

Historical development of ornithophily in the western North American flora

(hummingbird pollination system/evolution of mutualism/Arcto-Tertiary floristic elements/Madro-Tertiary floristic elements)

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ABSTRACT The 129 ornithophilous plant species in western North America have floristic affinities with one or the other of four geofloras: the Arcto-Tertiary flora (101 species), Madro-Tertiary flora (19 species), Madro-Tethyan flora (8 species), and Neotropical flora (1 species). The last three floras have been in continuous contact with hummingbirds since some time early in the Tertiary, and ornithophily is old in this subset of western ornithophilous plants. The Arcto-Tertiary flora had no contact with hummingbirds in Eurasia or in its early history in North America. Ornithophily is a new condition in Arcto-Tertiary plant groups, dating from the first significant contact of these plants with hummingbirds in the Eocene. Buildup of the hummingbird pollination system in the Arcto-Tertiary flora is expected to be gradual and stepwise for several reasons. Ornithophilous plant groups with Arcto-Tertiary affinities in the modern western flora form a graded series with respect to taxonomic rank, taxonomic size, and ecological diversity. The series consists of one large genus (*Castilleja*), three small genera (*Zauschneria*, etc.), species groups in several genera (*Penstemon*, *Aquilegia*, etc.), single ornithophilous species in otherwise nonornithophilous genera (seven genera—e.g., *Pedicularis*, *Monardella*), and ornithophilous races in otherwise nonornithophilous species (known in two species). It is suggested that the gradations in size of the groups approximately reflect stages in their development, with the largest ornithophilous genus being oldest, with single ornithophilous species being relatively recent, and with ornithophilous races being most recent. The observed distribution of numbers of ornithophilous species among genera is in agreement with the expectation of a gradual and stepwise development of ornithophily.

Hummingbirds and hummingbird flowers form a flourishing mutualistic association in western North America. This association is composed of about 129 plant species, with flowers adapted for foraging and pollination by hummingbirds, and 11 species of hummingbirds (1–3). The mutualistic dependence of the birds and plants is not absolute. Individual birds can and do sustain themselves for a time on bee flowers, insects, and stored food reserves, and some ornithophilous plants can accomplish pollination and seed set with the aid of bees or other insects or by selfing. Nevertheless, the mutual dependence is strong, as indicated by the fact that breeding and nesting hummingbirds generally occur near populations of ornithophilous plants, while plant taxa with ornithophilous floral characters are absent in regions such as the Great Plains of Nebraska, Wyoming, and Montana, which are outside the distribution range of hummingbirds.

How does a mutualistic association such as that involving western North American hummingbirds and ornithophilous plants develop? This question can be approached from several standpoints. The approach adopted here is a historical one.

MATERIALS AND METHODS

Western North America is defined for this study as the area from the Rocky Mountains to the Pacific coast, and from the Mexican border to southwestern Canada and southern Alaska.

The ornithophilous plant species in this area are listed in Table 1. The list includes 129 species in 39 genera and 18 families. Hummingbird pollination records are available for 43 of the species; the other species have inflorescence and floral characters similar to those in the 43 documented species (1, 2). Some ornithophilous species may exist in nature but be undetected and omitted from the list; if so, their number would be small, and the listed species provide a good sample for the purpose of this study.

Taxonomic disagreement exists concerning the rank of four small genera in Table 1. Some taxonomists treat *Diplacus*, *Keckiella*, and *Zauschneria* as subgenera of other larger genera (*Mimulus*, *Penstemon*, and *Epilobium*, respectively), while other students, myself included, see them as good minor genera. *Diplacus*, *Keckiella*, and *Zauschneria* all differ significantly from their related genera in floral and vegetative characters and, in one case, in basic chromosome number; they represent distinct branch lines; and they have all moved into a new adaptive zone, hummingbird pollination. The fourth small genus, *Galvezia*, is construed broadly here to include the related *Gambelia*.

A genus problem exists also in *Castilleja*. *Castilleja* is close to *Orthocarpus* and the character differences separating the two groups break down in some species. Pennell (7) recognized the problem but maintained the two taxa as separate genera. Chuang and Heckard (8) have recently reorganized *Orthocarpus* and transferred a block of *Orthocarpus* species to *Castilleja*. I follow the genus concept of Pennell for *Castilleja*; consequently, this taxon as discussed in this paper is equivalent to *Castilleja* subgenus *Castilleja* of Chuang and Heckard (8).

