The Lopezieae present an interesting mixture of ancestral and derived characters: some members of the tribe retain the basic onagraceous chromosome number \((n = 11)\), but the flowers are advanced in that they are mostly zygomorphic and always have a two-merous androecium. Species differ in the position of the nectaries, also in the way in which floral parts are united above the inferior ovary. These differences, when analyzed with information from a new monograph of the Lopezieae, provide the basis for a phylogenetic tree. It is inferred that ancestral Lopezieae were bird-pollinated woody perennials with regular flowers, two fertile stamens, and no floral tube distal to the ovary. Evolutionary events accompanying the emergence of modern taxa included abortion of the abaxial stamen (all surviving Lopezieae except Lopezia lopezioides), development of an epigynous floral tube (L. riesenbachia, L. semelandra), decrease in floral symmetry without conversion to insect pollination (in two independent lines), and decrease in floral symmetry with conversion to insect pollination (in at least two independent lines). The prominent tubercles on upper petals of certain insect-pollinated species apparently evolved from the less prominent swollen areas still present in some of the bird-pollinated species. The tubercles and an associated snapping mechanism arose in response to increasing selection for fly pollination. Densely staining areas in some specimens may be osmophores; if so, scent plays a supplementary role in the orienting of insects to the upper petals. Interstaminal nectaries and the absence of a floral tube link the Lopezieae to Ludwigia; the relationship of these two taxa to Epilobium is presently unclear. Fossil records indicate that the Onagraceae had evolved by the beginning of the Tertiary Period and that the Ludwigia line is very old. The family’s ancestral features are retained to a greater degree in Fuchsia, however, than in Ludwigia.

WE KNOW NO previous anatomical work on flowers of the onagraceous tribe Lopezieae Spach save that of Baehni and Bonner (1948), who studied five or six species obtainable from botanical facilities in Geneva, Switzerland. With one exception, these specimens were known to Baehni and Bonner only as herbarium specimens. The investigation we report here was carried out in conjunction with a taxonomic revision of the Lopezieae by Plittmann, Raven, and Breedlove (In press). Aided by these monographers, we made observations on 18 of the tribe’s 22 species, and most of our work was done with flowers preserved in FAA or other alcoholic preservative. Another difference between our investigation and the earlier one is that Baehni and Bonner were primarily concerned with floral vasculature and its interpretation, whereas we emphasize evolutionary changes in floral symmetry and the differing ways in which epigynous floral parts are united.

Peter Raven coordinated our efforts with those of his research group, passing specimens from worker to worker, providing us with pollination observations and with other data obtained by his group, and incorporating into their monographic study inferences resulting from our investigation. Thus, our work was aided substantially, though indirectly, by a series of grants from the National Science Foundation to Raven and by specimens that personnel of the University of California Botanical Garden (Berkeley) collected for Raven. Raven also transmitted to us a set of slides prepared by Sherwin Carlquist at a time when Carlquist planned his own anatomical investigation of the Lopezieae. Having put aside the Onagraceae, at least temporarily, for other research interests, Carlquist generously allowed us free use of these preparations, which included two species we might not otherwise have studied.

Alcoholic collections from which our slides were prepared are listed in Table 1. We also sectioned dried flowers of two rare species known (when our investigation began) only as herbarium collections; Lopezia hintonii Foster, Hinton 14902 (US), Guerrero; and L. suffrutescens Munz, Ortega 4264 (US), Durango. Among Carlquist’s preparations were sectioned flowers of two additional taxa: L. cornuta S. Wats., Breedlove 15547

\[771\]
Table 1. Collections of Lopezieae—all now classified as Lopezia species—preserved in liquid and sectioned for this investigation. Localities (except Panama) are Mexican states

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. clavata Brandeg.</td>
<td>Moran 11786 (DS), Baja California¹</td>
</tr>
<tr>
<td>L. gentryi (Munz) Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 15551 (DS), Durango</td>
</tr>
<tr>
<td>L. gracilis S. Wats.</td>
<td>Breedlove 15553 (DS), Durango</td>
</tr>
<tr>
<td>L. grandiflora Zucc. subsp. macrophylla (Benth.) Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 16963 (DS), Sinaloa</td>
</tr>
<tr>
<td>L. laciniata M. E. Jones subsp. ovata Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 15548 (DS), Durango</td>
</tr>
<tr>
<td>L. longiflora Decne.</td>
<td>Breedlove 7161 (DS), Chiapas</td>
</tr>
<tr>
<td>L. lopezioides (Hook. &amp; Arn.) Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 8044 (DS), Morelos</td>
</tr>
<tr>
<td>L. langmaniae Miranda</td>
<td>Breedlove 8052 (DS), Nayarit</td>
</tr>
<tr>
<td>L. nuevo-leonis Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 14225 (DS), Nayarit</td>
</tr>
<tr>
<td>L. paniculata Seem.</td>
<td>Ripley &amp; Barneby 13659 (DS, NY), Nuevo León¹</td>
</tr>
<tr>
<td>L. racemosa Cav.</td>
<td>Dressler s.n. (DS) Panamá¹</td>
</tr>
<tr>
<td>L. riesenbachia Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 7030 (DS), Chiapas¹</td>
</tr>
<tr>
<td>L. semeliandra (Hook &amp; Arn) Plitm., Raven &amp; Breedl.</td>
<td>Breedlove 9882 (DS), Oaxaca¹</td>
</tr>
<tr>
<td>L. suffrutescens Munz</td>
<td>Anderson &amp; Laskowski 4492 (MICH), Guerrero¹</td>
</tr>
<tr>
<td>L. trichota Schlecht.</td>
<td>Breedlove 24534 (MO), Durango</td>
</tr>
<tr>
<td></td>
<td>Rzedowski 20375 (DS), Hidalgo²</td>
</tr>
</tbody>
</table>

* Material taken from progeny cultivated at Stanford University

We imbedded our flowers in Paraplast and sectioned them transversely (mostly at 15 μ) with a rotary microtome, staining some series with chlorazol black E and Pianese 111-b (Wilcox and Marsh, 1964), others with tannic acid, FeCl₃, safranin, and fast green. Eventually we abandoned the first staining method because the safranin-fast green combination proved better for emphasizing nectaries. We prepared no longitudinal sections, for the longitudinal sections of flowers among Carlquist’s preparations did not seem to provide enough additional information to merit the effort; however, we cleared and dissected whole flowers of most species to supplement observations made on the cross sections.

