1962

Pollination and Evolution in Pedicularis (Scrophulariaceae)

Elizabeth F. Sprague
Sweet Briar College

Follow this and additional works at: <https://scholarship.claremont.edu/aliso>

Part of the [Botany Commons](#)

Recommended Citation

Sprague, Elizabeth F. (1962) "Pollination and Evolution in Pedicularis (Scrophulariaceae)," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 5: Iss. 2, Article 6.

Available at: <https://scholarship.claremont.edu/aliso/vol5/iss2/6>

POLLINATION AND EVOLUTION IN PEDICULARIS (SCROPHULARIACEAE)¹

ELIZABETH F. SPRAGUE

Sweet Briar College, Sweet Briar, Virginia

Pedicularis is a circumboreal and North Temperate genus of semi-parasitic herbs belonging to the tribe Euphrasieae. The complex flower shape is typical of bee flowers. The mode of pollination for seven species occurring in California has been studied. The purpose of this paper is to present data on pollination mechanisms of some western North American species and to relate these findings to the evolution of the genus.

The seven species observed all fall into Li's (1948) infrageneric group, *Allophyllum*, of alternate-leaved species with alternate flowers and terminal spicate or racemose inflorescences. They represent six of the eleven coastal series recognized by Pennell (1951) as natural groups having very homogeneous vegetative and floral characters.

The following species were observed in California:

P. crenulata occurs in the Rocky Mountains in Colorado, Wyoming, west into Nevada, and in a tiny relictual outpost of 25-30 white-flowering plants on Convict Creek, Inyo County, California.

P. dudleyi is an endemic almost confined to the stream banks in Portola State Park, Santa Cruz Mountains, California.

P. racemosa is abundant throughout the northwest from northern California to British Columbia, east into Montana and south to Colorado.

P. attollens occurs in the Sierra Nevada and north into Oregon.

P. groenlandica extends from the high elevations in the Sierra Nevada north to the coast of Alaska and east through Canada to Greenland.

P. semibarbata is found at moderate elevation in the California mountains and north into Oregon.

P. densiflora occurs in Baja California along the coast to Oregon, then east to the western slope of the Sierra Nevada as far south as Fresno County.

OBSERVATIONS ON THE POLLINATION OF THE CALIFORNIA SPECIES

HEAD POLLINATION BY BUMBLEBEES

Pedicularis crenulata (fig. 2-4)—This is a common species of grassy meadows and stream banks. It occurs at moderately high elevations in Colorado, Wyoming and west into the mountains of Nevada; a tiny relictual outpost occurs on the banks of Convict Creek, Inyo County, California, where the observations were made. The flowers of these 25 to 30 plants were white in contrast to the purple commonly found in other populations. They grow at an acute angle from the dense firm spike. The oblique lip (fig. 2d) with three expanded lobes is shorter than the galea. A median ventral groove (fig. 4n) is extended to

¹This paper is adapted from a portion of a doctoral dissertation prepared at the Rancho Santa Ana Botanic Garden and the Claremont University College, Claremont, California.

Fig. 1. *Pedicularis palustris* showing habit. This is a classical example of a species pollinated by bumblebees (after Hegi).

the nectary (fig. 4h) by the channel between the two ventral filaments (fig. 4f) which bear trichomes similar to those on the ridges. The straight-backed galea arches distally (fig. 2c) so that the anterior "crest" is vertical. Two slender teeth (fig. 2b) behind a truncate apex (fig. 2a) occur only in this one California species. The ventral galea margins (fig. 2l) are closely appressed below the hood. The acute tips (fig. 4o) of the anthers, at least the ventral pair, are often just visible behind the teeth.

The visitors included small bees (one an *Osmia*) and the largest California *Bombus*, *B. fervidus*, the most effective visitor. The bee was observed to work every open flower of seven adjacent spikes and then repeat visits to two of these spikes. Although this bee must feed largely elsewhere it surely takes advantage of this eminently suitable flower when it is available.

Pedicularis crenulata exhibits the "classical" type of bumblebee pollination in which the head, in some cases other parts of the dorsum, effects the transfer of pollen. When feeding in rapid succession the bee approaches the flower with proboscis outstretched. This is inserted through the narrow groove leading to the nectary as the forelegs grasp the lower lip margins and middle and hind legs cling to the subtending bracts and adjacent flowers. The comparative rigidity of the flower and the strict and compact inflorescence result in very little displacement of the floral parts when visited. As the bee's face is inserted into the throat (fig. 2m) the stigma brushes across the back of the head and onto the anterior edge of the thorax.

The pressure of the head on the galea teeth (fig. 2b) plus the lateral expansion of the throat by insertion of the face allows the anthers to separate and drop a large amount of nearly white pollen on the bee's head or on the anterior margin of the thorax. As the head goes deeper into the throat, the anterior margins of the teeth shove some pollen onto the thorax. As the bee feeds, the stigma which projects anteriorly to the teeth is rubbed into this pile of pollen, probably a mixture of self and foreign. Although the stigma is covered with long glandular papillae, pollen does not adhere readily. A process as vigorous as this may be necessary if sufficient pollen is to remain.

In addition to *Bombus fervidus*, the small bees observed could have effected incidental pollination. An *Osmia* visited numerous flowers and hit the stigma of some. It fed for 40 to 70 seconds with head and thorax far down the tube. It backed out via the lower left lobe avoiding any possible contact with the stigma. (Left and right of the flower refer to these positions as an observer views them from the vantage point of the axis). A similar but more slender bee hit the stigma and teeth and then lit on the lower lip and crawled into the tube. Pumping movements indicated it fed for as long as two minutes. Pollen was seen on the head as it rested between visits. Possibly the momentary pressure of these small bees' heads on the teeth releases the anthers sufficiently for some pollen to fall. The abundance of trichomes on ridges and filaments may indicate that these flowers are more or less dependent upon these small bees which are constant visitors in the absence of or between the rare visitations of *Bombus fervidus*. As the large bee did not seem to use the trichomes, these would be of no selective advantage to the flower in this relationship. These hairs may serve as a deterrent to insects too small to be effective pollinators, as aids in capillary conduction of the nectar, or it may be that *P. crenulata* is in part dependent upon smaller bees. Also, the trichomes may be vestigial structures for however hirsute the vegetative parts may be, the presence of the trichomes in the corolla in *Pedicularis* seem to correlate with their apparent use by the regular visitors.

A second question involves the true function of the teeth. They usually have been interpreted as guides for pollen deposition, or as a means of preventing excess lateral dispersion. Anthers of *P. crenulata* lack the lateral trichomes of some similar species so teeth may serve that purpose; but if that is their prime function, why do bidentate flowers like

those of *P. sylvatica* have trichomes on the backs of the anthers that seem also to serve this function? Apparently even a small bee can hit these teeth and thus release pollen for a functional load. Those insects observed were symmetrically loaded rather than one-sided as would be the case if they hit one tooth only. In observations on *P. canadensis* in the Blue Ridge, Virginia, the function of the teeth could be interpreted to reduce lateral dispersal of pollen, to provide additional leverage to open the galea distally and also to shove some pollen posteriorly.

A remarkable correlation between pollinator and flower was in the parallel size and curvature of the head and thorax of *B. fervidus* and that of the galea of *P. crenulata*. They more obviously complement each other in these respects than do any other observed species of *Pedicularis* and their pollinators. Because *B. fervidus* does not extend to the Rocky Mountains one cannot help but wonder whether another species comparable in its large size replaces it for those populations. It seems probable that populations of *P. flavida* and *P. bracteosa* of similar size, mechanism and rigidity of inflorescence found to the north where *B. fervidus* occurs are also pollinated by this very large *Bombus*. The nectary in these species is well developed and at least in *P. crenulata* produces a generous amount of nectar. This is so typical of the genus that Kugler (1955) among others has used *Pedicularis* to demonstrate the exploitation of nectar to reduce the amount of pollen consumed.

Pedicularis dudleyi (fig. 5-7)—This is probably another relictual Pleistocene population which has been able to maintain itself only in the cool moist redwood forest of Portola State Park in the Santa Cruz Mountains. The small plants with a few large lax leaves hang from the road banks or recline on damp duff above the stream. The raceme bears a few lavender flowers (20-25 mm. long) which become pale with age. The visitors observed were *Bombus sitkensis* and *B. edwardsii*.

The outthrust proboscis of the visiting bumblebee is inserted through a small triangular opening into the deep median groove of the throat. The first two pairs of legs grasp the gular folds as the body weight depresses the lower lip, flattening its base. This allows insertion of the head, expands the opening laterally and in turn causes the "breaking" of the galea at the arched vein. The pollen falls on the abdominal dorsum of the bee.

Pollen appears to be transferred as the bee enters a second flower and hits the bilobed stigma while still on the wing, for as it alights the body immediately drops down. Some visitors were seen to tip their abdomens up just as they entered the flower. This may enable the head to enter the throat at a better angle for deeper penetration of the tube and it would also bring about firmer contact between abdomen and stigma. This mode of pollination is similar to that described for many European species and like that of *P. crenulata* is typical for the genus.

Pedicularis attollens (fig. 14-16)—The range of *Pedicularis attollens* extends from Inyo County in the Sierra Nevada and in the White Mountains north to the Cascades in Oregon. This species occurs in drained areas of meadows and in soil caches of steep Sierran slopes. The observation localities were at Norden, Placer County, Echo Pass and Fallen Leaf Lake, Eldorado County, and several areas in the Tioga Pass area, Mono County. *Pedicularis attollens* has a compact spike of pink flowers with purple markings. The lateral lobes of the lower lip are reflexed, the center one is smaller and often cucullate. The short galea with its two conspicuous dark "eyes" terminates in a beak which turns abruptly up and to the right; the tip is nearly centered just anterior to and above the galea. From the beak, which supports the slender style, projects the stigma which has the same dark hue as the margins of the galea beak. The resulting flower looks like a miniature elephant's head with a raised trunk (fig. 14), justifying the common name, "elephant snouts."

