially in 1984. A full crossing program was carried out the following year. Because many of the crosses were lost due to storms at the beginning of March 1985, more crosses were made in the 1986 summer to compensate for losses.

RESULTS—*Floral morphology and development*—Flowers of *Quinchamalium chilense* are arranged in congested spikes, each containing around 32 flowers which mature gradually in a centripetal fashion. The curved actinomorphic yellow to orange-yellow perianth comprises a slender tube with five reflexed tips (Fig. 1). The five stamens have long slender filaments which are adnate to the perianth tube for most of their length. The inferior ovary is crowned with a nectar secreting disc.

Thrum flowers of *Quinchamalium chilense* have perianths which measure an average of 13.8 mm in mature flowers (Table 1; Fig. 1). In this flower type the perianth tube is essentially constant in width. The filaments are fused to the perianth up to a point near the entrance to the tube and the anthers protrude about 2 mm beyond its mouth. Thrum styles measure 6.6 mm in length, exceeding over half the length

of the perianth tube. Pin flowers have shorter perianth tubes and larger ovaries than thrum flowers (Table 1; Fig. 1). They are readily distinguished from the latter by the perianth tube which is conspicuously inflated in the upper portion (Fig. 1). The filaments are adnate to the perianth tube for around $\frac{2}{3}$ its length. The anthers of this floral form fit into the inflated portion of the perianth tube and can be seen only when the perianth lobes are folded back. Styles of the pin flowers are exerted 1.5–2 mm beyond the perianth tube. Pin flowers produce a larger number of smaller pollen grains than thrum flowers (Table 2). The anthers and stigmas of the two floral forms are not in truly reciprocal positions (Fig. 1; Table 1). Pin anthers and thrum stigmas are at relatively similar levels, but thrum stigmas are situated much lower down in the perianth tube relative to pin anthers. All differences between pin and thrum flowers are statistically significant (Table 1, 2).

Tracing a curve through the points in Fig. 2a, 2b shows that style growth is sigmoidal with respect to stamen growth. The morphological differences between the two floral types arise as a result of differences in the relative rates of growth for the organs involved. In very small buds (less than 2.5 mm), the anthers are situated above the level of the stigma in both morphs. In thrum flowers (Fig. 2a), following this early stage up to the 6.5 mm bud stage, growth of the style and stamens proceeds at roughly the same rate. Before anthesis, however, style growth slows relative to stamen growth. By the time thrum flowers are open, the styles have almost reached their maximum length; the perianths and adnate stamens, in contrast, grow another 5–6 mm following anthesis. The style and stamen growth rates of pin flowers diverge at a very early stage of floral development (Fig. 2b). In 5 mm long buds, the stigma already overtops the anther level, due to a much faster growth rate of the style relative to the stamen and perianth. After anthesis, as a result of a decline in the growth rate of the style, pin styles and stamens grow at roughly the same rates, each of the two kinds of organs gaining an extra 3–4 mm length. Superimpos-