We thank Cynthia Warner for technical assistance during early stages of the investigation. Photographs are by Smithsonian photographer V. Krantz, drawings by A. Tangerini (Fig. 16) and C. Reinecke.

Observations—The Lopeziae are shrubs and herbs—annual, biennial, or perennial—ranging through various parts of Mexico and Central America. Flowers are four-merous except for a two-merous androecium. In all species but Lopezia lopezioides, the lower member of the androecium is a petaloid staminode. Two conspicuous areas of densely cytoplasmic cells associated with the base of the stamen and staminode secrete an abundance of nectar in some of the species. We shall refer to all such areas as nectaries, whether or not nectar is produced. As in other Onagraceae, the ovary is inferior, and a marked constriction separates it from the epigynous parts of the flower. The style is terete and, in younger flowers, terminally concave. At maturity, the stigma is usually described as capitate or subcapitate. Each of the four locules may contain one, a few, or many ovules, depending on the species. The ovules of pluriovular species frequently disrupt the interior of the ovary as they develop into seeds, tearing septa and penetrating the fleshy placental region. In some pluriovular species, the locules connect through small openings (compita) at the summit of the ovary. We have not seen these openings in species with one ovule or with very few ovules per locule—L. cornuta, L. gracilis, L. lopezioides, L. nuevo-leonis—nor have we seen them in L. clavata, L. gentryi, or L. laciniata. Cross sections through the ovary wall show two main tissue zones: (1) beneath the epidermis, a zone of parenchyma in which large raphide-containing cells are distributed, often in pairs; (2) an endocarp the cells of which enlarge in conformity with the cross-sectional outline of the locule (Fig. 13, 14). Differential staining indicates that the walls of most endocarp cells signify...
Fig. 1. Flower buds of Lopetiae. *Lopezia longiflora* (a), *L. semeiandra* (b), *L. grandiflora* (c), *L. langmaniae* (d) *L. lopezoides* (e), are bird-pollinated. Other illustrated species— *L. riesenbachia* (f), *L. trichota* (g), *L. paniculata* (h), *L. laciniata* (i), *L. racemosa* (j), *L. gracilis* (k)— are insect-pollinated or autogamous. When fully expanded, flowers of *L. semeiandra* are longest. Brackets on *L. longiflora* enclose sequence shown in Fig. 2. Sequences in Fig. 3 and Fig. 6–10 pass through roughly equivalent segments in other species. Sequences in Fig. 4, 5 traverse longer segments. All × 3.5.
as the fruit develops, while the single layer of cells immediately surrounding the locule remains un lignified. In _L. semeiandra_ the ovary (like the floral tube and calyx) is densely covered with slender hairs, most of which have rounded or capitate apexes and heavily staining contents. Similar trichomes, but fewer, are found in _L. clavata_, _L. laciniiata_, _L. lopezioiides_, _L. riesen- bachia_, and _L. trichota_. The ovary of _L. gentryi_ is distinctive in having sharply pointed unicellular trichomes on raised pluricellular bases.

We found, as Baeahi and Bonner (1948) did, that the vascular system of the ovary is much the same in all _Lopezia_ species. There are eight main longitudinal bundles, four of them in the septal radii and the other four in locular radii; branches from the bundles on the locular radii enter the trichomes on raised pluricellular bases.

The most obvious differences in floral structure among the _Lopezia_ are associated with different modes of pollination. As would be expected, bird-pollinated species have larger flowers than species that are mostly insect-pollinated or autogamous (Fig. 1). The extremes are _L. semeiandra_, with flowers up to 8 cm long, and _L. gracilis_, with flowers as little as 3 mm long. Some species have a tubercle, more often a pair of tubercles, on each upper petal, a feature first linked with insect pollination more than a century ago. The tuberculate petals are also geniculate and usually clawed, and the tubercles occur at the junction of claw and blade, where the petals bend. Microscope sections through well-developed tubercles show a palisade-like epidermis.

Munz (1961) divided the tribe into five genera. Plitmann et al. (1973), partly as a result of our investigation, put all _Lopezia_ in the genus _Lope- zia Cav_. Our comparison of species begins with _L. longiflora_ the flowers of which are nearly actino- morphic, unlike those of other _lopezias_.

_Lopezia longiflora_—The massive nectaries (more than 2 mm deep) appear in cross sections taken just above the floral constriction (Fig. 2a). Sections taken 1 mm or so above the constriction show the lateral sepals as discrete entities (Fig. 2b), although sepals remain marginally coherent in this species until the flower opens. Bases of the four linear petals are fairly well defined at this level (see also Fig. 2c, a section taken about 500 μ distal to 2b), but a distance of about 1 mm separates the divergence of the petals (Fig. 2d) from the divergence of the lateral sepals. Apparently, the lower petals of _L. longiflora_ always diverge at a slightly more basal level than the upper petals. Upper petals, upper and lower sepal, style, stamen, and staminode separate within a 200–300 μ segment (Fig. 2e, f). In some flowers the union of lower sepal and staminode (Fig. 2e) extends further than the union of stamen and upper sepal; in other flowers, the reverse is true. The nectaries terminate slightly beyond the level at which the last of these appendages become free.

Baeahi and Bonner figured several discrete vascular bundles in the stamen and the staminode of _L. longiflora_ ("L. insignis"). Our sections show a more or less solid mass of vascular tissue in both.