The obviously effective visitors to *P. attollens* were *Bombus bifarius nearcticus* and *B. occidentalis*; one specimen of the narrow-headed *B. flavifrons dimidiatus* was taken. Other

Fig. 2-7. Fig. 2-4. *Pedicularis crenulata*.—Fig. 2. Lateral view. $\times 3.5$.—Fig. 3. Front view. $\times 3$.—Fig. 4. Longitudinal section, semidiagrammatic. $\times 3.5$.—Fig. 5-7. *Pedicularis dudleyi*.—Fig. 5. Lateral view. $\times 3$.—Fig. 6. Front view. $\times 3$.—Fig. 7. Longitudinal section, semidiagrammatic. $\times 3$. (a. apex of galea; b. teeth, c. crest of galea; d. lower lip; e. dorsal filament; f. ventral filament; g. style; h. nectary; i. arching vein; j. "breaking" point; l. ventral margins of galea; m. proximal region of galea; n. ventral groove; o. anthers.)

visitors, obviously gleaners, included *Chloralictus*, syrphids, a vespid, and small flies (*Drosophila*). Long-winged flies fed particularly on the glandular calyx and occasionally went between corolla and calyx, presumably to feed on trichomes there. These flies also fed on the stigma; they may, however, have been feeding on glandular secretions rather than pollen. *Chloralictus* was seen to bite through the corolla at the level of the anthers; however, evidence of robbery was less frequent in *P. attollens* and *P. groenlandica* than in other species. The firm broad contact between the lower lip and the galea together with the infolded "teeth" may reduce the number of ineffective visitors in these two species.

When working *P. attollens*, the *Bombus* alights on the left side of the expanded lower lip. The body weight depresses the lip and allows the bee to move forward across the exposed midlobe. The outstretched proboscis is inserted into the tube from the right side of the galea. As the face is pushed into the throat the head raises the galea and spreads the base. This releases tension on the filaments and the anthers, now in a vertical position, separate. Pollen falls in a shower over the head and thorax of the visitor.

The forelegs cling to the margin of the lip at its juncture with the galea; the mid and hind legs are braced against the faint ridges of the lower lip. Without perceptibly moving its feet the bee relaxes *backward* for a moment, sometimes withdraws the proboscis but more often not. Another thrust forward is accompanied, like the first, by a loud buzz, vibration of the wings and scraping with the hind legs to pack pollen collected off the thorax. This is usually repeated two or three times, rarely five or six, on the same flower. In departing, the bee backs and veers to the lower left lobe, thus avoiding the stigma. From this position the bee crawls to another flower on the same spike or with equal frequency makes a short backward flight and proceeds as before.

As the bee approaches a second flower, the pollen-covered head brushes the stigma. The dark style and stigma are poorly distinguished from the larger adjacent beak tip and even more conspicuous eye spots (fig. 14). Does the bee, approaching from above or in front, note the more conspicuous markings and thus pick up a heavier load of pollen as a result of hitting the less conspicuous stigma harder?

Guide lines are well developed only in *P. attollens* among the California species. Each lobe of the lower lip has a purple or maroon midline curving toward the galea as it continues under the hood. Lines arising at either juncture of galea and lower lip and running down the inside of the throat serve no recognizable function. The exposed margin of the twisted beak is dark and meets the midline. These, together with the margins of the lip, beak and galea point up clearly the center of the floral entrance. The two anterior, maroon "eye" spots on the pale galea may help orient the bee's approach from a greater distance, the guide lines serving only as the bee alights. The dark tip of the beak and the "eye" spots make a triangle; all three points may be required to insure contact of stigma with the bee's head. Microscopic examination showed that the guide lines are composed of cells lacking the cuticular relief of those of most of the corolla surface. This textured difference together with the structural margins and sinuses of the lower lip may serve as tactile as well as visual stimuli to point up the entrance. A sensory guide on the central lobe may be particularly important for the proboscis. These guide lines offer a distinct pattern on a corolla that is often of the palest tint as well as a pattern distinctive from that of the closely associated and similar *P. groenlandica*.

P. attollens has a faint odor somewhat like that of apple blossoms to which the *Bombus* responds even when the flowers are obscured by cages. There is no perceptible nectar or nectary. If nectar is present it must be very rich indeed to be worth the energy involved in the repeated "buzzes." No puncture marks or other evidence of damage within the corolla indicated the bees procured anything other than the copious pollen. Intermittent visits to adjacent *Perideridia* (Fallen Leaf, Phillips) to gather nectar only was further evidence of insufficient nectar to condition *Pedicularis* pollen for packing. As Michener (1953) has

pointed out for *Megachile*, *Bombus* working *Pedicularis* appears to be polylectic regarding nectar but pollen collecting is restricted. Table 1 indicates an apparent pollen constancy. Pumping of the abdomen, observed occasionally, was the only indication that nectar might be present; one wonders however, if this might be only a reflex action associated with the working of a flower. In such case the proboscis serves only as a levering or holding device.

TABLE 1. Pollen Loads of *Bombus*.

LOCALITY	SPECIES	LOAD PER SPECIMEN
Sonora Pass	<i>Bombus bifarius nearcticus</i> on <i>Pedicularis groenlandica</i>	#1 95% Pedic. 95% fertile
		#2 60% Pedic. 99% fertile 5% <i>Caltha</i> 35% undetermined
		#1 70% Pedic. 97% fertile
	<i>Bombus melanopygus</i> on <i>Pedicularis groenlandica</i>	
Tioga Pass	<i>Bombus b. nearcticus</i> on <i>Pedicularis attollens</i>	#1 98% Pedic. 98% fertile 2% Compositae
		#2 95% Pedic. 98% fertile 5% undetermined

Because the bees seem to visit only the largest fresh flowers the question arises as to what advantage may accrue from the precocious protogyny exhibited by this species. Bees crawling over the spike may hit an occasional stigma; the pollen is powdery and does scatter but not in the veritable "showers" of *P. groenlandica*. Updrafts must carry some pollen to young flowers, for gleaners (sundry flies) appeared to find sustenance over much of the spike; some of this pollen may adhere to young stigmas.

VENTER POLLINATION BY BUMBLEBEES

Pedicularis racemosa (fig. 8-10)—This is a common and widespread species which extends from northern California to British Columbia and east through the northern Rocky Mountains. This distinctively bushy little plant grows in cool wooded areas and often above streams. The single locality where it was observed was the southernmost area reported for the species in the Sierra Nevada, Rainbow Tavern on Highway 40, Placer County, about 10 miles west of Soda Springs. On a steep bank above the Yuba River the slight, woody little plants occupied an area of some 200 square feet under the shade of *Abies concolor*, *Sorbus sitchensis* and *Pinus monticola*.

A loose raceme of a few fragrant white flowers terminates each branch of this plant. Across the oblique and broadly expanded lower lip extends the highly arched galea. This tapers to a narrow, hooked (twisted) beak which first curves anteriorly and to the right; then it bends ventrally, crosses the outer edge of the gular folds almost in contact with the lower lip, and ends with an upturn of the bidentate tip so that the exerted style points upward (fig. 8). A bulge and consequent opening between the galea margins occurs just proximal to the apiculate tips of the anthers.

At the single observation locality the principal visitors were *Bombus bifarius nearcticus* and *B. edwardsii*. There was no recognizable difference in the way either species worked the flower. Some individuals repeatedly visited the adjacent *Ribes* in bloom, particularly during windy periods or if they were being observed at close quarters; those collected were *B. b. nearcticus*. Other visitors, including a small bee, *Chloralictus*, gathering pollen and with the scopa full were too short to effect pollination. *Drosophila* were numerous as gleaners, especially in the morning. Two wasps, one a vespid, syrphids, and other flies were also seen. One too small to reach the stigma repeatedly entered the flower from the crest of the galea and emerged covered with pollen.

The visiting *Bombus* approaches to the left of the flower, alighting in a position vertical with respect to the earth and at right angles to the longitudinal axis of the flower. The bee

Fig. 8-10. *Pedicularis racemosa*.—Fig. 8. Anterolateral view.—Fig. 9. Longitudinal section through corolla.—Fig. 10. Ovary with portion of style and half of calyx. All $\times 5$.

then turns right, or parallel with the galea axis, and simultaneously pushes with the hind legs on the lower lip which thus assumes a horizontal plane but with the upper surface facing down. As the bee turns, the stigma is brushed by the venter.

The hind legs are oriented by the marginal sinuses or ridges. The midlegs are astride the base of the beak, the forelegs cling to the margins at the base of the lower lip. Exact positioning must be crucial for the bee will adjust the legs once or twice and rather frequently must push at least twice with the hind legs to force the lower lip up and hence open the ventral aspect of the galea. With this movement the proboscis is inserted into the throat from the

Fig. 11-16. Fig. 11-13. *Pedicularis groenlandica*.—Fig. 11. Front view. $\times 4.4$.—Fig. 12. Lateral view. $\times 4.2$.—Fig. 13. Longitudinal section, semidiagrammatic. $\times 4.2$.—Fig. 14-16. *Pedicularis attollens*.—Fig. 14. Front view. $\times 6$.—Fig. 15. Lateral view. $\times 6$.—Fig. 16. Longitudinal section, semidiagrammatic. $\times 6$.

FIGURES 11-16

left side of the galea presumably along the median groove. The face enters at the pouched opening of the galea, then presses against its narrower base. The accompanying lateral expansion releases tension on the filaments so that the anthers separate and allow pollen to fall.

As the bee curves the abdomen forward, the terminal segments are brushed across the stigma which then springs back into position. The venter (now curved under the galea opening of the galea, then presses against its narrower base. The accompanying lateral exposed the venter presumably touches them so that additional pollen is dislodged. The entire venter is dusted, particularly the center left, and in addition the right side of head and thorax. When it stops feeding, the bee appears to drop off the flower; some individuals fall farther than others before coordinating themselves into oriented flight.

At irregular intervals of 1 to 20 minutes the bee would back out of the flower, cling by one foreleg to the margin of the lower lip and clean its entire body. Pollen was worked into tiny balls at the tip of the abdomen prior to transfer to the corbicula. Pollen left on the ventral segments must be that most effective in pollination as the region undoubtedly comes into firmer contact with the stigma than any other part of the body.

Visiting *Bombus* spent more time in selecting flowers of *P. racemosa* than was observed for any other species. The bees never landed on half-opened flowers, indicating that any attraction other than pollen is available only in mature flowers. Trichomes and other tissues of the tube and ovary do not differ from those of other *Pedicularis* species which have no conspicuous fragrance and do have a true nectary; however, no nectar was discerned. Does the proboscis serve only as a lever or holding device?