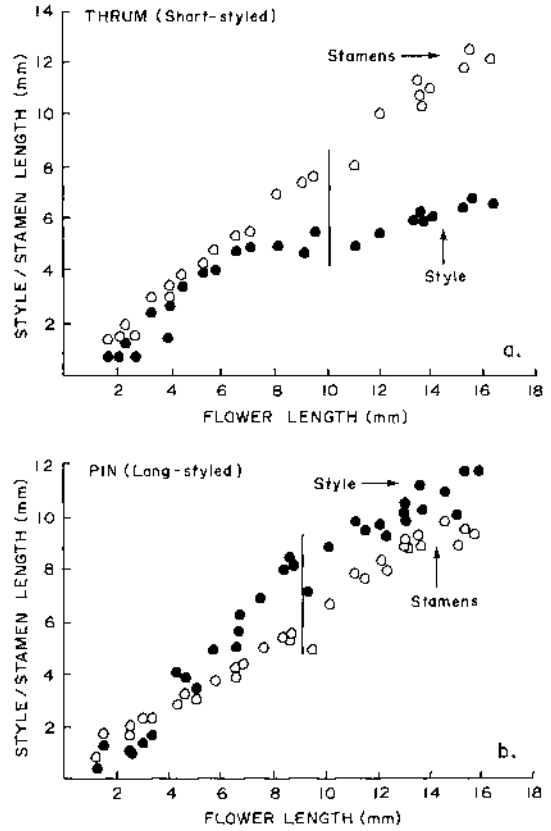


Fig. 2. Relationship between flower length and style and stamen lengths for thrum a) and pin b) flowers of *Quinchamalium chilense*. For comparison with Table 2, perianths of thrum flowers measure around 1.6 mm less than a complete flower, perianths of pin flowers measure around 1.9 mm less than a complete flower. The vertical line indicates the stage when the flower bud begins to open.

ing Fig. 2a over Fig. 2b shows that the two floral types pass through a stage of true reciprocity in the positions of the stigmas and anthers around the time the flowers open. The loss of this reciprocity as the flowers continue to grow is a result of allometric growth of the styles and stamens along developmental pathways established well prior to anthesis.

The mean perianth, stamen, and style lengths for flowers at the fruiting stage were similar to

TABLE 1. *Floral measurements (mm) for Quinchamalium chilense on Volcán Casablanca, Southern Chile*

	Pin			Thrum			t-test for means
	\bar{x}	S.D.	Rg.	\bar{x}	S.D.	Rg.	
Perianth length	12.35	1.09	10.00–14.50	13.80	0.95	11.00–15.50	'98 = 6.862; $P < 0.001$
Style length	9.85	1.05	8.25–12.00	6.62	0.38	5.60–7.50	'98 = 20.456; $P < 0.001$
Stamen length	8.50	0.72	7.00–10.00	11.32	1.01	8.50–12.50	'98 = 16.109; $P < 0.001$
Anther length	1.55	0.26	0.80–2.00	1.75	0.21	1.50–2.00	'64 = 2.740; $P < 0.01$
Ovary length	1.89	0.20	1.50–2.50	1.57	0.29	1.00–2.00	'98 = 6.426; $P < 0.001$

TABLE 2. Pollen characteristics of pin and thrum flowers of *Quinchamalium chilense*

	Pin		Thrum		t-test for means
	\bar{x}	S.D.	\bar{x}	S.D.	
Pollen size					
Long axis (μm)	16.97	1.84	27.58	0.98	$'38 = 22.768; P < 0.001$
Short axis (μm)	16.52	1.75	23.63	0.54	$'38 = 17.367; P < 0.001$
Pollen grains per flower	35,066	5,911	25,500	5,157	$'8 = 3.582; P < 0.01$

those illustrated for the final stages of development for non-fruiting flowers (Table 3). Occasional individual perianths nevertheless were larger. Also a number of the fruits measured were smaller than typical ovaries of flowers used to obtain prefertilization floral measurements, suggesting that we had inadvertently over-represented fruits from inflorescences more depauperate than average. Thus it cannot be conclusively established from these data that perianth growth ceases upon fruit development. In order to circumvent variation due to inflorescence vigor, the ratios fruit length/perianth length and ovary length/perianth length were compared (using the raw data of Tables 2, 3). For both morphs the first ratio was significantly higher when compared against the second using post-anthesis flowers of all sizes ($t_{68} = 13.59; P < 0.001$ for thrums; $t_{73} = 5.51; P < 0.001$ for pins) as well as those with the most developed ovaries (1.8–2.2 mm ovaries for thrums, $t_{35} = 8.52; P < 0.001$; 2.0–2.5 mm ovaries for pins, $t_{47} = 2.65; P < 0.05$). Thus any perianth growth, if it does continue once fruiting begins, must proceed at a much slower rate per increment in fruit size in comparison with the growth rate for equivalent increments in ovary size in unfertilized flowers.