_Lopezia lopezioiides_—No other _lopezia_ has two fertile stamens. As in _L. longiflora_, the nectaries are massive, but here they occupy a position more to the upper side of the flower (Fig. 3a), and they protrude as lobes for much of their length. The lower sepal diverges a little beyond the floral constriction (Fig. 3b, c). At the same level, the style becomes free in a depression formed by the united bases of the remaining appendages. Within another...
Fig. 2-5. Cross sections beginning a little beyond the floral constriction (a) and proceeding distally to show order in which floral parts diverge. 2. Lopezia longiflora. To identify floral parts, first examine f: style (arrow) is below stamen and above staminode; these are enclosed by four petals, then four sepals. Stippling indicates nectaries, pollen-transmitting tissue; solid or nearly solid markings indicate vascular tissue. ×7. 3. L. lopezioides, Breedlove 8052. ×7. 4. L. semianandra. Sequence passes through at least 2/3 of epigynous portion of flower. Free parts in i are four sepals, four petals, gynostemium; gynostemium separates into components in j, k. Further explained in text. ×7. 5. L. riesenbachia. Sequence passes through ca. 1/2 of epigynous portion of flower. Note similarity to Fig. 4. ×14.
100–200 μm the lower stamen diverges (Fig. 3d), and the lower petals separate at a somewhat more distal level (Fig. 3e). Scanning sections for another 200 μm or so, one observes the separation of the upper stamen from a unit comprising three sepals and the two upper petals (Fig. 3f). Slightly beyond this, the nectaries terminate. The remaining sepals and petals separate about 500 μm further on, more or less in one plane (Fig. 3g).

**Lopezia semeiandra**—This species and the succeeding one are the only lopezias in which the basally united appendages form a floral tube above the inferior ovary. Sections followed distally from the floral constriction show that the septum into two deep pockets lined with nectariferous tissue (Fig. 4a–c). Slightly beyond the level at which this tissue disappears, the staminal side of the septum separates from the floral tube (Fig. 4d, e). The distal continuation of the septum, incorporating the vascular bundles of stamen and staminode plus four discrete stylar bundles, is united to the lower side of the floral tube up to the level at which sepals and petals separate. This separation occurs about a third of the way from the floral constriction to the distal end of the flower, in the order shown in Fig. 4f–i. Style, stamen, and staminode remain united as a column or gynostemium for some distance. Components of the gynostemium separate about two-thirds of the way from the base of the perianth to its distal end, the stamen diverging a few mm in advance of the staminode (Fig. 4j, k).

**Lopezia riesenbachia**—Flowers of *L. riesenbachia* are smaller than those of *L. semeiandra* and they differ in shape (Fig. 1), but serial sections show structural similarities. As in *L. semeiandra*, the base of the floral tube is divided into two deep pockets lined with nectariferous tissue (Fig. 4a–c). Slightly beyond the level at which this tissue disappears, the staminal side of the septum separates from the floral tube (Fig. 4d, e). The distal continuation of the septum, incorporating the vascular bundles of stamen and staminode plus four discrete stylar bundles, is united to the lower side of the floral tube up to the level at which sepals and petals separate. This separation occurs about a third of the way from the flower, in the order shown in Fig. 4f–i. Style, stamen, and staminode remain united as a column or gynostemium for some distance. Components of the gynostemium separate about two-thirds of the way from the base of the perianth to its distal end, the stamen diverging a few mm in advance of the staminode (Fig. 4j, k).

**Lopezia grandiflora** and **L. langmaniae**—The two are enough alike that selected cross sections from *L. langmaniae* (Fig. 6a–f) will serve to illustrate the position of nectaries and the order of divergence in both. As in *L. lopezioides*, the free base of the style is surrounded by the united bases of other floral parts (Fig. 6d), but the divergence of the lower sepal is closer to the divergence of other appendages than is the case in *L. lopezioides*. In *L. langmaniae* and *L. grandiflora*, moreover, the two members of the androecium are basally united up to the level at which the lower petals diverge (Fig. 6e). Still another difference is that the nectaries of *L. grandiflora* and *L. langmaniae* do not appear in cross section as lobes associated with the upper petal bases; instead, they terminate distally in the filament of the stamen (Fig. 6f).

Sectioned herbarium flowers of *L. hintonii* resemble our sectioned flowers of *L. grandiflora* and *L. langmaniae*, with two notable differences: (1) the lower sepal diverges at a relatively more distal level in *L. hintonii*, and (2) the lateral sepals diverge at a relatively more proximal level. Thus, certain sections from *L. hintonii* show free lateral sepals separated by a central unit embodying the bases of the other epigynous parts. Somewhat more distal sections show the divergence of the lower petals. Slightly beyond this divergence, the lower sepal diverges, and a little beyond that the remaining parts diverge, more or less in a single transverse plane. The style emerges from a depression as in *L. grandiflora* and *L. langmaniae*.

**Lopezia paniculata**, **L. miniata**, and similar species—Figure 7a–e shows the order of divergence of floral parts in *L. paniculata*. The figured flower had lost one of its sepals during preparation, so a mirror-image sepal was added to the right side of each sketch for clarity. At the level of the nectaries (Fig. 7b, c), *L. paniculata* is less zygomorphic than *L. grandiflora* or *L. langmaniae*, and the style of *L. paniculata* does not arise from a depression. Levels of divergence are quite close together in this species. When sections are scanned distally, lateral sepals are seen to diverge first, followed by the lower petals, then by the upper petals and the style. Finally, the stamen and the staminode separate from the upper sepal and the lower sepal, respectively.

Sectioned flowers of *L. miniata* look like those of *L. paniculata*. The resemblance is not unexpected, for the two species are very similar in gross morphology and they hybridize freely (Plitmann et al., in press). *Lopezia trichota* differs from *L. paniculata* and *L. miniata* with respect to its underground parts and the form of its petals, but its flowers are not notably different in cross section. There is perhaps a greater degree of zygomorphy in *L. trichota*; that is to say, a greater displacement of the bases of epigynous parts toward the upper side of the flower. Sections through the bases of the lower petals of *L. trichota* show epi-
Fig. 6-10. Cross sections showing position of nectaries, order in which floral parts diverge. To identify floral parts, see text and Fig. 2. 6. *Lopezia langmaniae.* × 8. 7. *L. paniculata.* Upper sepal separates from stamen, lower sepal from staminode a few μ beyond e. × 14. 8. *L. racemosa, Breedlove 9882.* Sections from an expanded flower, showing divergence of style, upper petals, stamen, staminode. Level a is slightly distal to the level at which sepal and lower petals diverge. × 14. 9. *L. gracilis, Breedlove 15535.* Section a, slightly distal to the summit of the ovary, carries continuations of carpel midveins; other bundles (stippled) are poorly developed at this level. Stippling on upper petals in g indicates deeply stained epidermal and subepidermal cells; see Fig. 11 and text. × 14. 10. *L. clavata.* Section f, distal to style, passes through filament (long arrow), anther lobes of fertile stamen; short arrow indicates staminode. Arrows in g indicate sepal. × 14.
dermal papillae, which we have not seen in a comparable position in other species.