The very pleasant odor decreases by noon as does the frequency of visitations. Odor may be particularly important for this shade-growing plant, for the white flowers are not very conspicuous. In the Arctic where bees are less abundant and seasonal competition for pollinators is very great, Knuth, Porsild and others have commented on the considerable fragrance. One wonders whether the small population of *P. dudleyi* may be due in part to its lack of an odor or did it have a scent the observer did not distinguish?

One might expect on the basis of Kugler's work (1930) that guide lines would be important in the eccentric flower of *P. racemosa*. Although colored markings are lacking, the deep gular folds and associated median groove, the transverse region of the beak and ventral margins of the galea serve as tactile guides and the shadows of folds and openings may serve visually.

Pedicularis groenlandica (fig. 11–13)—This is the most widespread of the California species. It is found from high elevations in the central Sierra Nevada to the coast of Alaska, throughout much of the Rocky Mountains, east in Canada to Greenland. Typically it is found in wet boggy places, often in deep shade and with its roots in ice-cold running water. Observations recorded here were made in the central Sierra Nevada at elevations of 8,000–10,500 feet at Norden, Placer County, Sonora Pass, Tuolumne County, and at several localities in the region of Tioga Pass, Mono County.

The purplish flowers on a strict dense spike suggest a totem of miniature elephant heads. The domed galea gives rise to a long dark (maroon) narrow beak (trunk) (fig. 11) which extends first ventrally, later ventrally then anteriorly, and finally in anthesis, ventrally, anteriorly and distally upward, usually twisted, often to the right and then to the left so that with the exerted style and stigma an arc of some 300° may be described in its 8–14 mm. length. The lateral lobes of the lower lip are large and reflexed (resembling ears), the middle one largely concealed by the beak.

Although numerous bumblebees were observed visiting the flowers, the pollination mechanism of *P. groenlandica* remained an enigma even after two seasons' observation. When experimental bees on pins were forced into a flower pollen would fall on the head and thorax but these parts did not contact the stigma. Bumblebees were regularly seen visit-

ing the flowers but owing to the peculiar conformation of the galea and beak which enclosed the sexual organs, and the rapidity of the bees' visits, it was not evident how the bees could effect pollination. The clue was finally afforded by the observations of *P. racemosa* just described. It is the venter of *Bombus* which transfers the pollen in both species.

The principal visitors observed were *Bombus b. nearcticus* and *B. melanopygus*, the former being more common. Occasional visitors and gleaners collected were *Psithyrus*, one Anthomyiidae, two Empiidae, syrphids, one megachilid, and a Rufous hummingbird was seen. Syrphids and an unidentified fly fed on pollen; they approached the flower in the same fashion as *Bombus*; hence they could pollinate with pollen incidentally picked up. Syrphids were observed to eat pollen on the stigma.

The visiting *Bombus* inserts its usually extended proboscis to the right, under the galea, into the tube. Clinging with the forelegs to the base of the galea near its juncture with the lower lip the bee pushes with the midlegs, hindlegs or both pairs on the lower lip, bending the abdomen forward at the same time. The combined action of inserting the face so as to push up the galea and of pressing the lower lip well back while the abdomen is curved forward under the resultant galea opening, allows sufficient separation of the anthers to let the pollen fall. Lobes (or teeth, Prain, 1891) folded back into the galea are not displaced but may provide a firmer margin to the proximal galea opening and perhaps may prevent excessive lateral anther displacement.

Usually pressure on the lower lip is maintained by the hind legs while the midlegs are used to gather pollen; other times the proboscis must act as a levering and holding device, when the forelegs push back the lower lip and both mid and hind legs collect pollen and pack it into the baskets. Occasionally on alighting, the bees would clean face and thorax of pollen and pass it to the venter; at other times cleaning was done while hovering.

It is pollen on the venter that is effective in pollination. This occurs as the bee approaches a second flower. Contrasting with the light dome is the beak tip which is about in line with its dark base, the assumed focal point for the approaching visitor. The delicate, relatively inconspicuous dark style and stigma thus may be "accidentally" hit harder by the venter than if they were conspicuous objects more readily avoided.

Thus like *P. racemosa*, *P. groenlandica* is a *Bombus* flower which requires a "learned behavior" even more complex than that referred to by Olberg (1951) for *P. sylvatica*. In these species the bee must (1) use the proboscis as a lever; (2) push the lower lip well back with one or more pairs of legs; and (3) curve the abdomen forward so the venter receives the pollen. *P. contorta* of the northwest appears to have a similar mechanism. Among some of the many asiatic species with variously coiled beaks, this may be the floral mechanism also. In *P. groenlandica* the guide lines, if any, consist of margins of the lower lobes converging toward the entrance, the margins of the dark beak and the outline of the light galea against the purple lower lip. The base of the dark beak adjacent to the white area of the galea offers great contrast. If the light dome of the galea serves as a guide from a distance, the final positioning of the visitor is based on the guides formed by the various margins and the dark base of the beak.

Manning (1956a) has shown that at close range, reaction to scent takes precedence over color and accounts for visitation to color varieties of garden flowers; this would reduce visits to flowers of similar form with different scents. Microscopic examination revealed no typical glandular tissues of a nectary nor was any nectar observed. The proboscis must serve solely as a holding and levering device as in the case of *P. attollens* and *P. racemosa*. However, the behavior of the bees affirmed the presence of an odor the observer could not detect. That bees are more sensitive to the odor than to the colors of *P. groenlandica* and *P. attollens* is evidenced by their attraction to caged flowers of both species when, because of the nature of the cage, the flowers were virtually invisible. Not only were bees attracted by the scent but unerringly they would alight on that portion of the cage most nearly adjacent to freshly

matured flowers. That the odors of these sympatric species must differ was further indicated by the fact that bees visiting *P. groenlandica* went only to cages containing *P. groenlandica* and those working *P. attollens* only to *P. attollens* cages.

The peculiar and various orientation of the protogynous stigma raises the question of possible adaptations. The pollen is abundant and regular visitors become well covered by the yellow powder. Also, as they work some falls onto other parts of the flower and occasionally one can even see small amounts carried away on an air current. Some bees after feeding on two or three flowers and becoming well dusted clamber over the spike. These could effect some pollination, particularly when the head, which usually receives a visible amount of pollen, hits a down-turned stigma. A bee was seen to hit such a stigma as it approached the landing platform of the flower below.

Flowers which are seasonally very late do not complete the typical upward growth of the beak. In these the anthers dehisce when the beak extends the maximum in a downward direction; the stigma may still be enclosed and hence some pollen may adhere. Kerner (1894) and Knuth (1909) report such a mechanism for several species which they considered self-fertile; however, these species have shorter beaks which regularly grow to a vertical position. Pollen falling through such a down-turned beak and effecting pollination may offer another possible explanation for the consistently high seed set observed. It would be interesting to know to what extent the success of *P. groenlandica*, so widely distributed, has depended on its versatility with respect to pollinating mechanisms.

The colors of flowers belonging to advanced plant families presumably have their origin not only in the attraction of insects, but also in luring specific insects according to their color-sense. Thus, color may serve as an isolating mechanism which may help to insure pollination. In the genus *Pedicularis*, the majority of flowers is yellow with greater or lesser amounts of red splotches and lines; however, some have red galeas but many species are entirely pink, red, or various red-purples. Fewer are white which appears to be a mutant from red. A variety of colors is to be found among the California species. The yellow, variously red-suffused or streaked flowers of *P. semibarbata* are relatively inconspicuous while the pale lavender and white flowers of *P. dudleyi* and *P. crenulata* are more readily distinguished in their respective habitats as are the white, beaked flowers of *P. racemosa*. *P. groenlandica* and *P. attollens*, the two beaked species growing in the open, and often adjacent, are distinctively colored. If bees see only the blue in rose-purple shades, the purple flowers of *P. groenlandica* are presumably very distinct visually from *P. attollens* in which the pink has almost no blue in it.

The question of the relationship of flower color to structure has been raised by earlier investigators. Prain (1891) found a high degree of correlation between beaked species and color in examining plants of the Himalaya, the region of maximum floral diversity. This in turn must be interpreted as an area showing the maximum selective pressure through pollinator discrimination and where a high percentage is pollinated by Lepidoptera. On the assumption that the beaked corollas show greater specialization (to pollination) it is not surprising to find the higher percentage "red". Although Prain considered the correlations "indirect," a cursory examination of 72 North American and European species showed a similar though less remarkable relationship.

There are many examples of parallel corolla forms which differ principally in color. The color-form association may be the significant thing, as von Frisch has suggested. Thus a beaked deviant of a beakless form would be more readily distinguished if a color were associated with it and hence might have a selective advantage over a beaked variant of the ancestral color pattern. *P. attollens* may have been set apart from its putative *groenlandica*-like ancestor by its lighter color with almost no purple and its distinct guide lines. It is possible that *P. groenlandica* with the blue in it is the more successful, in part because of its color.

The very high seed set on very early and very late spikes of flowers indicated that *P.*

groenlandica and *P. attollens* might be self-compatible. Experiments in selfing, crossing and "autogamy" were carried out in the field as indicated in table 2. "Autogamy" in these experiments involved only the identification of flowers in bud at the time of caging, no artificial pollination. The results are not significant because of the numerous opportunities for contamination², a major problem when experimental material must be handled in the field because of its parasitism. The results are suggestive that the flowers are limitedly self-compatible and that autogamy may occur rarely.