Incompatibility and morph ratios—Fruit set was variable in each crossing treatment (Table 4). There was a tendency for higher fruit sets when small numbers of flowers per inflorescence were crossed, suggesting likelihood of some early fruit abortion on the highly congested inflorescences when ample numbers of flowers are pollinated. To investigate this trend,

results of all hand effected crosses, independent of type were divided into three groups (1–4, 5–8, 9 or more flowers crossed per inflorescence, respectively). Combining the results of 1985 and 1984, 27.3% of crosses in the first category resulted in 100% fruit sets, as opposed to none in the other two categories. In 1986 the corresponding values were 33.3% for the first category and 13.3% for the second (no crosses performed in 1986 belonged to the third category). Overall percent fruit set also increased across these categories. In 1985 and 1984 percent flowers crossed producing fruits was 42.4% for the 1–4 flower category, 26.7% for the 5–8 flower category and 14.4% for the nine or more flower category. The difference between the first and second category was significant ($G_{\text{adj}} = 9.64; P < 0.005$); a comparison of the second and third categories also produced salient results ($G_{\text{adj}} = 4.76; P < 0.05$). In 1986 the tendency persisted in the data: 50.7% of the flowers crossed corresponding to the 1–4 flower category formed fruits and 41.6% of the flowers corresponding to the 5–8 flower category produced fruits. However, this difference did not reach statistical significance ($G_{\text{adj}} = 1.28; P > 0.05$). These data also reveal that fruit set tended to be higher in 1986, probably as a result of the warmer summer that year. The difference between years for the 1–4 flower category did not reach statistical significance ($G_{\text{adj}} = 0.41; P > 0.1$); however, it did for the 5–8 flower category ($G_{\text{adj}} = 4.41; P < 0.05$).

The results of intra- and intermorph cross-pollination (Table 4) indicate that the two morphs of *Quinchamalium chilense* are self-compatible. Percent fruit set for thrum \times

TABLE 3. Floral measurements (mm) for pin and thrum flowers of *Quinchamalium chilense* persistent on young fruits

	Pin			Thrum		
	\bar{x}	S.D.	Rg.	\bar{x}	S.D.	Rg.
Perianth length	13.34	1.90	11.00–16.50	13.10	1.15	11.00–14.50
Style length	9.89	1.13	8.00–12.25	6.25	0.84	5.00–8.00
Stamen length	9.35	1.10	7.25–11.50	10.23	2.02	7.00–12.50
Fruit length	2.40	0.19	2.00–2.75	2.02	1.14	1.80–2.25

TABLE 4. Results of hand pollinations, spontaneous selfing tests and fruit set under natural pollination conditions in *Quinchamalium chilense* on Volcán Casablanca, Southern Chile

Cross or test	No. plants	Total fls. crossed	Total fruits formed ²		% Fruits formed per plant crossed or observed	
			No.	%	\bar{x}	SE
Pin × pin	11	76	8	10.5	18.7	9.5
Thrum × thrum	12	68	21	30.9	32.9	9.4
Pin × thrum ¹	14	55	16	29.1	28.9	9.6
Thrum × pin ¹	9	84	27	32.1	45.6	12.4
Pins hand selfed	14	56	37	66.1	69.4	8.4
Thrums hand selfed	14	58	17	29.3	31.5	11.5
Pins spontaneously selfed	9	123	26	21.1	45.2	13.7
Thrums spontaneously selfed	11	169	32	18.9	43.0	14.2
Pins naturally pollinated	6	197	75	38.1	36.6	6.1
Thrums naturally pollinated	8	221	48	21.7	20.1	3.6

¹ Pollen parent.² Fruits of *Q. chilense* contain one seed.

thrum and thrum × pin crosses is not significantly different ($G_{adj} = 0.02$; $P > 0.5$), suggesting that this morph is highly self-compatible. Percent fruit set for pin × pin and pin × thrum crosses is significantly different ($G_{adj} = 7.29$; $P < 0.01$). The lower fruit set for pin × pin crosses relative to pin × thrum crosses suggests that pins are less self-compatible than thrums. Because of the relationship between number of flowers pollinated on an inflorescence and final fruit set, these conclusions must be interpreted with care. The number of flowers pollinated per inflorescence in thrum × thrum crosses ($\bar{x} = 5.7$) was lower than in thrum × pin crosses ($\bar{x} = 9.3$). The number of flowers pollinated per inflorescence in pin × pin crosses ($\bar{x} = 6.9$) was higher than in pin × thrum crosses ($\bar{x} = 3.9$). As a result, real relative fruit set for thrum × thrum vs. thrum × pin crosses is probably lower than our results suggest at face value, while true relative fruit set for pin × pin versus pin × thrum crosses is probably higher.