Flowers of *L. cornuta* are also similar, but the level at which upper petals diverge is further from the divergence of lower petals than is the case in *L. paniculata* and *L. miniata*. There are additional differences in the number of ovules, those of *L. cornuta* numbering only one or two per locule, and in the upper petals, those of *L. cornuta* having areas of deeply staining papillose epidermis above the tubercles (Fig. 12).

In *L. nuevo-leonis* the bases of epignous floral parts are much like those of *L. cornuta*, but the nectaries are somewhat displaced to the upper side of the flower, whereas the nectaries of *L. cornuta* are positioned as they are in *L. paniculata*. Moreover, the lower sepal and staminode of *L. nuevo-leonis* diverge as separate appendages. In *L. cornuta*, *L. miniata*, *L.paniculata*, and *L. trichota* the lower sepal and staminode diverge as a unit (Fig. 7d), which separates into its two components at a slightly more distal level.

*Lopezia racemosa*—The four sepals and the lower petals diverge at about the same level from a four-sided structure (Fig. 8a). The style becomes free within this structure (Fig. 8b); then the other epignous parts diverge, more or less together (Fig. 8c). Thus, the base of the style is encircled for a short distance by the united bases of upper petals, stamen, and staminode. In this respect, *L. racemosa* is like *L. langmaniae*, but in *L. langmaniae* the base of the upper sepal is also a part of the unit that surrounds the free style.

*Lopezia gracilis*—Petals and sepals diverge together (Fig. 9a–d) from a central unit that incorporates basal portions of stamen, style, and staminode. In some specimens the lower sepal is slightly adnate to the staminodial side of this unit, but the upper petals do not diverge from the unit, as is the case in *L. racemosa*. The style becomes free (Fig. 9c) slightly below the level at which stamen and staminode separate (Fig. 9f). Sections through the tubercles on the upper petals reveal a localized area of densely cytoplasmic cells within each tubercle and in adjacent portions of the blade (Fig. 9g, 11).

*Lopezia clavata and similar species*—Flowers of *L. clavata*, *L. gentryi*, and *L. laciniata* differ from others in the genus in that the constriction separating perianth, style, and androecium from the ovary is a neck, that is, it has a linear dimension (Fig. 15). The neck carries the four principal vascular bundles of the flower as well as the pollen-transmitting tissue. This group of species is further distinguished by extreme zygomorphy. Floral parts—staminode and lower sepal excepted—are greatly displaced to the upper side of the flower.

In some specimens the displacement is even evident in the arrangement of bundles within the neck (Fig. 10a). Lower sepal and staminode diverge as a unit well in advance of the other parts (Fig. 10b–d), and they remain united roughly to the level at which the style and stamen diverge (Fig. 10c). The lower petals diverge substantially beyond this level (Fig. 10f). Upper petals, upper sepal, and lateral sepals separate at a still more distal level (Fig. 10g). The upper sepal carries a prominent tubercle (less prominent in *L. clavata* than in the other species) on its inner surface where this separation occurs.

**Discussion—Interpretation of floral structure**

—Bachni and Bonner (1948) reported multiple vascular bundles in the stamen and staminode of some *Lopezia*ae, and they took this to mean that the oligomericous androecium has evolved through the coalescence of a larger number of stamens, perhaps eight, as in other Onagraceae. We do not know that anyone has accepted this interpretation, nor have we been able to verify the observations on which the interpretation was based. Our transverse sections through the base of the stamen and the base of the staminode show a broad, more or less continuous area of vascular tissue in each, rather than multiple bundles. The difference between a single bundle and multiple bundles may be simply a matter of variation between individual plants, for Bachni and Bonner figured contrasting conditions in *Lopezia miniata* and *L. pumila*, now considered the same species.

The *Lopezia*es provide no clue to the origin of transeptal ovular bundles; that is, we find no indication of transition from an ancestral central system, the kind of ovular supply present in most syncarpous gynoeica with axile placentation (Eyde, 1967; Schmid, 1972a). We have seen central ovular strands, with transeptal strands completely lacking, only in *L. gentryi*, and not in all collections from that species. Since *L. gentryi* is one of the most highly evolved *Lopezia*es, these few instances of central vasculature can hardly be considered a retained ancestral condition. The occurrence of two kinds of ovular supply within one species supports the arguments of Carlquist (1969) and Schmid (1972b) against extreme or uncritical evolutionary interpretation based on the supposed antiquity of floral vascular patterns.