The option of basing a history of ornithophily directly on fossil evidence is not available because of the lack of an adequate fossil record of both hummingbirds and ornithophilous plants. No fossil records of hummingbirds are listed for North America in standard compendia (9, 10). Most ornithophilous plants in western North America are herbaceous and would be poorly preserved. However, the history of western North American floras is well known and is based on the fossil records of the dominant woody species. Furthermore, we know the floristic affinities of western North American ornithophilous plants. One approach to the problem used here is to infer the history of western ornithophilous plants from the known history of their plant communities.

A second approach is to use the taxonomic rank of natural groups of ornithophilous plant groups as an indicator of their relative ages. Supplementary criteria are the relative taxonomic size and ecological diversity of the groups. These criteria have to be used with discrimination and controls. A relict species can be older than a larger indigenous species group. This source of error is avoided by restricting the rank

Table 1. Native ornithophilous species in the western North American flora

Family, genus, and species	Family, genus, and species
Nyctaginaceae	Scrophulariaceae
<i>Allionia coccinea</i>	<i>Castilleja: affinis, angustifolia, applegatei, austromontana, brevilobata, breweri, chromosa, covilleana, crista-galli, cruenta, culbertsonii, elmeri, exilis, foliolosa, franciscana, fraterna, haydeni, hispida, hololeuca, inconstans, integra, lanata, latifolia, laxa, lemmonii, leschkeana, linariaefolia, martinii, miniata, minor, nana, neglecta, organorum, parviflora, patriotica, payneae, peirsonii, plagiotoma, pruinosa, rhexifolia, roseana, rupicola, stenantha, suksdorfii, subinclusa, uliginosa, wightii, wooteni</i>
Caryophyllaceae	<i>Diplacus: aurantiacus, longiflorus, parviflorus, puniceus</i>
<i>Silene: californica, laciniata</i>	<i>Galvezia speciosa</i>
Ranunculaceae	<i>Keckiella: cordifolia, corymbosa, ternata</i>
<i>Aquilegia: desertorum, elegantula, eximia, flavescens, formosa, shockleyi, triternata</i>	<i>Mimulus: cardinalis, eastwoodiae</i>
<i>Delphinium: cardinale, nudicaule</i>	<i>Pedicularis densiflora</i>
Saxifragaceae	<i>Penstemon: barbatus, bridgesii, cardinalis, centranthifolius, clevelandii, crassulus, eatonii, labrosus, lanceolatus, newberryi, parryi, pinifolius, rupicola, subulatus, utahensis</i>
<i>Ribes speciosum</i>	<i>Scrophularia coccinea</i>
Leguminosae: Papilionoideae	Acanthaceae
<i>Astragalus coccineus</i>	<i>Anisacanthus thurberi</i>
<i>Erythrina flabelliformis</i>	<i>Beloperone californica</i>
Cactaceae	<i>Jacobinia ovata</i>
<i>Echinocereus triglochidiatus</i>	Rubiaceae
Fouquieriaceae	<i>Bouvardia glaberrima</i>
<i>Fouquieria splendens</i>	Caprifoliaceae
Convolvulaceae	<i>Lonicera: arizonica, ciliosa</i>
<i>Ipomoea coccinea</i> (including <i>I. hederifolia</i>)	Campanulaceae
Polemoniaceae	<i>Lobelia: cardinalis, laxiflora</i>
<i>Collomia rawsoniana</i>	Onagraceae
<i>Gilia subnuda</i>	<i>Zauschneria: californica, cana, garrettii, septentrionalis</i>
<i>Ipomopsis: aggregata, arizonica, sancti-spiritus, tenuifolia</i>	Liliaceae
<i>Polemonium: pauciflorum, brandegei</i>	<i>Fritillaria recurva</i>
Boraginaceae	<i>Lilium: maritimum, parvum</i>
<i>Macromeria viridiflora</i>	<i>Brodiaea: ida-maia, venusta</i>
Labiatae	
<i>Monarda fistulosa</i>	
<i>Monardella macrantha</i>	
<i>Satureja mimuloides</i>	
<i>Salvia: henryi, lemmoni, spathacea</i>	
<i>Stachys: chamissonis, ciliata, coccinea</i>	
<i>Trichostema lanatum</i>	

Data are based on refs. 1, 2, and 4–6.

and size comparisons to nonrelictual ornithophilous groups belonging to the same historic flora.