TABLE 2. Data on Pollination Experiments on *P. groenlandica* and *P. attollens*

EXPERIMENT	NUMBER OF FLOWERS	CAPSULES		SEEDS
		NUMBER	PERCENTAGE	
Outcrosses				
<i>attollens</i>	73	12	16.5	15-9 poor
<i>groenlandica</i>	220	36 (81 set)	16.3	58
Exp. selfed				
<i>attollens</i>	127	32	25	aborted
<i>groenlandica</i>	217	75 (81 set)	34.5	30 small
Autogamy				
<i>attollens</i>	77	4 (aphids) (3 dehisced)	4.2	2
<i>groenlandica</i>	265	40 (aphids) (14 abort)	15	10
Crosses				
<i>attollens</i> × <i>groenlandica</i> ♂	196	21-5 dehisc.		31 small
<i>groenlandica</i> × <i>attollens</i> ♂	246	45-4 tiny		12 shrunken shrunken or empty

POLLINATION BY SMALL BEES

Pedicularis semibarbata (fig. 17-19)—The range of *Pedicularis semibarbata* extends from southern California to southern Oregon and east into adjacent Nevada. It is found in the drier, well drained, usually gravelly areas of yellow pine forests but may occur at higher elevations. The principal observation localities were near Lake Arrowhead and Wrightwood, San Bernardino County; other localities were at Mt. Pinos, Kern County, Echo Lake, El Dorado County, and Norden, Placer County. The yellow, often rose-suffused flowers are frequently hidden by numerous large pinnately compound leaves but the main spike is always exposed. A comparatively wide mouth and tube allow ready entrance to small bees. The abruptly truncate galea may be faintly crested, the arching vein (fig. 23i) forms a line of constriction and terminates at a slight indentation on the galea margins. It forms the line along which the "break" occurs. As in *P. crenulata*, *P. dudleyi* and *P. densiflora*, the lower lip curves and locks over the recurved margins of the galea. The oblique lower lip, shorter than the galea, has three expanded lobes that form an adequate landing platform; a middle groove is bounded by ridges bearing trichomes.

The principal visitors to *P. semibarbata* are various species of *Osmia* which are small enough to force their way into the funnel-shaped throat. Two species of *Anthophora* were taken but they fed mostly on pollen scattered on the lower lip. At two locations *Xylocopa* were observed to back out of the tube, then turn upside down under the galea presumably to get more pollen. Smaller bees, *Chloralictus* and *Erylaeus*, scavenged for pollen on flowers

²The powdery pollen is readily carried by air currents; it was difficult to make an 'adequate' amount adhere; thrips and aphids which multiplied rapidly in caged plants undoubtedly caused contamination. The capsules formed were small and such seed as was harvested was small and shrunken. The testa was normal size in some but the endosperm in such cases was shrunken; none germinated.

and bracts. Other visitors included a Bombyliid and an Anthomyiid. The species in so far as they were identified are as follows: *Osmia atrocyanea*, *O. densa*, *O. laeta*, *O. tristella*, *O. sp. Lasioglossum (Chloralictus)*, *L. (Evylaenus)*, *Xylocopa sp.*, *Anthophora edwardsii*, *A. pacifica*, Bombyliid, Anthomyiid.

The *Osmias* hover over several plants and finally settle on one. Selecting a single spike, they crawl over it for a time before working the first flower, and then they may work two to five more. It is puzzling that a clump or even a spike requires so much searching, for a selected flower often is visited four or five times by the insect which alternates with ten to thirty second rests in the sun. Although the powdery pollen scatters to some extent, the insects never seem to feed on this, but, as they brush past flowers, pollen scattered over the body pile must cause some incidental pollination.

From flight the bees (1) alight to the left of the lower lip, (2) hit the stigma with the terga as they turn into the throat, (3) force the head and thorax, or the entire body of smaller species and of most females, into the throat. This creates a lateral pressure which causes a distension of the galea walls and allows separation of the anthers. Pollen is deposited on the back of the visitor. Retreat is accompanied by vigorous wiggling which must release additional pollen and may increase opportunity for self-pollination. As the bee angles to its right, its weight displaces the lower lip downward and prevents self-pollination.

The abdomen may press against the subulate-tipped anthers as the bee alights, although this was only experimentally observed with dead bees. The corolla is relatively firm and the visitors are small bees; it seems likely that contact is made during entrance and is in part due to the locking device at the angle of upper and lower lips. This delay in downward displacement of the lower lip may help insure contact with the stigma (as well as in *P. crenulata* and *P. dudleyi*), and also reduce the visits of ineffective visitors. The lateral pressure on the throat by the face, then the head, and often the thorax allows pollen to fall on the head, thorax, and limitedly on the abdominal dorsum. The absence of subulate anther tips in similar species suggests that such anthers may be of adaptive significance here.

Bees often approach the flower from one side, particularly a second flower on the spike; if so, any part of the back may brush the stigma which is displaced to the right. Such stigma displacement facilitates entrance by providing easier access to folds and trichomes that offer good footholds and that may also serve as obscure guide lines. The central groove leading to the nectary undoubtedly offers a good mechanical guide for the proboscis.

Frequently bees enter the flower upside down, particularly in young turgid flowers offering no landing platform. The weight of the bee at the apex of the galea in these firmer flowers may help to cause the "breaking" and hence release pollen. Because *Osmia*, the chief pollinator, carries pollen in a ventral scopa, this reversed entry and exit must provide reasonable assurance of pollination in these protogynous flowers. So often was the lower lip used only as a means of exit that one questions how essential it is as a "landing platform." Even when it was so used the bee often entered at such angle as to grasp the style with the hind leg and pull the stigma against the venter. At one locality (Wrightwood) *Osmias* regularly entered and departed from the flower on the left side but they also frequently turned more or less upside down and followed the edge of the galea as they backed out of the tube; this would seem to increase the possibility of selfing.

No European observer has reported a species of *Pedicularis* pollinated only by small bees. *P. semibarbata* in the drier mountains of California is such a species. The structure is so similar to that of bumblebee species that it is difficult to understand why long-tongued bees do not take advantage of it. *Bombus* does occur at the observation localities of *P. semibarbata* but not one was seen to investigate these flowers over a period of three seasons. It seems probable that other species, as *P. furbishiae*, also are pollinated by small bees but no observations have been recorded.

POLLINATION BY HUMMINGBIRDS

Pedicularis densiflora (fig. 20–23)—This species is found along the coast from Baja California to southern Oregon, east through the mountains to the west slope of Sierra Nevada and south to Kern County. It grows in a variety of ecological conditions within this area. Southern populations are associated with chaparral composed primarily of *Adenostoma*. In the Santa Lucia Mountains some populations are in stands of Coulter pine; in the Monterey peninsula they are under Monterey pine; in the San Francisco Bay area they are usually associated with madrone and Kellogg oak, but on Mt. Diablo with *Adenostoma* as well; in the Siskiyou-Trinity Mountains they were in stands of Douglas fir and scrub oak; and in the northern Sierra Nevada the subsp. *P. d. aurantiaca* was observed largely with yellow pine. All these populations save that on the Monterey peninsula were represented in the observation localities.

The flower of *Pedicularis d. densiflora* is distinguished by its red color, the greater size (25–35 mm. long), the proportionately longer truncate galea and a very reduced lower lip. The subspecies *P. d. aurantiaca* (Sprague, 1957), has a flower still longer (35–45 mm.), the galea larger and the color yellow to orange-red. The corolla tube, long-exserted from the calyx, enlarges distally but sufficiently abruptly in the subspecies so as to form a more distinct short throat. In some populations a contrasting chartreuse or white area (fig. 20, 21) occurs in the sinuses of the lower lip and in an area at the angle of the galea and lower lip which is covered with large pyramidal cells (fig. 23k). The margins of the upper lip recurve proximally, over which the lower lip curves to form a very effective locking device as in *P. semibarbata*. As the flower ages, a growth difference in the distal region of the tube (fig. 23j) causes the more distal portion to become increasingly horizontal and the self-colored style and stigma which extend two to three millimeters beyond the apex of the galea become vertical. A firm vein (fig. 23i) which arches distally and terminates at the mid-point of the galea margin forms the line along which the worked flower "breaks."

The principal visitors were four species of hummingbirds. No difference was noted between feeding methods of different species and some individuals of all four species were observed with pollen at the base of the bill or on the crown after feeding from *Pedicularis*. The resident Anna hummingbird was the principal species in coastal populations and the Rufous in the Sierra Nevada; migrant Allens were observed in coastal mountains and at Mt. Diablo, where Black-chinned hummingbirds were also seen. The birds usually hovered while feeding; an adjacent spike or the ground on occasion tempted them to perch. As they frequently worked in sequence two or more spikes on the same rootstock the percentage of cross-pollination must be reduced. Repeated visits to the same flower indicate that the copious nectar supply had been rapidly replenished or else little diminished on the first visit.

The population at Phoenix Lake, Marin County, was worked vigorously by *Bombus vosnesenskii* during the day where mechanisms similar to those in bird pollination were in operation. The area of pollen deposition and consequent transfer area was the top and back of the head and thorax. The bees hovered as they probed, especially while working the more mature flowers with no landing platforms. On the denser spikes with young flowers they more often alighted, the hind legs on bracts, midlegs grasping the calyx edge and front legs on the lower lip. As the anthers do not dehisce until the galea is exserted one-half to two-thirds the length of the calyx, only nectar was sought in the younger flowers. In many populations quantities of nectar are secreted as soon as the stigma is visible. Since hummers were not observed to feed on such young flowers and few populations were visited by bees, the significance of this precocious nectar secretion is not known.

In the Phoenix Lake area where *Bombus* worked *Pedicularis* flowers during the day the birds concentrated their attention on the abundant thrip-laden panicles of *Arbutus menziesii*, feeding heavily on *Pedicularis* only at dusk. It may be that the bees were a deterrent

Fig. 17-22. Fig. 17-19. *Pedicularis semibarbata*.—Fig. 17. Front view. $\times 3$.—Fig. 18. Lateral view. $\times 3$.—Fig. 19. Longitudinal section, semidiagrammatic. $\times 3$.—Fig. 20-22. *Pedicularis densiflora*.—Fig. 20. Lateral view. $\times 2$.—Fig. 21-22. Views such as might be seen by visiting hummingbirds. $\times 2$.

to the hummingbirds (which they often chase from syrup cups) or more likely, as it was nesting season, the proteinaceous thrips were a more desirable food for the young.

In three localities *Anthophora pacifica* or *A. edwardsii* were observed; they worked younger flowers where there seemed some possibility of their reaching the nectar. Quantities of pollen on face and labrum indicated the possibility of incidental pollination. At one population *Apis mellifera* was present, gathering pollen but surely getting little nectar. Most populations showed holes through the galea opposite the anthers; three populations had

frequent holes in the tube indicating nectar stealers. Small bees and sundry flies were observed gleaning pollen from the surface of the flowers. The powdery pollen, occasionally caught by air currents while a "legitimate" visitor fed, may account for some incidental pollination. In some populations where stamens were frequently pulled out of the galea or became flaccid with age and fell from the galea, even more pollen must be carried by air currents to the protogynous stigmas.