Comparisons of fruit set following hand self-pollinations and intermorph cross-pollinations provide further evidence for self-compatibility in *Quinchamalium chilense* (Table 4). Percent fruit set for hand self-pollinated thrum plants and thrum × pin crosses is not significantly different ($G_{adj} = 0.13$; $P > 0.5$), once again suggesting considerable self-compatibility for this morph. Nevertheless, as the number of flowers hand self-pollinated per inflorescence ($\bar{x} = 4.1$) was lower than in thrum × pin crosses ($\bar{x} = 9.3$), true relative fruit set for these crosses is probably lower than indicated by the results as they stand. Contrary to the impression gained in comparing pin × pin and pin × thrum crosses, a significantly higher fruit set in hand-selfed pins compared with pins crossed by thrums ($G_{adj} = 15.39$; $P < 0.005$)

suggests that pins are highly self-compatible. Numbers of flowers pollinated per inflorescence for these crosses were similar ($\bar{x} = 4.0$ for hand-selfed pins; $\bar{x} = 3.9$ for pin × thrum crosses). A high level of self-compatibility for pins is further suggested by the significantly higher fruit set for hand selfed pins in comparison with hand selfed thrums ($G_{adj} = 15.60$; $P < 0.005$).

Both morphs may undergo spontaneous selfing to some degree (Table 4). Percent fruit set for spontaneously selfed and hand-selfed thrums was not significantly different ($G_{adj} = 2.58$; $P > 0.05$), giving the impression that thrums are potentially strongly autogamous. For the equivalent crosses on pin plants, however, the difference was significant ($G_{adj} = 33.56$; $P < 0.005$), fruit set being lower following spontaneous selfing (18.9%). Thus the potential for spontaneous selfing is clearly lower in the pin morph, yet because of the apparently lower level of self-compatibility in the thrum morph, fruit set following spontaneous selfing when compared directly for the two morphs is not significantly different ($G_{adj} = 0.21$; $P > 0.5$). It must be assumed that most spontaneous selfing on the pin morph, considering that the stigma is situated above the level of the anthers, occurs through pollen being vibrated out of the anthers, possibly from nearby flowers as well as from any one flower under consideration. Most spontaneous selfing in thrum flowers, in contrast, probably results mainly from intraflower pollen deposition. The number of flowers hand-selfed per inflorescence in the two morphs ($\bar{x} = 4.1$ for thrums; $\bar{x} = 4.0$ for pins) was considerably lower than the number observed for spontaneous selfing ($\bar{x} = 15.4$ for thrums; $\bar{x} = 13.7$ for pins). Thus in both cases, selfing potentials, if anything, are probably underestimated.

TABLE 5. Ratios of pin and thrum morphs of *Quinchamalium chilense* on Volcán Casablanca, Southern Chile

	Plants sampled	Pin		Thrum		Ratio P:T	Deviation from 1:1 ratio
		No.	%	No.	%		
Cuadrat-1	227	93	40.97	134	59.03	1:1.44	G = 7.445; P < 0.01
Cuadrat-2	288	115	39.93	173	60.06	1:1.50	G = 11.760; P < 0.005
Cuadrat-3	200	86	43.00	114	57.00	1:1.33	G = 3.934; P < 0.05
Pooled data	715	294	41.12	421	58.88	1:1.43	G = 22.678; P < 0.005

Mean fruit set under natural conditions of pollination failed to exceed 40% on either morph (Table 4). No single individual produced more than 54% fruit. Mean percent fruit set per plant was significantly higher for pin plants ($t_{12} = 2.22$; $P < 0.05$; arcsine transformed data), which produced almost twice as much fruit as thrum plants. This result is interesting in view of the fact that fruit set for pin \times thrum and thrum \times pin crosses is not significantly different ($G_{adj} = 0.14$; $P > 0.5$) or in other words the two morphs have similar potential fertility levels. Natural fruit set for thrum plants, moreover, is not significantly different from fruit set following spontaneous selfing ($G_{adj} = 0.46$; $P > 0.5$), whereas it was for pin plants ($G_{adj} = 10.33$; $P < 0.005$).