For reconstructing phylogenetic relationships, I use the traditional method in which one draws inferences from comparative morphology, biogeography, and ecology. I use this method in preference to the currently popular method of cladistics for well considered reasons.

FLORISTIC BACKGROUND

The higher plants of western North America, including the native ornithophilous species, are derived from several Tertiary geofloras, two of which—the Arcto-Tertiary and Madro-Tertiary floras—are especially important. The Arcto-Tertiary forest flora occurred in the northern temperate zones of Eurasia and North America, and the Madro-Tertiary flora occurred in a warmer and drier zone in the southwest and Mexico. In the Eocene, the two floras met and interdigitated in hilly or mountainous terrain in interior regions of the southwest. The Madro-Tertiary flora expanded its range to the north and west after the Eocene in response to climatic changes and by Miocene time was in Nevada and California. This extended the zone of contact between the two floras (11–13).

A shift in vegetation type occurred in Nevada in the mid-Miocene as the amount of summer rainfall decreased. The older Arcto-Tertiary flora declined in abundance, while Madro-Tertiary elements expanded. This shift came rapidly ≈15 million years ago in fossil sites in northwestern Nevada (14, 15).

Contacts between the Arcto-Tertiary and Madro-Tertiary floras resulted in numerous exchanges of floristic elements. Nevertheless, Arcto-Tertiary elements predominate today in the central and northern parts of western North America and decline in abundance to the south, while Madro-Tertiary elements predominate today in the arid southwest, and drop out progressively to the north.

In the mid-Pliocene each geoflora segregated into various modern subdivisions in response to further climatic and tectonic changes (11, 16, 17). Climatic and tectonic changes during the Tertiary and Quaternary also opened up new habitats, which were occupied by new indigenous plant groups (13).

A third Tertiary flora, the Madrean-Tethyan flora, also of at least Eocene age, occurred in a warm subhumid belt across southern North America, the Mediterranean region, and the Black Sea and Caspian Sea areas (13, 18). The Madrean or North American province of this flora occupied much of the same territory as the Madro-Tertiary flora (18). Some elements in the modern western flora can be traced directly to a fourth historic flora, the old Neotropical flora.

RESULTS AND DISCUSSION

Floristic Relationships of the Ornithophilous Plants. The genera listed in Table 1 can be assigned to one or the other of the above-mentioned floras. However, it is necessary to recognize different degrees of floristic affinity.

Some Arcto-Tertiary floristic elements retain a close association with modern subdivisions of the Arcto-Tertiary flora (e.g., *Aquilegia*). Other genera have their origin in the

Arcto-Tertiary flora but have radiated into numerous other communities in the modern flora (*Castilleja*). And some genera have their phylogenetic roots in an Arcto-Tertiary genus but have evolved extensively in Madro-Tertiary communities (*Diplacus*). This latter type is classified as a remote Arcto-Tertiary element.

Parallel degrees of floristic affinity are found among Madro-Tertiary elements. Some of these remain in modern Madro-Tertiary communities (*Fouquieria*). Others have invaded Arcto-Tertiary territory (*Ipomopsis*). Still others have crossed over into Arcto-Tertiary communities to such an extent that they should be designated remote Madro-Tertiary elements (*Collomia*).

The following genera in Table 1 are straightforward Arcto-Tertiary elements: *Silene*, *Aquilegia*, *Delphinium*, *Ribes*, *Monarda*, *Monardella*, *Stachys*, *Trichostema*, *Castilleja*, *Mimulus*, *Pedicularis*, *Penstemon*, *Scrophularia*, *Zauschneria*, *Fritillaria*, *Lilium*, *Brodiaea*. *Diplacus* and *Keckiella* are remote Arcto-Tertiary elements.