The oligomery of the *Lopezia* androecium and the appearance of the tubercles on upper petals of most insect-pollinated species indicated to Barnes (1944; see also Morren, 1850) that these petals may actually be "composite structures in which petals and stamens are combined." We have found no evidence to support this idea or the earlier idea that the upper petals are actually "two stamens early developed, and partaking, in consequence, of a petaloid character" (Meehan,
Fig. 11-15.—Fig. 11. *Lopezia gracilis*, Breedlove 15535. Cross section of flower, showing deeply staining areas in distal portions of tubercles and adjoining parts of upper petals. × 65. 12. *L. cornuta*. Floral cross section distal to tubercles, showing deeply staining epidermis on upper petals. At this level, stigma (center, with opening), overlying stamen, broad underlying staminode, and upper petals are encircled by each lower petal. Preparation courtesy of S. Carlquist. × 41. 13. *L. longiflora*. Cross section of ovary. Large bundles on septal radii supply ovules via transeptal strands. × 34. 14. *L. gentryi*, Breedlove 16963. Cross section of ovary; ovules supplied by two longitudinal bundles at center. There are no transeptal bundles in this flower. × 86. 15. *L. gentryi*, Breedlove 7231. Longitudinal section of flower, showing central ovular supply, neck between ovary and epigynous parts, prominent tubercle (arrow) on upper sepal. Preparation courtesy of S. Carlquist. × 34.
1867). An explanation for the origin of tuberculate petals more in keeping with modern evolutionary concepts is suggested by the presence of swollen areas on the upper petals of two bird-pollinated species, *L. grandiflora* and *L. langmaniae*. In *L. grandiflora* the dilation may be scarcely visible or it may give each upper petal a slightly lobed appearance near its base; in *L. langmaniae*, the swellings are more conspicuous (see illustrations in Miranda, 1962; Plitmann et al., In press). By clearing and dissecting flower buds, one may observe that the dilated areas, like the much more prominent tubercles of small-flowered lopezias, fit closely above the nectaries and conform in outline to the nectaries prior to anthesis. We believe the close conformity of these structures is due to a developmental peculiarity described and illustrated by Payer (1857). Payer showed that *Lopezia* petals are initiated unusually late in floral development and begin to expand after the stamen and staminode are almost completely formed. We reason that the last appendages formed must expand into the crevices between previously formed structures or into spaces unfilled by other appendages, including the space immediately above each nectary. If the petals then elongate greatly, as in *L. longiflora*, the early conformity to the outline of the nectary is lost. The petals of *L. grandiflora* elongate less than those of *L. longiflora*, and the upper pair consequently retain a visible record of the expansion. In *L. langmaniae* the petals are quite small, and the dilated areas are correspondingly more prominent. We hypothesize that petals of this type, i.e., with localized swellings on their adaxial surfaces, preadapt the flower for the shift from bird pollination to insect pollination. (In a subsequent section we explain why bird pollination must be ancestral in *Lopezia.*) Any evolutionary change that would alter the proportions of floral appendages relative to each other could simultaneously increase the prominence of the dilated areas. And, if the dominant avian pollinators should become unreliable, swellings prominent enough to focus the attention of insect pollinators would be selected for, thus promoting the evolutionary development of geniculate petals with tubercles.

Our collections included an anomalous flower of *Lopezia racemosa* that seems to fit our hypothesis. It had five petals rather than the usual four, and all five resembled the lower petals of normal flowers. We take the absence of tubercles and geniculation to mean that no petal was positioned during development so as to expand tightly and conformably above a nectary.

The foregoing remarks do not apply to the solitary median tubercle of *Lopezia clavata*, *L. gentryi*, and *L. laciniata*. The epipetalous position of this structure and its general appearance indicate a somewhat different origin from that of the epipetalous tubercles in *L. racemosa* and allied species. It is not unlikely, however, that the two kinds of protuberances have evolved under the influence of similar selective factors. Raven's group has observed that insects are frequent on flowers of *L. laciniata*, and the prominent median tubercle may well play a role in attracting them.

An old error in the interpretation of the epipetalous tubercles is worth mentioning because it is perpetuated in the famous Ware Collection of glass flowers in the Botanical Museum of Harvard University. Vaucher, apparently the earliest observer to comment on the function of the tubercles, described them as nectaries in a letter to A. P. de Candolle (published by de Candolle, 1832; see also Vaucher, 1841). Ogle (1869), Müller (1873), and Biedermann (1890) also misidentified the tubercles as nectaries. Biedermann's mistake is puzzling because Hildebrand (1869) and Delpino (1873, p. 273) had already set the matter straight. Model 743 in the Ware Collection, a beautiful sequence demonstrating syrphid pollination of *Lopezia racemosa* ("L. coronata"), is apparently based partly on Biedermann's account: it shows a glass fly about to take glass nectar from a glass tubercle.

The snapping phenomenon—Some of the earliest workers to examine *Lopezia racemosa* observed that the flowers are markedly protandrous, with the stamen and immature style held under tension by the staminode so as to snap apart when touched (Curtis, 1794; Jacquin, 1796). Meehan (1867) observed that flowers of *L. miniata* snap in the same way, and the process is now known to occur in a number of other species. Although nineteenth-century naturalists recognized the role of snapping in insect pollination, skeptics Goebel (1920, p. 321) and Troll (1922) undertook to disprove the adaptive value of the mechanism. Troll's arguments contain some misinformation (he claimed, on the basis of an erroneous literature report, that flowers of *L. miniata* do not snap), but he was the first to illustrate the gradual rotation of the developing filament of *L. racemosa* before anthesis. When the anther springs free from the staminode, it is twisted 180° into the extrorse position.

The arguments of Goebel and Troll against the selective value of snapping are now largely obsolete. Observations on *Lopezia* under natural conditions and in cultivation (Breedlove et al., in preparation) demonstrate that syrphid flies are the effective pollinators of certain species and that the behavioral responses of these agents are related to floral structure. Syrphidae are poor pollinators of flowers with exposed pollen because they can move from one such flower to another without carrying much pollen (Robertson, 1924a, b). Fly-pollinated lopezias have overcome this
difficulty by evolving a mechanism for flinging pollen against the underside of the fly’s body.

It is now known that the fertile stamen twists in all lopezias, including the bird-pollinated species (see illustrations in Plitmann et al., In press). Raven has pointed out to us that bird-pollinated lopezias grow near bird-pollinated species of other genera and that precise positioning of the anther is important because different kinds of pollen are often carried in different places on the same bird. More-

Fig. 16. Evolution of Lopezieae, certain species omitted. Gametic chromosome numbers in parentheses. In addition to characters indicated in diagram, most branches reflect differences in the union of floral parts. See text for details.
The diagram incorporates chromosome numbers. Plitmann et al. (In press). In general, directions of chromosome numbers are synonymous for the resemblance of these preparations to some other plant group for which this change is postulated.