In the three quadrats of *Quinchamalium* sampled the thrum and pin morphs were represented by similar percentages respectively (Table 5). Thrums are statistically over-represented with respect to a 1:1 ratio in all cases (G-test for Goodness of Fit). The pooled data give 41.1% pins and 58.9% thrums or a pin:thrum ratio of 1:1.43.

DISCUSSION—The heterostyly of *Quinchamalium chilense* on Volcán Casablanca exhibits many features (e.g., dimorphic pollen, different numbers of pollen grains produced by the two morphs, larger corollas on the thrum morph) of more typical distylous species (Ganders, 1979). However, in its possession of self-compatibility, excess of the thrum morph in populations, higher fruit set on the pin form and the non-truly reciprocal positions of the stigmas and anthers in mature flowers, *Q. chilense* is unusual. Self-compatibility has been reported in heterostylous species of *Pulmonaria* (Darwin, 1877), *Amsinckia* (Ray and Chisaki, 1957; Ganders, 1975; Weller and Ornduff, 1977), *Palicourea* (Sobrevila, Ramírez, and Xena de Enrech, 1983) and in *Cryptantha* (Casper, 1985). Excess of the thrum form has been documented in four species of *Cordia* (Opler, Baker, and Frankie, 1975). The most striking feature of *Q. chilense*, undoubtedly, is its basic floral morphology. Studies of floral development in heterostylous species (e.g., Richard

and Barrett, 1984) indicate that style and stamen growth is usually highly canalized, with development of all organs complete by the time the flowers open. In *Quinchamalium* considerable flower growth occurs after anthesis and the stage at which the stigmas and anthers are in reciprocal positions is a transient one which gives way to a final wider separation of the stigmas and anthers on the thrum morph in comparison with the pin form. Pin stigmas and thrum anthers, nevertheless, attain quite similar levels as a result of the peculiarities of their respective growth curves. The stigmas and anthers of the pin morph are placed more closely together than in the thrum morph in three species of *Cordia* (*C. curassavica*, *C. dentata* and *C. inermis*) (Opler et al., 1975). In this genus however, unlike in *Quinchamalium*, the final positions of the organs mentioned are attained by the time the flowers open.

The unusual floral morphology of *Quinchamalium chilense* could result in differential pollen flow between thrum and pin plants with consequent gender specialization (*sensu* Lloyd, 1979) or a tendency towards functional dioecism. A number of authors have provided examples of dioecism derived through distyly (Ornduff, 1966; Lloyd, 1979; Beach and Bawa, 1980). In *Q. chilense* the relatively similar levels attained by the stigma of the pin morph and the anthers of the thrum morph should allow unrestricted pollen flow from the latter to the former. Pollen flow is less likely to occur between the pin anthers and the thrum stigma in view of their different levels. The thrum morph thus acts more strongly as a pollen parent, and the pin morph acts as the predominant ovule parent. Evidence for some gender specialization in *Q. chilense* is perhaps seen in the smaller thrum ovaries. Thrum plants, moreover set only just over one-half as much fruit as pin plants in natural populations, in spite of non-significant differences in the fertility levels of the two morphs when pollinated by hand. Higher fruit set on the pin morph cannot be attributed to more spontaneous selfing, as the amounts of fruit resulting from spontaneous selfing for the two morphs were not significantly different. Pins, nevertheless, might be

more susceptible to pollinator-mediated geitonogamous selfing and intramorph crossing, in view of the closer placement of their stigmas and anthers. Male-biased sex ratios are common in dioecious species (Godley, 1964; Lloyd, 1973). The excess of thrums in *Q. chilense*, which seem to be allocating fewer resources to fruit set than pins, is also consistent with some gender specialization in the direction of dioecism.