In working the flowers of *P. densiflora* the hummingbird slips the bill through the slight opening at the proximal part of the galea. As the bill enters the tube along the central groove which is continued by the ventral filaments, the bird may tip the flower up, particularly in older flowers with an obvious break (fig. 23j). This results in pressure of the stigma against the base of the bill in Anna hummingbirds working coastal populations and on the crown of Rufous hummingbirds in the Sierran subspecies. The broader base of the bill (or the face

23

Fig. 23. *Pedicularis densiflora*. Longitudinal section, semidiagrammatic. $\times 3.4$. (a. apex of galea; c. crest of galea; e. dorsal filament; f. ventral filament; g. style; i. arching vein; j. "breaking" point; k. pyramidal cells or "prickles"; h. nectary.)

in Rufous) distends the throat, the galea widens and the distal portion "breaks" along the arching vein. This releases tension on the filaments; the anthers separate and pollen falls on the feathers at the base of the bill (or upon the crown of Rufous and Allens). Probably the acute-tipped anthers are touched and thus increase the amount of pollen dislodged. As the bird withdraws, it drops lower and prevents self-pollination. Because the stigma projects and is well in advance of the anthers, approach to a second flower would seem to insure cross-pollination if flowers on another rootstalk are visited.

The most distinctive floral adaptation among the California species is found in *P. densiflora*, the reddest *Pedicularis* in California, and the only hummingbird-adapted species in the genus. This is not surprising since most flower-birds and bird-flowers are found in the tropics and sub-tropics whereas this is a north temperate genus with only two species approaching the equator. *P. densiflora*, however, grows within the resident and migratory range of four hummingbirds, all of which take advantage of its abundant nectar supply. Furthermore, observations indicate that they are the principal, when not the sole, pollinators.

Whether or not red is the typical bird-flower color continues to be disputed with no adequate statistical data to settle the question. It may well differ in various provinces but in the southwest red is strongly associated with hummingbirds as evidenced by red species of *Castilleja*, *Penstemon*, *Ipomopsis*, *Diplacus*, etc. It is of some import that birds can see red whereas bees cannot. Competition during the day is thus reduced if not eliminated and at night the flowers are virtually invisible. If, as Porsch (1930) suggests, red is the color most visible to the eye of vertebrates, red flowers are a particular advantage for birds which feed

early in the morning when other colors are less visible. Visibility must be increased for flowers in the coastal populations where the luminous quality of the translucent purple-red corolla is enhanced by the long rays of aural and crepuscular hours, the periods of greatest hummingbird activity. It is also in these southern populations growing in the shade under *Adenostoma* where the contrasting color at the angle of galea and lower lip is more prevalent. It poses the question whether it is important as a guide.

There is a further interesting, possibly coincidental, correlation between the flower color of *P. densiflora* and its principal visitor. In the coastal populations, at least as far north as Lake County, *P. d.* subsp. *densiflora* is primarily red with purple overtones whereas *P. d.* subsp. *aurantiaca* in the Sierra is bright orange with red added. On the coast the principal pollinator is the Anna hummingbird with a gorget of the same luminous purple-red; in the Sierra, the Rufous hummingbirds, with orange-red gorgets, are the summer residents and migrants. Scott-Elliott (1890) found a similar correlation between the color of the breast of *Cinnirys* sp. which fed on flowers of different families (labiates, irids, aloes, legumes) of which many species had become bird-flowers and were of the same hue. Werth (1915) has pointed out a similar correlation. It is probable that a conditioned response, however slight, might form for flowers of the same color as the one important in the nuptial courting going on concurrently with the flowering. A similar color might be expected to produce a quicker response, particularly in the breeding season, and give some selective advantage to flowers possessing it. Müller (1881), Lovell (1918) and Eltringham (1919) have reported similar responses in butterflies.

Many students of floral ecology have pointed out the various characteristics of bird-flowers. They include, in addition to color, correlated size, lack of a landing platform, shape and structure of the tube, presence of nectar and lack of odor, the nature of the pollen and the floral mechanism. Comparative measurements of the floral tube and bird bill, and the introduction of birds' heads (museum specimens) into fresh flowers indicate that, with the extensibility of the tongue, the nectar is easily reached. The Sierran race with a larger, wider tube and throat requires that the bird's face be inserted to accomplish the "breaking" and to enable this smaller bird to feed readily; at the same time it insures that the crown will serve as the effective area for pollen transfer. Additional pressure on the stigma resulting from the bending of the distal region of the galea must increase the chance that some pollen will adhere.

In *P. densiflora* the short, narrow lower lip offers no platform and hence discourages visitors too small to be effective pollinators. The narrow tube admits the hummingbird's bill, a narrower organ than the head of a bee, with a proboscis long enough to reach the nectar, whereas a bee of such size that, while hovering, it can reach the nectar is probably a reasonably efficient pollinator as was indicated at the Phoenix Lake station.

Melin (1935) and Werth (1956) consider a large size and firmness to be correlated with bird pollination. *Pedicularis densiflora* has the largest flowers of any California species and probably as large as any North American member of the genus; only the long-tubed Himalayan ones are conspicuously larger. The tube of this flower is no firmer than that of *P. crenulata* and *P. semibarbata*. It does have large pyramidal cells on the inner as well as the outwardly rolled proximal margin of the galea. Kerner (1895) examining *P. sylvatica*, considered these as "prickles" to be avoided by the insect and hence to define the path into the flowers, hardly the *raison d'être* for the less sensitive bird bill. They appear to stiffen this area and it is assumed they are supportive in function.

The nectar of *P. densiflora* is abundant, fairly thin and has long been relished by Indian children and flickers alike (Chestnut, 1900). It is secreted from a fairly large ventral nectary, the hypogynous disc typical for the genus. It is large and more expansive ventrally than that of other California species; this may possibly be related to the protection of the ovules from the probing bird bill (Grant, 1950a). The nectar is conducted a short way along the

canal formed by the ventral filaments. Porsch (1924) claims that conduction from the place of origin is important to maintain maximum secretion. The bill per se rarely endangers the ovary as it probably does not often extend beyond the "break." The tongue is readily protruded the ensuing distance and in any case is the organ that licks and pumps up the nectar.

Whether the bird primarily seeks nectar, insects, or both remains a contended point. Investigations of stomach contents are contrasted with observations at syrup cups. Lowland species seem more dependent on nectar than the more insect-dependent mountain species. Whether it is a matter of availability, the need for more liquid in warmer regions, or nutritional requirements which change with the season, has not been shown. The nature of the prime focus does not detract from the fact that birds, particularly hummingbirds, and flowers, notably nectariferous ones, are intimately associated. That this association is of long standing is indicated by the modified brush and tubular tongue of the hummingbird which is characteristic of flower-birds, particularly nectar-feeding ones.

Pedicularis densiflora seems to lack odor; at least none has been noted. The lack of odor in bird-flowers has been noted by Melin, Porsch and others. Odor seems to play little if any role in attracting birds to flowers. In fact, when flowers have an odor which attracts insects the birds seem frequently to feed upon the insects rather than the nectar (Porsch, 1933).

The floral mechanisms of the tubed flower associated with bird pollination are typical of the genus; dichogamy, stigma exserted, and a correspondence between flower proportions and the principal pollinators. The largest of the California hummingbirds, the Anna (bill 16–19 mm. long and 0.9–1.0 mm. wide at midpoint), feeds upon the coastal population of *P. d.* subsp. *densiflora* having the larger tube and the shallower galea; the smaller Rufous hummingbirds with slightly shorter, more slender and rapidly tapering bills (15–17 mm. long and 0.7–0.8 mm. wide) feed on *P. d.* subsp. *aurantiaca* with a narrower tube and larger, deeper galea. In the coastal populations the larger tube admits Anna's larger bill which is wide enough to expand the galea, so that, with the "breaking," pollen will be deposited at the base of the bill. The smaller galea, together with the feathers and bristles at the base of the bill, provide adequate lateral protection to prevent lateral loss of pollen. In the Sierran form the narrower tube admits the smaller bill of the Rufous and yet the large throat admits the introduction of the face, thus providing the necessary lateral pressure to cause "breaking of the galea." The large galea, more or less enclosing the crown of the bird where pollen is deposited, prevents lateral dispersal.

To look for a progenitor of this fine bird-flower it is not necessary to go far. Its habit of growth, the large leaves from a woody crown with a few fleshy storage roots giving rise to annual fibrous roots connecting with the host, dense spikes of flowers only later surmounting the foliage (see fig. 1) and physiological adaptations to a more arid condition place *P. densiflora* close to section *Centrantherae*. A flower form possessing the less specialized characteristics of its two species, *P. semibarbata* and *P. centranthera*, could have given rise to all these related species in the Pleistocene.

Although the two species, *P. densiflora* and *P. semibarbata*, are nowhere sympatric, the similar vegetation and habit suggest a relationship in which Dr. Li concurs (personal communication). In addition, if speciation through floral isolation were to occur, *P. semibarbata* becoming adapted to small bees and *P. densiflora* becoming adapted to hummingbirds, other barriers might not arise. Flowers of *P. semibarbata* were cross-pollinated with *P. densiflora* but not the reciprocal cross because of the difference in blooming periods of the two species; *P. densiflora* is nearly out of bloom when *P. semibarbata* begins. No capsules resulted from these crosses (table 3). Experimental selfing indicates both species may be limitedly self-fertile, which could account in part for the high seed set, but that between species internal barriers do exist.

TABLE 3. Data on Pollination Experiments in *P. densiflora* and *P. semibarbata*

EXPERIMENT	NUMBER OF FLOWERS	CAPSULES		SEEDS
		NUMBER	PERCENTAGE	
Outcrosses				
<i>densiflora</i>	76	17	22.4	52 good
<i>semibarbata</i>	92	3	4.	7
Exp. selfed				
<i>densiflora</i>	185	27	14.6	23 good
<i>semibarbata</i>	101	4	4.	9 good
Autogamy*				
<i>densiflora</i>	79	14	17.7	1-2 ea.
<i>semibarbata</i>	192	8	4.15	11
Crosses				
<i>densiflora</i> × <i>semibarbata</i>	46	0		

*Autogamy in these experiments involved only the identification of flowers in bud at the time of caging, no artificial pollination.

Pedicularis densiflora is the only ornithophilous species that has evolved in this bumblebee genus. That facultative bee pollination still occurs in some populations of *P. densiflora* may indicate a vestige of a less specialized mode of pollination, or the versatility necessary for long-term success, perhaps for future evolution.