The following genera are considered straightforward Madro-Tertiary elements: *Allionia*, *Erythrina*, *Echinocereus*, *Fouquieria*, *Gilia*, *Polemonium*, *Ipomopsis*, *Macromeria*, *Anisacanthus*, *Beloperone*, *Jacobinia*, *Bouvardia*, *Lobelia*. *Collomia* is a remote Madro-Tertiary element.

Astragalus, *Satureja*, and *Salvia* belong to the Madrean-Tethyan flora, and *Lonicera* may belong here also (13, 18, 19). *Galvezia* occurs on the Pacific coast and offshore islands of North and South America. Since it is related to *Antirrhinum*, which is a Madrean-Tethyan floristic element, it can perhaps be considered a remote Madrean-Tethyan element.

Ipomoea section *Quamoelit*, which includes our ornithophilous species *I. coccinea*, is primarily a tropical American group. *I. coccinea* is probably best classified as a remote element of the Neotropical flora in the southwestern (and southeastern) United States.

The Tertiary geofloras differ as regards their relationship with hummingbirds. Hummingbirds are basically a tropical American group (3, 20). Madro-Tertiary floristic elements must have been in contact with hummingbirds since sometime in the early Tertiary. Ornithophily is old in this geoflora in general as well as in many of its modern representatives in the southwestern part of the United States. Plants belonging to the Madrean province of the Madrean-Tethyan flora and remote elements of the Neotropical flora have also presumably had a long historic association with hummingbirds. The origin and early development of ornithophily has become obscured by age in these floras.

Hummingbirds were not originally a part of the biota to which the Arcto-Tertiary flora belonged. The Eurasian branch of this flora was completely outside the range of hummingbirds, and the original North American branch in northern and central regions of the continent was probably outside the range of these birds too. The first contact between Arcto-Tertiary plants and hummingbirds most likely occurred in the zone of interdigitation of this flora and the Madro-Tertiary flora in interior southwestern North America in the Eocene. The zone of contact would have spread along with the expansion of the Madro-Tertiary flora to the north and west after the Eocene.

Ornithophily is thus a relatively new feature in the Arcto-Tertiary flora, particularly in the northern and central parts of this flora. This makes it possible to search for stages in the development of ornithophily in the Arcto-Tertiary component of ornithophilous plants. Accordingly, the Arcto-Tertiary contingent of western ornithophilous plants is emphasized in the following analysis.

Frequency Distribution of Ornithophilous Species Among Genera. The number of ornithophilous species per genus was tabulated for the subsample of genera with Arcto-Tertiary floristic relationships (Table 2). One genus has numerous, at

least 48, ornithophilous species, and one has 15 such species, but many genera have only 1 or 2 ornithophilous species each.

This distribution, which plots as a hollow curve, is familiar in ecology. Diverse examples are cited by Williams (21), who interprets it as a result of relative success in evolution. One or a few groups are very successful in a given habitat or adaptive zone, whereas many groups are moderately or only slightly successful.

This concept can be extended to include relative age in the case of western ornithophilous plant groups with Arcto-Tertiary floristic affinities. The one large ornithophilous genus, *Castilleja*, is inferred to be large and successful because it developed ornithophily first, ahead of other plant groups. Other lines of evidence support this inference as discussed below. Genera with a moderate number of ornithophilous species and those with only one or two ornithophilous species are believed to represent younger stages of development of ornithophily.

Castilleja. This genus is a member of the tribe Euphrasiaeae (Scrophulariaceae) along with *Rhinanthus*, *Pedicularis*, *Cordylanthus*, *Orthocarpus*, and other genera. The tribe has a predominantly northern hemisphere distribution (7). *Castilleja* itself is a large genus of ≈200 species occurring almost exclusively in North and South America. Its main center of distribution is in western North America. Pennell (22) lists 71 species in the Pacific states, and Munz (23) lists 33 species in California.

Bee pollination is the basic and widespread condition in the tribe Euphrasiaeae, occurring in *Rhinanthus*, *Pedicularis*, *Cordylanthus*, *Orthocarpus*, etc. Some species of *Castilleja* have bee flowers or butterfly flowers, but most of the species, particularly in western North America, have corollas and floral bracts modified for hummingbird pollination. Ornithophily is clearly derived from a bee-pollination system or mellitophily in *Castilleja*.