Scent areas in the upper petals?—One would judge from the literature on Lopezia pollination that flies are attracted and oriented by visual cues alone, that is, by floral symmetry and by the color and shiny surfaces of the tubercles. The occurrence of densely staining areas in upper petals of L. cornuta and L. gracilis (Fig. 9g, 11, 12) suggests that a volatile chemical attractant may supplement these visual cues, at least in some Lopezias. The stained material is cytoplasmic, rather than vacuolar; the areas are not associated with markings visible to the human eye; and Raven informs us that they look no different from the rest of the petal in photographs taken with ultraviolet light. Our suggestion that the areas emit a scent is offered cautiously, because we have obtained the staining reaction from only two species, one of which (L. gracilis) is almost exclusively self-pollinated. If emission areas do play a role in attracting insects to Lopezia flowers, one would expect to find them in some of the other species. Vogel (1962) has shown, however, that the microscopic appearance of a scent area changes before and after the emission of the volatile substance: this could explain why we have seen the dark areas in only a few of our stained preparations. At any rate, we would be remiss if we did not point out the resemblance of these preparations to some of the stained preparations in Vogel’s photographs (Abb. 37, 42). Furthermore, a dual system of attractants would not be unusual. Experiments show that flowers attractive to honeybees commonly have one or more scent areas in addition to optical stimuli and that the boundaries of these areas are not always identical to the boundaries of the optically attractive areas (Lex, 1954). Other experiments show that Ophrys orchids elicit a sexual response from insect visitors by means of a chemical emission in combination with tactile stimuli and an insect-like appearance (Kullenberg, 1961).

Evolutionary relationships within Lopezia—Figure 16 summarizes our views concerning the origin and relationships of most Lopezia species. In addition to our observations on floral structure, the diagram incorporates chromosome numbers and other indications of evolutionary status from Plittmann et al. (In press). In general, directions of evolutionary change are diagrammed in accordance with well-known trends among angiosperms: zygomorphy from actinomorphy, one-staminate flowers from two-staminate flowers, floral tubes from free appendages, one-ovulate locules from pluriovulate locules, herbaceous annuals from woody perennials.

The one evolutionary change that may appear unorthodox is the shift from bird pollination to insect pollination. The opposite change is believed to be more common (Grant and Grant, 1968, 1970): indeed, there is good evidence that bird-pollinated species have originated from insect-pollinated species elsewhere in the Onagraceae (Lewis and Raven, 1961). We are confident that bird pollination is ancestral in Lopezia, however, because the most nearly actinomorphic species (L. longiflora) is bird pollinated and because only bird-pollinated species have 11 gametic chromosomes, the basic number for the tribe and for the family (Carlquist and Raven, 1966). The direct shift from hummingbird pollination to syrphid pollination may be unique. In scanning the literature on pollination systems, we have found no other plant group for which this change is postulated.

The diagram treats four well-developed stylar bundles as ancestral because the typical angiosperm style (including that of most Onagraceae) carries a distal continuation of each carpel mid-vein. Our failure to observe discrete stylar bundles in most Lopezias is somewhat perplexing since Baehni and Bonner (1948) figured four well-marked bundles for every species that they studied. It is possible that developmental differences are partly to blame for the discrepancy between their observations on flowers cleared after anthesis and our observations, most of which are recorded from sectioned flower buds. Developmental differences cannot explain the discrepancy completely, however, because we also sectioned and cleared a number of flowers with mature styles. Whether or not vasculature changes appreciably as the style matures, we believe it is systematically significant that some species have four discrete stylar bundles in the bud and others do not. Incidentally, Carlquist’s (1969, p. 338) assertion that vasculature should increase with evolutionary increase in floral size does not apply here. Lopezia riesenbachia, a species with well-defined stylar bundles in the bud, has much smaller flower buds and a much shorter style than one finds in L. longiflora, a species with poorly defined stylar bundles.

Sprague and Riley (1924) grouped the species of Lopezia according to the number of tubercles on the upper petals (Unituberculatae vs. Bituberculatae). Our diagram does not make this distinction because we consider the tubercles—also the auricles that sometimes accompany the tubercles—too susceptible to evolutionary change to have much taxonomic significance. For example,
we have observed that L. trichota, which commonly has a single tube at each upper petal like L. racemosa, more closely resembles L. miniatu and L. paniculata in the way its floral parts are united. Among the other species that seem to have only a limited value for identifying evolutionary trends and systematic relationships among Lopezia species are ovule number, trichome type, and pollen color. For instance, L. lopezioides consistently has only one ovule per locule (at maturity, a distinctive winged seed), but other species with few ovules, such as L. gracilis and L. nuevo-locleoni, are unlike L. lopezioides and not very similar to each other. The capitate trichomes of L. clavata and L. lacinata appear to have a separate origin from the similar trichomes of L. semeiandra and L. riesenbachia, and an independent origin for the capitate trichomes of L. trichota also seems likely. Pollen is bluish in most lopezias, including L. lacinata, but L. clavata, with internal floral structure almost identical to that of L. lacinata, has yellow pollen. Lopezia riesenbachia and L. semeiandra, the only other lopezias with yellow pollen, share important floral peculiarities not found in L. clavata.

Some of the shared features of L. riesenbachia and L. semeiandra—for instance, the basally separated floral tube with the distal continuation of the septum adnate to the lower side of the flower (Fig. 4, 5)—are not found elsewhere in the tribe. In addition, these two species share the same chromosome number and the discrete stylar bundles previously discussed. Accordingly, we view L. riesenbachia and L. semeiandra as the only members of an early diverging evolutionary line. By virtue of its floral tube, nectar pockets, size, and general appearance, the flower of L. semeiandra can be considered the most highly specialized of all Lopezia flowers for hummingbird pollination. The structural similarity to the small self-pollinated flowers of L. riesenbachia (cf. Fig. 1b, 1f) is therefore rather startling. The difference in floral size is related to a difference in habitat. Lopezia semeiandra, like most other lopezias, grows in oak-pine forests at middle elevations; L. riesenbachia occurs in xeric situations at low elevations. We infer that the latter evolved from marginal populations among the common ancestors of L. riesenbachia and L. semeiandra when severe environmental conditions made outcrossing disadvantageous or impossible. Field observations and experimental work with other groups, including the onagraceous genus Clarkia (Moore and Lewis, 1965), indicate that the shift from outcrossing to selfing is often accompanied by an evolutionary decrease in floral dimensions, but we know of no other group in which the resultant size difference rivals that of L. riesenbachia and L. semeiandra.