POLLINATION OF PEDICULARIS IN AREAS OTHER THAN CALIFORNIA

The ten species of California *Pedicularis* make up but a small segment of and do not form a natural group within the 600 or more species of the genus. The European species with flowers highly specialized for insect pollination have been described by numerous students of floral morphology. The spectacular long-tubed species of the Himalaya stimulated comment by Li. Other geographic areas which should prove to be of interest in relation to the pollination of *Pedicularis* are the arctic as a whole, eastern North America, and Mexico south to Ecuador.

Since Sprengel first described the flower of *Pedicularis sylvatica* (1793) the European species have been noted for the generally high degree of specialization for insect pollination. In general the mechanism seems to be very similar to that of *P. crenulata*. A few species of short-tongued Lepidoptera have been recorded on some of the shorter-tubed species. Many species are reported as having mechanisms insuring self-pollination should cross-pollination fail.

The species of eastern North America all appear to be bumblebee-pollinated. *Pedicularis flammula* and *P. furbishiae* with comparatively small flowers may be pollinated by shorter-tongued species of *Bombus* or smaller bees. It is the close correlation between tube width and length and the proportionate length of the galea, which houses the anthers distally, that prescribes the effective visitors.

Observations on the pollination of arctic species have been reported only from northern Europe and adjacent areas. It seems possible that a correlation exists between some of the commoner circumboreal species (*P. flammula*, *P. lanata*, *P. euphrasioides*, *P. sudetica*), the infrequent occurrence of *Bombus* in some arctic areas and at least the potentiality of autogamy. Even in Spitzbergen where *Bombus* has been reported absent or at least rare, Knuth (1906) reports on the maintenance of vigor and seed production of *P. hirsuta* via autogamy. In Nearctic regions, however, *Bombus* is so regular a visitor to some species of *Pedicularis* that the common name is "bumblebee plant" (Anderson, 1950). These species have a most conspicuous fragrance and abundant nectar. Examination of herbarium specimens of these

species indicates that most have a comparatively primitive flower with only short beaks or truncate galeas and appear admirably adapted to pollination by bumblebees.

Seven species of *Pedicularis* are found in Mexico and Central America, one in the Colombian-Ecuadorean Andes. These probably represent isolated remnants from the southernmost extension of the genus during Pleistocene ice periods. The four species endemic to four isolated mountain areas tend to bear this out. These species are similar in their strict habit of growth and three have well developed beaks. The corolla tubes are comparatively narrow and long so that only long-tongued bees or butterflies could reach the nectar. According to C. D. Michener (personal communication) the exceptionally long-tongued bees of the genus *Euglossa* could be expected in these areas, even endemic species. The more widespread species may be pollinated by species of *Bombus*; one of these, however, *P. procera*, which extends north to Colorado, has flowers so large as possibly to require a bee the size of *Euglossa* also.

The Himalaya appear to be the area which has stimulated maximum diversity in the genus and also offers the flowers of greatest interest to the floral evolutionist. Many species have exploited lepidopterans in the cause of pollination. Some of these are characterized by a long narrow tube (up to 11 cm.), a large conspicuous lower lip, a compact inflorescence, rather dense with numerous flowers approaching a vertical position but becoming more lax with age as the inflorescence opens. Most of the very long-tubed species have a beak which is variously coiled, twisted laterally, crested, or even horned. As Prain (1891) noted, the twisting in nearly all cases removes the stigma from the lip which is presumably the landing platform (fig. 24-29).

Many species grow low to the ground in colorful mats with the flowers displayed well above the foliage. Presumably nothing other than a hawkmoth could utilize the twenty or more species in which the tubes are 4 cm. to 11 cm. long. To what extent the length of tongue must correlate exactly with the length of tube is unknown for within such slender tubes (1-2 mm. external diameter) considerable capillary rise of nectar could occur. A majority of these high mountain species is described as red, rose, pink, purple, or crimson; fewer are yellow or white. Ilse (1928) states that butterflies can see red and presumably diurnal moths do likewise. The dark color of many of these species indicates that the pollinators are diurnal, a hypothesis not inconsistent with the cold of these high meadows. Possibly related to lepidopteran pollination is the development of connate bracts, a character distinguishing the series Superbae (e.g., *P. rex*). Such support to the flower's base could enhance the rigidity and upright position of the tube, a character associated with butterfly adaptation. Some of the normally red-flowered species have white-flowered subspecies of distinct geographic distribution. Nocturnal moths may replace the diurnal pollinators in these areas.

Some of the conspicuously small flowered species have "typical" corollas of purple-red or deep pink, colors which may provide the ultraviolet wave length to which the bees respond. The lower elevations of 1500-2000 meters would be somewhat warmer, which might allow for the proliferation of bee species including small bees. *Pedicularis excelsa* has a corolla with a notably short tube, so twisted within the calyx tube that the flower is quite upside down in anthesis, reminiscent of some *Erythrina*s in appearance. Interestingly, this is the only corolla reported to be caducous in the genus. Another species with the position of upper and lower lips reversed has a long narrow tube suitable for butterflies.

In summary it might be said that no valid grounds exist at present for stating the particular method of pollen reception and transfer on the basis of flower form alone. It was only after extensive examination of *P. racemosa* and *P. groenlandica* that these flowers yielded their clue, the reception of pollen on the curved-under abdomen, which is so essential to their pollination mechanism. The contortions of the beak in many of the Himalayan species likewise cannot be explained functionally without actual observations. The peculiar

horns and crest on some species are present only in some populations; in others they are constant characters. They may be due to some real selective pressure, or, rarely, to random fixation, or this variability may represent the evolving status of the species (Li, 1948).

It can be pointed out in summary that the genus *Bombus* and the genus *Pedicularis* are coextensive. There is also evidence, however, that when *Pedicularis* has migrated, it has exploited local pollinators; these include smaller bees, Lepidoptera, and hummingbirds. This utilization of endemic insect (and bird) populations may be responsible for the larger number of endemic species within the genus. This could be explained largely by selection pressures upon numerous corolla mutations.

DISCUSSION

The widespread species of *Pedicularis* in Europe, Asia, North America and the Arctic are all *Bombus* pollinated. Those features of *Pedicularis* flowers which appear suited to bee pollination are: (1) the robust zygomorphic corolla in which the lower lip offers a landing platform (or departing platform) and a concealed entrance to the rather narrow throat; (2) the common pollen chamber formed by the anthers, which is opened only when the galea base is distended laterally, and in many cases subulate-tipped anthers indicating actual contact with the pollinator; (3) attractive color, the presence of nectar, a pleasant odor, and guide line; and (4) a size at least relative to that of the local *Bombus* population. Combinations of these characteristics, resulting in flowers eminently suitable for *Bombus* pollination, are found in five of the California species observed. Two species, *P. semibarbata* and *P. densiflora*, which occur in habitats among the most arid for the genus, have distinctively modified flower structures.

ADAPTIVE RADIATION

Pedicularis is an arctic-alpine genus for which the Pleistocene provided the most suitable period for its wide dispersal. Presumably the pluvial periods provided opportunity for it to migrate to lower elevations and far south of its typical habitat. In fact, it surely must account for the two species which approach the equator, *P. incurva* of the Colombian Andes and *P. zeylandica* of Ceylon; others found in warm regions occur in Mexico, Central America, and in the drier environments of southwestern United States.

Prain (1891) believed the many endemic Himalayan species lent support to his theory of geographic isolation and were a direct result of Pleistocene glaciation. Pennell developed its role for the American province and believed there had been more than one wave of migration from west to east. Li (1948) also indicates the ideal situations that would have occurred during the several periods of glacial retreat for the migration of the genus: new habitats comparatively free from competition and also ones offering moist cool conditions.

The presence of *P. densiflora*, *P. semibarbata*, and *P. centranthera* in the drier environments of southwestern United States can be attributed likewise to pluvial periods and consequent physiological (host-parasite) adjustments rather than the altitudinal or latitudinal migration of most species. A warmer (interpluvial) period might have provided a climate suitable for hummingbirds to migrate within the range of the primitive *P. centranthera*-like species. Variants with longer, redder galeas, larger flowers more conspicuously displayed on taller spikes, reduced lower lips and more nectar (whether these characters occurred singly or in combinations) would have a selective advantage if hummingbirds were concerned. The onset of a pluvial period would create conditions favorable for migration southward and

Fig. 24-29. Chinese species of *Pedicularis*.—Fig. 24. *Pedicularis macrorhynca*.—Fig. 25. *Pedicularis przewalskii*.—Fig. 26. *Pedicularis armata*.—Fig. 27. *Pedicularis tenuituba*.—Fig. 28. *Pedicularis cyathophylla*.—Fig. 29. *Pedicularis decorissima*. (after Li, 1948). All $\times 0.9$.

FIGURES 24-29

coastward. Some such conditions might provide the possibility of natural selection to account for the *P. densiflora* of today. Smaller, yellowish flowers could have been exploited by small bees which are more numerous in warmer habitats; selection pressure could have resulted in the *P. semibarbata* of dry western mountains.

An associated factor which appears to have been effective in the adaptive radiation of this genus is based on the host-parasite relationship. Reports on the European species show the genus as a whole to be highly facultative; members of the Gramineae and Cyperaceae are parasitized indiscriminately, although other moor and meadow plants are utilized (Hayek and Hegi, 1914). A few European species show a strong predilection for specific hosts as do *P. verticillata* for *Sesleria caerulea* and *P. recutita* for *Deschampsia caespitosa*. The species also differ in what they utilize; some take water only; others take some organic material (Hayek and Hegi, 1914).

Among the California species observed, the Sierran forms, *P. groenlandica*, *P. attollens*, and *P. crenulata*, were associated with a mixture of meadow plants (*Poa* sp., *Deschampsia* sp., *Phleum alpinum*, *Carex* sp., *Trifolium monanthum*). *Pedicularis racemosa* was associated with *Abies concolor* but root connections were not identified. *Pedicularis semibarbata* was rarely found on other than yellow pine, *Pinus ponderosa*. *Pedicularis densiflora*, distributed over a wide range of habitats, showed host preferences by each ecological race; that farthest south was associated most often with *Adenostoma fasciculatum*; populations in the coast ranges were on *Adenostoma* or associated with *Pinus coulteri* and *Arbutus menziesii*; in the San Francisco region populations were largely confined to madrones and Kellogg oak; the Sierran subspecies was never found on other than yellow pine.