Castilleja differs from other western American genera containing ornithophilous species in several significant respects. First, *Castilleja* has at least 48 ornithophilous species in western North America (1) (Table 2) and thus contributes heavily to the total western contingent of ≈129 ornithophilous species. Second, the proportion of the total number of species that are ornithophilous is unusually high in *Castilleja*. For example, 27 of the 33 species of *Castilleja* in California are ornithophilous. In most western genera containing ornithophilous species, ornithophily is a minority condition. Third, ornithophily is broad-based in *Castilleja*, occurring in 13 taxonomic sections.

A fourth feature of ornithophily in *Castilleja* is its ecological amplitude. An analysis of the treatment of *Castilleja* in Munz's *A. California Flora* (23) reveals that one ornithophilous species or another occurs in 24 of the 29 plant commu-

Table 2. Number of genera with a given number of ornithophilous species in western North American genera with Arcto-Tertiary floristic affinities

No. of ornithophilous species per genus	No. of genera	Genera
48	1	<i>Castilleja</i>
15	1	<i>Penstemon</i>
7	1	<i>Aquilegia</i>
4	2	<i>Diplacus</i> , <i>Zauschneria</i>
3	2	<i>Stachys</i> , <i>Keckiella</i>
2	5	<i>Silene</i> , <i>Delphinium</i> , <i>Mimulus</i> , <i>Lilium</i> , <i>Brodiaea</i>
1	7	<i>Ribes</i> , <i>Monarda</i> , <i>Monardella</i> , <i>Trichostema</i> , <i>Pedicularis</i> , <i>Scrophularia</i> , <i>Fritillaria</i>

nities recognized in the state. Some of the habitats occupied by *Castilleja* are old, others (e.g., the alpine zone) are recent.

These features all point to the conclusion that ornithophily had an early origin and continuous development in *Castilleja*. The extensive speciation and radiation of ornithophilous taxa in this genus suggest that ornithophily is older here than in the other western genera with Arcto-Tertiary floristic affinities.

Penstemon. The large, nearctic, predominantly bee-pollinated genus *Penstemon* is the second largest contributor to the western ornithophilous flora with 15 ornithophilous species (Tables 1 and 2). Here, however, the systematic distribution of the ornithophilous species is very different from that in *Castilleja*. The ornithophilous species are scattered in different taxonomic sections of *Penstemon*, where they occur together with bee-pollinated (or wasp-pollinated) species. This indicates that the shift to ornithophily has taken place independently in different phyletic lines in *Penstemon*. The moderate number, low proportion, and scattered systematic distribution of ornithophilous species in *Penstemon* suggest that ornithophily is substantially younger here than in *Castilleja*.

Aquilegia. This genus is closely associated with the Arcto-Tertiary flora. Its center of distribution lies in temperate Eurasia. The center of origin is probably in Eurasia also; the most primitive species, *A. ecalcarata*, occurs in the Himalaya Mountains (24, 25). The Eurasian species are pollinated by bees—usually bumblebees (26).

The North American *Aquilegia* are clearly immigrants from Eurasia. Several species in northern North America retain the ancestral condition of mellitophily, but two groups, the *A. formosa* group in western North America and *A. canadensis* in eastern North America, have changed over to hummingbird pollination (4, 25). These ornithophilous taxa occur in modern subdivisions of the Arcto-Tertiary flora that sorted out in western and eastern North America, respectively, in the mid-Pliocene (11, 16).

The *A. formosa* group consists of seven species ranging from Alaska to the southern California mountains and the southern Rocky Mountains. The montane forest habitat of these plants is semicontinuous in the Pacific Northwest, and here the group has a semicontinuous distribution. In the southwest, by contrast, montane forest has a disjunct distribution, and the *A. formosa* group breaks up into disjunct allopatric semispecies treated as separate taxonomic species. Thus, wide disjunctions separate *A. formosa* var. *truncata* in the Sierra Nevada from *A. shockleyi* in the eastern Mojave desert mountains, and the latter from *A. triternata* in the eastern Arizona mountains (4, 25).

Furthermore, some taxa have crossed over from Arcto-Tertiary plant communities to Madro-Tertiary communities in the southwest. *A. shockleyi* occurs in pinyon-juniper woodland in the Mojave desert mountains.