Our linking of Lopezia grandiflora with L. langmaniae contradicts the late Faustino Miranda’s (1962) claim that the two should be in separate genera. We are unimpressed by Miranda’s list of distinguishing characters. At least one of the supposed distinctions—stamen and staminode basally united around the free-standing base of the style—describes L. langmaniae as well as L. grandiflora. The floral parts of these two species are adnate in a manner not duplicated elsewhere in the tribe, and they share the same chromosome number; therefore we infer that they had a close common origin.

The diagram shows Lopezia lopezioides as an early evolutionary offshoot, not closely related to other species with markedly zygomorphic flowers. Two considerations make the isolated position of L. lopezioides necessary: (1) it is the only species with two fertile stamens and therefore not likely to have evolved from ancestors with one fertile stamen, and (2) to add additional species to the same evolutionary line with L. lopezioides would require at least one more arrow marked “Lower stamen infertile”—a needless hypothesis. The branch leading to L. riesenbachia and L. semeiandra is also seen as an early offshoot because we cannot imagine the kind of adnation one finds in these species originating from ancestors in which the style, stamen, and staminode are adnate to the upper side of the flower.

All other taxa appear to be derived from extinct ancestors that were more akin to Lopezia longiflora than to any other extant species. No doubt the ancestors had shorter flowers than L. longiflora, and they must have had 11 gametic chromosomes, unlike L. longiflora, which is a tetraploid.

The extinct precursor of L. longiflora apparently gave rise to three evolutionary lines in addition to L. longiflora itself. The ancestral relationship with birds was retained in the line leading to L. grandiflora and L. langmaniae, while the flower became zygomorphic. Increased zygomorphy—that is, a greater degree of basal displacement of floral parts—probably provides additional space for the accumulation of nectar, thereby tightening the bond between flower and pollinator. If, as we would guess from very limited evidence, L. hintonii belongs on the same evolutionary line with L. grandiflora, it would have to be placed closer to the extinct precursor than either of these species because our sectioned herbarium flowers show less basal adnation of floral parts in L. hintonii. Alternatively, L. hintonii might be placed where the branch leading to L. grandiflora and L. langmaniae diverges from the branch leading to L. paniculata and L. miniatu, for its flowers have characters in common with both pairs of species.

The line leading to Lopezia paniculata, L. miniatu, and their derivatives (with a side branch leading to L. racemosa and L. gracilis) embraces the majority of insect-pollinated lopezias. We
have drawn this part of the diagram in such a way as to make the snapping adaptation a single evolutionary event. Flowers of L. paniculata and L. miniata are less zygomorphic than the very similar flowers of L. cornuta, L. nuevo-leonis, and L. trichota. With this in mind, and mindful also of the chromosome numbers, we see L. paniculata and L. miniata as forms ancestral to the other three. The staminode and lower sepal are not basically united in L. nuevo-leonis, a self-pollinating species, as they are in L. paniculata and L. miniata. For this reason, L. nuovo-leonis might have been placed on a side branch diverging from below L. paniculata and L. miniata, but the difference seemed too slight to merit further complication of the diagram. Of the trio L. cornuta, L. nuovo-leonis, and L. trichota, no species appears to be derived from another. Lopezia trichota stands apart because of its capitate trichomes. The floral parts of L. cornuta are not displaced to the upper side of the flower to the degree observed in L. nuevo-leonis, and L. cornuta has the higher chromosome number; but L. nuovo-leonis is autogamous and has the higher ovule number, so neither species is the likely progenitor of the other. Lopezia suffrutescens might have been placed next to L. nuevo-leonis, but suitable anatomical material reached us after Fig. 16 had been prepared for publication. Flowers of L. suffrutescens are similar to those of L. nuevo-leonis, and the derived chromosome number of L. suffrutescens (n = 9, fide W. Tai) is not out of keeping with this similarity. A separate side branch is necessary for L. racemosa because of its capitate trichomes. The floral parts of L. cornuta are not displaced to the upper side of the flower to the degree observed in L. nuevo-leonis, and L. cornuta has the higher chromosome number; but L. nuevo-leonis is autogamous and has the higher ovule number, so neither species is the likely progenitor of the other. Lopezia suffrutescens might have been placed next to L. nuevo-leonis, but suitable anatomical material reached us after Fig. 16 had been prepared for publication. Flowers of L. suffrutescens are similar to those of L. nuevo-leonis, and the derived chromosome number of L. suffrutescens (n = 9, fide W. Tai) is not out of keeping with this similarity. A separate side branch is necessary for L. racemosa because of its capitate trichomes.

After some reflection, we decided to derive Lopezia gracilis from L. racemosa, even though this derivation runs counter to the general trend toward increasing zygomorphy. Lopezia gracilis is autogamous, but the totality of characters place it among the fly-pollinated loppezias (Raven's collaborators have seen a few syrphids on the flowers), and there are more similarities to L. racemosa than to any other species. We might have avoided the implication of evolutionary reversal by postulating a close common ancestry for the two species rather than a direct derivation of L. gracilis from L. racemosa. We have not done so because we doubt that our few sectioned flowers of L. racemosa show the complete range of variation in floral structure: as presently delimited (Piltmann et al., in press), L. racemosa is a highly polymorphic species, and some of its variants may have floral parts as free as those of L. gracilis.

The remaining branch of the phylogenetic tree leads to L. clavata and L. laciniiata; L. gentryi, an autogamous derivative of L. laciniiata, is omitted from the diagram. Flowers in these species are specialized for fly pollination, but differ structurally from those of other fly-pollinated loppezias (see OBSERVATIONS). Lopezia clavata has shifted to self pollination (Piltmann et al., In press), but its flowers retain most of the structural features associated with fly pollination. Brandegee (1889, p. 158) conjectured quite wrongly that the epipetalous tubercle of L. clavata, flanked by slight but epipetalous protuberances (the latter apparently homologous with the tubercles of snapping species), constitutes a semicircular disk "to be regarded as a modification of the disk which in many of the Onagraceae lines the calyx-tube."