Pedicularis semibarbata and *P. densiflora* occur in habitats which deviate most widely from the typical cool alpine meadows (Sprague, in press). They thrive in comparatively warm dry regions of coastal chaparral, woods, or the gravelly well-drained areas of yellow pine forests. The host plants are long-lived perennials with large roots which should insure adequate water supply for the annually produced haustoria. Among California species these two also show the greatest divergence from specialization for *Bombus* pollination, *P. semibarbata* for small bees and *P. densiflora* for birds. It seems possible that a correlation exists between these species, which are highly modified as to habitat preference as well as to the nature of their hosts and the apparent host specificity. Mayr (1942, p. 208) points out that . . . "biological races may live in the same localities without mixing, if reproduction takes place only on the host. New biological races may develop almost spontaneously as single individuals become conditioned to new hosts. It is conceivable that species may evolve from these 'chemically' separated races through mutations that affect reproduction behavior and sterility."

Another aspect of the physiological isolation exhibited by some species is that exemplified by the micro-ecological separation of *P. attollens* and *P. groenlandica*. *Pedicularis attollens* is confined to the open drier margins of meadows, dry grass-grown areas on stream banks, or the drier soil caches of rocky mountain slopes. *Pedicularis groenlandica* grows in boggy areas, in ice-cold running water, often in dense shade along streams or in the middle of willow patches. Even where they occur within a few inches of each other as at Slate Creek, Mono County, this preference is easily recognized. An insufficient number of hosts was specifically identified to determine whether the host-parasite relationship correlated with this distinct ecological environment.

FLORAL ISOLATION

What has stimulated this great diversification of corolla form which Li (1948) states is likely unequalled by that of any other genus? Although only hinted at by Prain (1891), the importance of the pollinator was repeatedly emphasized by Pennell (1948) in his study of the Scrophulariaceae. The genus *Pedicularis* represents a remarkable utilization of

environmental resources, particularly potential pollinators. Some mutations of species entering new areas (particularly areas opened up by retreating glaciers) may have allowed them to continue utilizing the same pollinator and others may have enabled a new pollinator, also migrating into a new area, to be exploited. Thus, in the Himalayan region there occur the only very long-tubed species which are probably dependent on Lepidoptera. In the somewhat lower, warmer regions of Asia and in western North America, species of bees are more numerous and a few species of *Pedicularis*, apparently dependent upon small bees, do occur. The result is that various families of two orders of insects have been exploited in addition to hummingbirds. Li states that "the different species have a remarkable potentiality inherent in the genus as a whole, to be able to respond to their insect pollinators in the shaping of the corolla tube."

Among the California species, exploitation of potential pollinators has occurred and in at least one instance is accompanied by ethological isolation. In the two Sierran species (*P. groenlandica* and *P. attollens*), often separated only micro-ecologically, the same species of *Bombus* are utilized but a different floral mechanism is involved. A third species, *P. racemosa*, quite unrelated to these, has a southern outpost in the Sierra but it is outside the range of the other two. The pollination mechanism is similar to that of *P. groenlandica* and one species of pollinator occurs in common. At the eastern foot of the Sierra Nevada, *P. crenulata* exploits a much larger species of *Bombus* (the largest in the state), while on the coast the locally endemic species, *P. dudleyi* utilizes a fifth species. More distinctive as to pollinators are the two species associated with drier areas, *P. semibarbata* depending on small bees and *P. densiflora* pollinated principally by hummingbirds. Apparently competition for pollinators is sufficiently critical so that modifications of corolla form have high selective value and this genus has been able to utilize either different pollinators or pollinators in a new way in a new geographic area.

Li, in his recent taxonomic revision of the Chinese species, comments on the role of the pollinator in the parallel evolution of corolla forms in the very different groups of the genus. He states:

"There is evidence that two different species of unrelated stock may have developed in the same, or sometimes in different regions, both of them showing a similar form of corolla in response to the same or similar insect pollinators. And there is also evidence that one species may give rise to another with like vegetative characters but with different form of corolla induced by the presence of a new insect visitor." (Li, 1948, p. 231)

He also states that "the large number of locally endemic species testifies to the *obligatory requirement* of insect visitors of many of the species" (italics mine). Among others, he presents the example of the series *Superbae* which, on the basis of a very distinctive character, connivent bracts forming a cup at each floral node, is judged to be monophyletic. Within this one group are found toothed and toothless, straight-beaked, and short- and long-tubed flowers. Li's interpretation is that convergent evolution of the corolla has repeatedly occurred among the various series of alternate- and opposite-leaved groups, and on this presumption he proposes the first really usable classification. Selective pressure for such exceptional corolla variation must be closely correlated with the pollination mechanism and hence with the insect (or bird) vectors. In no other genus can one recognize a greater divergence of corolla form.

Among the California species floral isolation is best defined between the sympatric species, *P. attollens* and *P. groenlandica*. These, together with *P. incurva* of the Andes, were considered by Pennell (1935) to form the most characteristic series of the American province. Like other bee-pollinated plants they are distinguished by floral characters (Grant, 1949). It is the proportions of corolla parts together with their conformation which principally distinguishes them, a fact which holds for nearly all the 600 species in the genus. The two sympatric Sierran species are separated, in part, by their floral mechanism and by

constancy of the pollinators.

Their floral mechanism differs. In *P. attollens* pollen is deposited on the stigma and more is picked up by the head of the bee. The bee works hard to procure the dry pollen but its great quantity, or the nectar, if any be present, is adequate reward. In *P. groenlandica* pollen is deposited on the stigma via the abdominal venter as the bee approaches. More falls on the venter when the bee, using the proboscis as a lever, pushes the lower lip back and curves the abdomen under the galea. The principal pollen load then is picked up on two very different areas of the body by the bees working these two species. It must be recalled, however, that other areas are often liberally dusted because the pollen is so powdery. Mechanical isolation then is not complete.

Ethology provides a second barrier between these two species. Observations over two seasons indicate that bees collecting pollen are constant to a given species. This tends to corroborate Manning's work (1956a, b) in which he found *Bombus*, at least on occasion, to attain a high level of constancy comparable to that of *Apis*. In the Slate Creek and Tioga Pass localities, individuals of *B. nearcticus* visited either *P. groenlandica* or *P. attollens* although the two species were within a few feet (or inches) of each other. Bees often had to pass over or avoid the plants of *P. groenlandica* when feeding on *P. attollens*, or vice versa. This is comparable to the observations of Mather (1947) where honeybees after feeding on *Antirrhinum majus* would fly a distance of 400 feet over *A. glutinosum* to locate and continue work on the first species. On only three occasions in over 100 hours of observation were individual bees working on one *Pedicularis* species seen to investigate the other sympatric species. Because memory is important in the matter of bee constancy, these aberrant visits might well have been by young individuals, possibly even on a first trip. (From a distance human observers may also confuse the two species). In some localities where only one species existed, bees visited other genera sparingly. This constancy of the pollinators results in ethological isolation which reinforces the mechanical isolation.

Another partial barrier is the difference between the blooming periods of the two species. *Pedicularis groenlandica* blooms two to three weeks earlier and may be past its peak when *P. attollens* begins to flower. There is, however, an extensive overlap. Individual plants of *P. groenlandica* growing in deep shade, or cold streams, often bloom much later and the long spikes of the flowers open slowly over an extended period. A few spikes may flower even longer than the shorter-spiked *P. attollens*.

Because of its distribution and certain floral characteristics *P. groenlandica* appears to be the more primitive species. It is possible that a mutant *P. attollens*, preadapted to head pollination could arise and presumably would be selectively advantageous over a flower requiring a "learning" process (*P. groenlandica*). Any preadapted mutant to be successful must present deviations that fall within the limits of discrimination of the pollinator; a totally new type of pollination presumably would provide this.

The close relationship between the morphology of a given flower and its pollinators has fascinated many field observers. Correlations between size, shape and floral mechanisms have come to be accepted so readily that classifications have been set up and flowers and visitors readily pigeonholed from the convenience of the armchair. There is no substitute for field observations when considering interrelationships of living things, no matter how cautious and apparently soundly based the theorizing may be.

HYBRIDIZATION

The probability that hybridization has played an important part in the evolution of the genus was discussed by Prain (1891). He suggested that during the repeated migrations along mountain routes, particularly during interglacial periods, mountain passes provided an opportunity for the interchange of genes. Several European observers particularly interested in the genus reported hybrids, some of them named forms. Most recently Hayek and

Hegi (1914) listed ten crosses between nine species which "show the characters of both parents." It is of note that these reports repeatedly involve many of the same parent species with similar floral mechanisms and within the range of the same species of *Bombus*. Where observations of most of these hybrids have been made there is some overlapping of species ranges and habitats. Between flowers with similar pollinating mechanisms ethological isolation could be extremely important in preventing swamping of the parent species and in maintaining the so-called "adaptive-peak." It is also under such conditions that floral evolution may be important in the origin of sympatric species (Grant, 1949).

Li pointed out (1948) that an occasional Himalayan specimen appears intermediate between two species but notes that the difficulty of cultivating the genus obfuscates the proof. Comments of Hultén on the variability of numerous amphi-Atlantic (1958) and Alaskan (1949) species suggest some hybridity or introgression may be the cause. However, no experimental crossing or cytogenetic work or even population studies utilizing modern methods for analyzing hybridization have been reported to verify these observations. None of the California students of natural hybridization have recognized hybrids in the Sierran or other California species.

Attempts to determine interspecific compatability of *P. groenlandica* and *P. attollens* were not successful. Tables 2 and 3 (pp. 193, 200) indicate crosses attempted. The results are only suggestive because of the many difficulties involved when experimental work is done in the field. It does appear that foreign pollen will often stimulate growth of the ovary in *P. attollens* and *P. groenlandica*. However, the fact that no hybrids have been reported by any field observer indicates that some internal barriers, in addition to the several partial external ones, do exist. Whatever its role in evolution, ethological isolation appears to be an important isolating factor in maintaining the two Sierran species and it may be even more important in Europe and similar areas where several species occur in close juxtaposition.