The forest (and woodland) communities with which the *A. formosa* group is associated today occurred at lower elevations in the past when moister, cooler climates existed and before recent uplift of mountain ranges in the Pliocene–Pleistocene (27). Warming trends set in after the period of cool climates. The disjunctions of the *A. formosa* group in the southwest, and the differentiation into geographically isolated semispecies there, have probably developed since the early period of cool climate and lowland distribution, as the warming trends forced taxa to higher elevations in mountains.

Ornithophily is thus inferred to have been in existence by mid-Pliocene time in *Aquilegia*, while a Pleistocene age is inferred for the development of the disjunct taxa of the *A. formosa* group in the southwest. These estimates of age are consistent with estimates from a different approach. The evolution of ornithophily from the ancestral bee-pollination system, probably by geographical speciation, is one time-

consuming process; range expansion and divergence of the western *A. formosa* and eastern *A. canadensis* are another such process; and the diversification of the *A. formosa* group in the southwest is still another. The estimate of at least a Pliocene–Pleistocene age for ornithophily in *Aquilegia* allows a reasonable amount of time for development of the ornithophilous *Aquilegia* to their present state.

Interspecific differences in DNA sequences are infrequent in *Aquilegia* as compared with the related *Isopyrum* and *Thalictrum* (28). Hodges and Arnold (28) conclude that *Aquilegia* is a product of a relatively recent radiation. This conclusion may or may not be at variance with the one reached here based on historical phytogeography, depending on the definition of recent.

Small Genera. In *Diplacus*, *Keckiella*, and *Zauschneria* there are small but distinctive groups of three or four ornithophilous species. Each genus is an offshoot of a larger, more widespread, predominantly bee-pollinated genus with Arcto-Tertiary floristic affinities. *Diplacus* is an offshoot of *Mimulus*, *Keckiella* is an offshoot of *Penstemon*, and *Zauschneria* is an offshoot of *Epilobium* (1). Each genus has expanded in Madro-Tertiary communities. *Diplacus*, for example, occurs in coastal scrub, chaparral, and live oak woodland. The genera are limited in geographical area as well as taxonomic size. These features suggest that the divergence of the three genera from their ancestral stock is of intermediate age. Ornithophily is inferred to be younger in *Diplacus*, *Keckiella*, and *Zauschneria* than it is in *Castilleja* but older in these groups than in exceptional ornithophilous species belonging to large nonornithophilous genera.

Exceptional Ornithophilous Taxa in Nonornithophilous Genera. Seven genera with Arcto-Tertiary relationships have one ornithophilous species each in western North America, and five Arcto-Tertiary genera have two ornithophilous species each in the western flora (Tables 1 and 2). The genera in question are large or moderate in size. The primary pollination system is bee pollination in most of the genera, or lepidopteran pollination in some (*Silene*, *Lilium*), and ornithophily is an exceptional derived condition (1). The ornithophilous species are indigenous in one region or another of the western flora.

This pattern presents the appearance of opportunism by latecomers to the hummingbird pollination system. The systematically and geographically scattered ornithophilous species are not only indigenous but also probably relatively new. Ornithophily at the single species level of divergence is inferred to be younger than ornithophily in small genera or sections of genera.

Some basically mellitophilous genera with Madro-Tertiary relationships have invaded Arcto-Tertiary floras and given rise to single ornithophilous species in their new areas. Examples are *Collomia rawsoniana* in the Sierra Nevada and *Polemonium brandegei* in the Colorado Rocky Mountains. These are inferred to be young ornithophilous taxa also.

Young Stages. Two cases are known of ornithophilous races in otherwise nonornithophilous species. *Lonicera involucreta* var. *ledebourii* and the San Bernardino mountain race of *Gilia splendens*, both in California, are the examples (1, 6). Ornithophily in these cases is judged to be in a younger stage of development than it is in whole ornithophilous species. Another young stage is represented by plant species with facultative bird and bee flowers, such as *Phacelia minor* (Hydrophyllaceae) and *Sarcodes sanguinea* (Ericaceae) (refs. 1 and 6; unpublished data). The larger groups to which these species belong are predominantly bee-pollinated, and the species in question appear to be in transition from bee pollination to ornithophily.