Some of our own inferences are more conjectural than others, and we expect future work on Lopezia to show our direct derivation of one taxon from another to be, at best, oversimplified. We take comfort in the conviction that careful investigators can improve on the systematic conclusions of their predecessors. After all, our predecessors (Baehni and Bonner, 1948) concluded that the Lopeziaeae are a heterogeneous group, with similarities attributable to convergent evolution.
is primitive? Influenced by the “Age and Area” concept and by a desire to link Onagraceae with Trapa, Broekens assumed Ludwigia (“Justeaeae”) to be the most primitive onagraceous genus. Takhtajan (1959, 1966) takes a similar view for somewhat different reasons. Despite the antiquity of Ludwigia (see subsequent discussion), an effort to make it the most primitive genus of Onagraceae runs into difficulty. The aquatic habit, eight gametic chromosomes, and deeply intrusive placentas of Ludwigia species are derived features. Fuchsia, with (basically) 11 gametic chromosomes, fleshy fruits, and unspecialized placenta- tion, appears to be the modern genus closest to the ancestors of all Onagraceae; and a floral tube is present in all Fuchsia species, as in most other Onagraceae. Examining families presumed to have a common ancestry with Onagraceae—Lythraceae, Melastomataceae, Myrtaceae—we find a floral tube in all but a few taxa, and the exceptions are remote from the Onagraceae. It can scarcely be doubted, then, that ancestral Onagraceae also had a floral tube.

The linking of Lopezia with Ludwigia presents some problems. No Lopezia species has deeply intrusive placentas, and no Ludwigia species has other than eight gametic chromosomes or a multiple thereof. Moreover, the interstaminal nectaries are not identically placed in the two genera: in Ludwigia, the nectaries extend upward along the summit of the ovary; in Lopezia, the nectaries extend upward along the stamen. Nevertheless, the evolutionary shift from one of these positions to the other—or from a common ancestral position to both—can be envisioned more easily than the evolution of a Lopezia nectary from, say, a Circaea nectary or a Fuchsia nectary. We cannot yet account for the cytological and palynological similarities or the similarities in habitat that seem to unite Ludwigia with Epilobium (Carlquist and Raven, 1966, p. 389). If we are right in linking Lopezia with Ludwigia, future work on floral structure may reveal how these two genera connect with Epilobium. It should be borne in mind, however, that similarities between Epilobium and Ludwigia could have evolved independently. Fossils show that the family is old enough for considerable parallelism and convergence.

The fossil record may in time contribute much to our understanding of relationships among the Onagraceae, but published records are presently of limited application. Among the less informative remains are badly eroded (redeposited?) Fuchsia-like grains from Antarctica (Cranwell, 1959) and the London Clay fruit Palaeeeucharidium, which Chandler (1961) retains in Onagraceae only because “no more likely relationship can be suggested at present.” On the other hand, the fossil fruit record of Circaea (Szafer, 1947; Nikitin, 1957; Dorofeev, 1963, 1969) is convincing and serves to show that Circaea existed as early as the Oligocene Epoch. All other pre-Pleistocene records known to us are pollen records, difficult to interpret because reporting authors differ as to whether the older grains can be placed with confidence in modern genera. By citing selected literature, one may start the Ludwigia record with Eocene occurrences in various parts of the world: Colombia (González Guzmán, 1967), British Columbia (Rouse, 1962), Soviet Far East (Bratskev, 1969). Boisdwuala is reported from the Oligocene of British Columbia (Piel, 1971), Fuchsia from the Awamooan of New Zealand (Couper, 1960), now considered mid-Miocene (Jenkins, 1971). Xylonagra has been identified in the Oregon Miocene (Wolfe, 1962) and in the Oligocene Florissant flora (Wolfe, personal communication). Mulier's (1970) "Range chart of identified pollen types" starts the record of Epilobium-type pollen in the Lower Eocene and refers the user to Krutzsch (1968) for details. Consulting Muller's source, one finds Krutzsch reluctant to assign Paleogene pollen to modern onagraceous genera ("Es ist in der Regel nicht ohne weiteres möglich, die dispersen Fossilien auf jeweils eine bestimmte Gattung zu beziehen"). Corsinipollentes ludwigioides, the oldest species he is willing to link with a single modern genus ("Als botanischer Vergleich dürfte in erster Linie die Gattung Ludwigia in Frage kommen"), begins at the Oligo-Miocene boundary. Krutzsch is inclined to accept even the earliest (Lower Paleocene) Corsinipollenites as onagraceous, however, and his summarizing table shows gradually increasing diversity from the Eocene upward. Some of these ancient Onagraceae shed their pollen in tetrads, like most modern Ludwigias. Corsinipollenites oculusnoctis parvus, which can occur in tetrads (Krutzsch, 1970), extends from the Lower Eocene into the Pleistocene; and it includes forms transitional to C. ludwigioides and to C. graciliporus, another Ludwigia-like fossil. Unfortunately, the tetrad character alone is not sufficient to link a fossil form with modern Ludwigia, for the pollen of most Epilobium species is shed in similar tetrads. It is now possible, however, to distinguish Epilobium pollen from Ludwigia pollen through a combination of light microscopy and electron microscopy (J. Skvarla, in preparation). The same combination of methods, when applied to fossil pollen, should aid in reconstructing the ancestry of Ludwigia, and this in turn may clarify the affinities of Lopezia.

The earliest Onagraceae presumably were insect pollinated, for hummingbirds are thought to have evolved after the Eocene Epoch. Among the Lopezieae, however, and probably among extant Onagraceae as a whole, bird pollination is primitive. To resolve this apparent contradiction, it may become necessary to postulate an extinct group of insect-pollinated Onagraceae, older than
all bird-pollinated Onagraceae. For the present, postulating such a group would be premature, as no one has yet studied floral structure and evolution in the key genus Fuchsia.

LITERATURE CITED


Curtis's Bot. Mag. 7, no. 254. [Plate plus 4 pages of text not numbered]


GONZÁLEZ GUTZMÁN, A. E. 1967. A palynological study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene; Tibú area, Colombia). E. J. Brill, Leiden.


OGLE, W. 1869. The fertilisation of salvia and of some...


Rouse, G. E. 1962. Plant microfossils from the Bur-