Almost certainly no one factor enables any two species to live sympatrically, nor plays the important role in evolution. Rather, a combination of all the isolating mechanisms has led to the diversification observed in the genus. Nonetheless, the exploitation of numerous pollinators in numerous ways (and of different kinds of hosts) has surely been a major contributing influence in the evolution of *Pedicularis*.

CONCLUSIONS

Pedicularis is an arctic-alpine genus of some 600 species which exhibit a variety of corolla forms that may be unparalleled in any other genus. The flowers, like those of all members of the tribe Euphrasiae, are among those most highly specialized for insect pollination. The basic floral structure allows ready exploitation by species of *Bombus*, the principal pollinator. The bee (1) lands on the lower lip, (2) inserts the proboscis through the closed throat to the ventral nectary, and (3) receives pollen on some part of the dorsum which contacts the stigma of the next flower visited. Various modifications of the basic pattern have enabled the numerous species to exploit not only *Bombus* of all sizes but small bees, Lepidoptera and hummingbirds.

Among the seven species of California *Pedicularis* observed, two species, *P. dudleyi* and *P. crenulata*, have corollas for which the basic pollination mechanism holds. These two species appear to be relictual populations; *P. dudleyi* is endemic to a very small area in the Santa Cruz Mountains and the population of *P. crenulata* is a white-flowered outpost of a usually purple-flowered species widely distributed in the central Rocky Mountains. A third species, *P. attollens*, differs in having a very short tube and long reflexed beak, but so oriented that head pollination occurs. Two species of *Bombus* taken regularly on the flower were working it and good seed was set.

The species, *P. racemosa* and *P. groenlandica*, which are also *Bombus* pollinated, have a floral mechanism requiring learning on the part of the bee which results in venter pollina-

tion. The release of pollen depends upon reflexing the lower lip and the attendant expansion of the galea for the opening of the pollen chamber. In both these species a pollen-collecting bee must (1) use the proboscis, at least in part, as a lever, (2) reflex the lower lip with one or more pair of feet, (3) curve the abdomen under the pollen chamber so that the venter receives the load. In *P. groenlandica* the stigma, supported by a long beak, extends well in advance of the lower lip; it is struck by the venter of the bee as it approaches the flower. In *P. racemosa* the stigma projects from the beak just above the margin of the median lobe of the lower lip; it is brushed by the venter as the bee assumes a working position.

The flowers of *P. semibarbata* have a lower lip which is adequate for the landing of small bees, principally *Osmias*, and the large throat admits the head, thorax or more, enabling these short-tongued bees to reach the nectar. A more distinctive floral mechanism is that of *P. densiflora* adapted to hummingbird pollination. The minute lower lip offers no landing platform; the long tubular corolla has no odor but a copious supply of nectar. It is red in color with a purple overtone in coastal populations where the Anna hummingbird (with a gorget of the same shade) is the principal pollinator; in the Sierran subspecies where pollination is dependent principally on Allen hummingbirds (which have a red-orange gorget) it is orange-red. The question is raised whether a selective advantage accrues to a flower of the same hue as that to which the principal pollinator is conditioned.

Observations of pollination in other geographic areas have been made principally in Europe where most flowers have a typical *Bombus* type of floral mechanism, although butterflies have been observed on them. The long-tubed species of the Himalaya undoubtedly require Lepidoptera. For such flowers as those of *P. armata* with a tube 11 cm. long and 1 mm wide, some long-tongued moths appear the probable pollinators.

Field and experimental observations indicate that the species may be limitedly self-compatible. Self-pollination, rare in *P. attollens* and unlikely for most other species, can occur; the powdery pollen, readily carried by micro air-currents, facilitates this.

The California species, which fall into several different series, and include both toothed and toothless, beaked and beakless forms, illustrate four distinctive pollination mechanisms; that which is basic to the genus, head pollination by bumblebees; a modification requiring venter pollination; one which appears to have arisen very few times in the genus, for small bees; and one which has occurred only once, for hummingbirds. The species utilizing these last two methods live under conditions of maximum aridity for the genus and have developed distinctive physiological requirements in the host relationship.

Presumably the Pleistocene with its cold or pluvial periods and with large arctic areas exposed due to lowering of the water level, would have provided opportunity for the migration of arctic-alpine plants. This period must have allowed species of *Pedicularis* to become widely dispersed. Following this period or during some of the inter-pluvial periods, species may have exploited new environments and under these circumstances utilized new pollinators, even in a new phylum.

Geographic isolation has been combined with a response to the pollinators in the speciation of *Pedicularis*. *Pedicularis attollens* and *P. groenlandica* are partially isolated by having different pollination mechanisms. They also show partial seasonal and ecological isolation. Some internal barriers may exist. Although both species of *Pedicularis* are worked by the same species of *Bombus*, none were observed to go from one plant species to the other. Analysis of pollen loads verified this constancy of vectors. It appears that ethological isolation is one of the more important barriers between these two species.

It is postulated that *P. semibarbata* and *P. densiflora* diverged principally in response to different types of pollinators. The exploitation of totally different vectors would confer an advantage by the reduced competition, of mutual advantage to pollinator and to flower. Adaptations to meet the xeric conditions of their present habitats would have allowed these species to survive to the present.

ACKNOWLEDGEMENTS

It is to Dr. Verne Grant I particularly wish to express appreciation for suggesting the problem, supervising the research and offering many constructive criticisms in writing this paper and the thesis from which it was taken. I am also indebted to Drs. Sherwin Carlquist and Philip A. Munz for their assistance and guidance both in research and in writing. Illustrations have been prepared with the assistance of Messrs William Klein, Richard Beasley and Dr. Stephen Tillett. The very real help and encouragement of a great many others made the completion of this paper possible. Research carried on while the investigator was a guest at Rancho Santa Ana Botanic Garden was partially financed by two grants from Claremont University College, Claremont, California, and a fellowship from the Southern Fellowship Fund, Chapel Hill, North Carolina. A grant from the University Center, Richmond, Virginia, assisted with typing and photographic expenses.

LITERATURE CITED

- Anderson, J. P. 1950. Flora of Alaska and adjacent parts of Canada. Iowa State College Jour. Sci. 24: 2.
 Chesnut, V. K. 1900-1902. Plants used by the Indians of Mendocino Co., California. Contrib. U. S. Nat. Herb. 7: 388.
 Eltringham, H. 1919. Butterfly vision. Trans. Entomol. Soc. London pp. 1-49.
 Grant, V. 1949. Pollination systems as isolating mechanisms in Angiosperms. Evolution 3: 82-97.
 ———. 1950. The protection of the ovules in flowering plants. Evolution 4: 179-201.
 Hayek, A. von, and G. Hegi. 1914. Illustrierte Flora von Mittel-Europa. J. F. Lehmann's, München. 6(1): 112-128.
 Hultén, E. 1949. Flora of Alaska and Yukon. Part IX. C. W. K. Gleerup, Lund. pp. 1401-1420.
 ———. 1958. The Amphi-Atlantic plants. Kungl. Svenska Vetensk. Handl. Fjärde Ser. 7(1).
 Ilse, D. 1928. Über den Farbensinn der Tagfalter. Zool. vergl. Physiol. 8: 658-692.
 Kerner, A. 1904. The natural history of plants. Translated by F. W. Oliver. The Gresham Publishing Co., London. 2 vol.
 Knuth, P. 1909. Handbook of flower pollination. Vol. 3. Translated by J. R. Davis. The Clarendon Press, Oxford. pp. 205-216.
 Kugler, H. 1930. Blütenökologische Untersuchungen mit Hummeln. I. Der Farbensinn der Tiere—Die optische Bindung in der Natur—Das Saftmalproblem. Planta 10: 229-280.
 ———. 1955. Einführung in die Blütenökologie. Gustav Fischer, Stuttgart. 278 p.
 Li, Hui-Lin. 1948. A revision of the genus *Pedicularis* in China, Part 1. Proc. Acad. Nat. Sci. Phila. 10: 205-378.
 Lovell, J. H. 1918. The flower and the bee. Charles Scribner's & Sons, New York. 286 p.
 Manning, A. 1956a. The effect of honey-guides. Behavior 9: 114-139.
 ———. 1956b. Some aspects of the foraging behavior of bumblebees. Behavior 9: 164-201.
 Mather, K. 1947. Species crosses in *Antirrhinum*. I. Genetic isolation of the species *majus*, *glutinosum*, *aurantium*. Heredity 1: 175-186.
 Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York. 334 p.
 Melin, D. 1935. Contributions to the study of the theory of selection. II. The problem of ornithophily. Uppsala University. Arsskrift 16.
 Michner, C. D. 1953. The biology of a leafcutter bee (—Megachile). Univ. of Kansas Sci. Bull. 35: 1659-1748.
 Müller, H. 1881. Alpenblumen. Wm. Engelmann, Leipzig. 611 p.
 Olberg, G. 1951. Blute und Insekt. Akademische Verlag. Geest & Portig K-G, Leipzig. 104 p.
 Pennell, F. W. 1935. Scrophulariaceae of eastern temperate North America. Acad. Nat. Sci. Phila. Monograph 1.
 ———. 1948. The taxonomic significance of an understanding of floral evolution. Brittonia 6: 301-308.
 ———. 1951. Scrophulariaceae. in Abrams, L. Illustrated flora of the Pacific states. Vol. III. Stanford University Press, Stanford, pp. 802-810.
 Porsch, O. 1924. Vogelblumenstudien I. Jahrb. wiss. Botan. 63: 553-706.
 ———. 1930. Kritische Quellenstudien über Blumenbesuch durch Vogel. Biologia Generalis 6: 133-246.
 ———. 1933. Der Vogel als Blumenbestäuber. Biologia Generalis 9: 239-252.
 Prain, D. 1891. The species of *Pedicularis* of the Indian empire and its frontiers. Ann. Roy. Botan. Gard. Calcutta 3: 1-196.
 Scott-Elliott, G. E. 1890. Ornithophilous flowers in South Africa. Ann. Botan. 4: 259-263; 265-280.
 Sprague, E. 1957. A new subspecies of *Pedicularis densiflora*. Aliso 4: 130.
 ———. Parasitism in *Pedicularis*. Madroño. In press.
 Werth, E. 1915. Kurzer Überblick über die Gesamtfrage der Ornithophilie. Botan. Jahrb. 53: 314-378.
 ———. 1956. Bau und Leben der Blumen. Fernand Enke, Stuttgart. 204 p.