Buildup of Ornithophily in a Single Locality. The development of ornithophily in western American plant groups with Madro-Tertiary and Madrean-Tethyan floristic affinities is a

continuation of a preexisting hummingbird–plant association. For plant groups in the western flora with Arcto-Tertiary affinities, on the other hand, ornithophily is a new condition, derived usually from bee pollination or sometimes from lepidopteran pollination. The development of ornithophily in these groups requires an explanation. The explanation presented here consists of a hypothesis and a summary of the evidence for it.

A certain difficulty surrounds the initial start of ornithophily in a flora. Bee-pollinated or lepidopteran-pollinated species cannot begin to change over to hummingbird pollination if hummingbirds are not regular foragers in their area, but hummingbirds cannot be regular foragers for very long if there are no hummingbird flowers.

The first contact between Arcto-Tertiary plants and hummingbirds probably occurred in the zone of interdigitation of the Arcto-Tertiary and Madro-Tertiary floras in the Eocene. The Madro-Tertiary communities contained old ornithophilous plants and their hummingbird flower foragers. Such hummingbirds had their regular food resource, but hummingbirds are constantly exploring for new food sources and would make visits to neighboring Arcto-Tertiary bee and lepidopteran flowers.

The numbers of pollinators and the numbers of flowering plants are not in perfect balance. Fluctuations in population size are normal and result in temporary imbalances. A shortage of Madro-Tertiary hummingbird flowers in one period, and a corresponding excess of hummingbirds, can be expected to drive hummingbirds to make more frequent visits to neighboring bee flowers. Conversely, an excess of Arcto-Tertiary bee-pollinated plants relative to the number of bees in any period can leave many such plants undervisited or unpollinated. If bee pollinators are in short supply and hummingbirds are available at the same time, the combination of factors will favor adaptive changes for hummingbird pollination and hence a development of new ornithophilous characters in some Arcto-Tertiary plant populations.

The new association of hummingbirds and Arcto-Tertiary plants would necessarily be small in numbers of individual birds and plants at first, but it would be a start, and it could build up gradually. More hummingbirds would support more hummingbird-pollinated populations and species, and more of the latter would support more hummingbirds, which in turn could expand their exploratory foraging flights in Arcto-Tertiary plant communities. The buildup is autocatalytic.

Buildup at Multiple Loci. The expansion of the Madro-Tertiary flora to the north and west after the Eocene must have brought hummingbirds into contact with other parts of the Arcto-Tertiary flora. The opportunities for Arcto-Tertiary plants to switch to hummingbird pollination, which was geographically localized in the Eocene, thus became more widespread after the Eocene. The mid-Tertiary migrations of the Madro-Tertiary flora created starting points for the buildup of ornithophily in different localities at different times.

The composition of the North American branch of the Arcto-Tertiary flora was not static throughout the Tertiary. Some plant groups were present in the North American branch in the early Tertiary, while others migrated from Eurasia to North America later in the Tertiary. *Aquilegia* is a probable example of the latter case. The starting time for the development of ornithophily would differ as between old members and late emigrants in the North American branch of the Arcto-Tertiary flora.

As the number of ornithophilous groups increased in the flora, they would support larger numbers of hummingbirds, which would then provide an ecological opportunity for the divergence of additional ornithophilous groups. The hummingbird pollination would be expected to increase progressively in extent in the Arcto-Tertiary flora as a whole.

The systematic distribution of ornithophilous species in groups with Arcto-Tertiary affinities in the modern flora, as described in this paper, is consistent with the expectation of a gradual and stepwise buildup of ornithophily. The gradation in size of ornithophilous groups appears to reflect a series of stages of development. The first Arcto-Tertiary group to become successfully adapted for hummingbird pollination, and to remain extant, would be the largest ornithophilous group now (*Castilleja*). Small ornithophilous genera (*Zauschneria*) and ornithophilous species groups (in *Penstemon*, *Aquilegia*, etc.) probably represent younger stages of development. Single ornithophilous species in otherwise nonornithophilous genera (*Pedicularis*, *Scrophularia*, etc.) represent a relatively recent stage.

We do not now have the kind of paleontological evidence needed for assigning ages to particular ornithophilous plant groups or to their various stages of development.

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