Two distinct classes of hypotheses have been advanced for dioecious trends in heterostylous groups. Ornduff (1966) observed incomplete self-incompatibility in *Nymphoides peltata*. He suggested that dioecism in other species of the same genus could have arisen to compensate for inbreeding. Differences in the amount of pollen transported to the stigmas of the two morphs as a result of peculiarities of pollinator behavior have been hypothesized as an alternate cause for gender specialization. Syrphids are more efficient at pollinating the pin morph of *Jepsonia heterandra*, while bees are more effective for the thrum morph (Ornduff, 1975). An excess of pin pollen on the stigmas of both morphs of this species (Ornduff, 1971) underscores that pollinator activity may result in unexpected patterns of pollen flow. Beach and Bawa (1980) suggested that insects with short mouth parts provoking pollen flow preferentially from thrums to pins could precipitate the evolution of dioecism from distyly. In the case of *Quinchamalium chilense* possibly both these kinds of selective force have been operating on the breeding system. Corroborating earlier findings for *Q. majus* in the central Chilean Andes (Arroyo et al., 1982), *Q. chilense* on Volcán Casablanca is visited by butterflies and flies. *Q. majus* was originally referred to as *Q. chilense* in Arroyo, Primack and Armesto (1982). Recent examination of the original illustration of *Q. majus* suggests that this name is more appropriate. Flies and butterflies are characterized by distinct foraging habits which should be reflected in different propensities for these insects for effecting geitonogamous pollinations and the quality of outcrossing resulting from visits. Flies (except for some advanced orders such as Bombyllidae, Nemestrinidae with hovering capacities) generally crawl over flowers when they are tightly packed in inflorescences, whereas butterflies alight, probing individual flowers from above. Long flight distances are typical for butterflies (Pyke, Pulliam and Charnov, 1977; Courtney, Hill and Westerman, 1982). Webb and Bawa (1983) showed that 70% of the pollen deposited on the stigmas of *Cnidocolus urens* by butterflies was derived from other individuals. Al-

though we are unaware of any data on flight displacement for flies, it seems unlikely that they would forage over the long distances reported for butterflies. Butterflies, in comparison with flies, are probably not only better adapted for effecting outcrossing over large distances, but also less prone to transporting pollen between flowers on an individual. The much elongated perianth tubes of *Q. chilense*, while ideally suited to foraging by butterflies, should act as a convenient deterrent to many fly groups from gaining access to the deeply seated nectary. The distal cause of some gender specialization in *Q. chilense*, consequently, might be selection for larger flowers favoring pollinators less likely to effect geitonogamous selfing, the flowers being produced within the constraints of allometric growth.

The floral morphology of *Quinchamalium chilense* and associated gender specialization might alternatively reflect the role of individual flowers in pollinator attraction at the level of an inflorescence. Prolonged development of flowers after anthesis producing an array of flower sizes and colors provides an excellent vehicle for greater division of labor within an individual inflorescence. On the tightly congested inflorescences of *Q. chilense* the outermost orange-yellow flowers with reflexed tips contrast strongly against younger, more recently opened yellowish flowers with erect perianth lobes and unopened greenish buds towards the center, as well as with very old browner perianths persistent on the larger fruits, producing a target effect. Gender specialization thus is perhaps the inevitable result of selection for increasing the life spans of flowers in order to provide this target effect, the entire system being viable because a tendency in the direction of functional dioecism provides the same outcrossing advantages as true distyly. Indeed, it seems quite possible that flowers in their terminal stages of maturity function entirely in pollinator attraction, the optimal period for pollination being midway between the time the flowers open and the time they reach their maximum sizes, over a range of breeding situations from perfect distyly initially to finally subdioecy. Considerable variation in the results of our crossing tests is suspected to be due to fruit abortion. Higher fruit set for smaller numbers of flowers pollinated could also be expected if the optimal period for stigma receptivity is more restricted in duration than represented in larger arrays of flowers crossed on the same inflorescence. Studies on pollinator foraging and nectar flow schedules, precise detection of the periods of stigma receptivity, and pollen presentation and determination as to whether

more selfing via geitonogamy contributes to the excess of fruits on pin plants—all beyond the scope of the present work—are clearly needed to further unravel the adaptive significance and true functional implications of the unusual kind of distyly in *Q. chilense*.

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