

LEAF FORM AND EVOLUTIONARY PATTERNS IN *PEDICULARIS*

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(Received 9 November, 1977)

The mid-latitude North American *Pedicularis* species have evolved very rapidly from probably a single Asiatic immigrant. Pinnately dissected leaves with narrow segments are highly efficient heat dispersers and allow several species to survive severe insolation on dry alpine areas. The leaf form is modified when species revert to shaded habitats.

INTRODUCTION

Pedicularis (Scrophulariaceae-Rhinanthoideae-Rhinantheae) contains about 500 species, and about three-quarters of them are found in the Himalayan region. Both abundance and extreme morphological variability suggest that the Himalayan region is the evolutionary centre of the genus. From this centre radiants have spread northward (with several species becoming circumpolar), westward or eastward.

Li (1948) suggested that flower morphology in the Asiatic species has repeatedly adapted to available pollinators. Such adaptations were also revealed among mid-latitude North American species by Sprague (1962) and Macior (1968a, 1968b, 1969, 1970, 1973, 1977). The mechanisms that have evolved to attract bees (notably *Bombus* spp.), and to ensure pollination by them, are too varied and complex to describe here in detail. Macior has shown that some *Pedicularis* species have evolved structures that demand different behaviour even by the same species of bee. A dramatic and complex adaptation is that of *Pedicularis densiflora* to pollination by hummingbirds (Trochilidae). This species occurs from Baja California to southwestern Oregon, mainly near the coast, in a region frequented by several migrant or resident hummingbirds. *Ped. densiflora* has long, slender, orange to red corollas, a target that hummingbirds in the region recognize as an abundant nectar source, which is largely neglected by red-blind insects. *Ped. densiflora* is visited by at least four hummingbirds, but is also visited by some bees. The purpose of this paper is to show, using these American species, that leaf morphology may also be rapidly altered in response to varied ecological conditions.

ORIGIN OF AMERICAN SPECIES

A group of about 25 species in the middle latitudes of North America, mostly in the cordilleran region, seems to have arisen, largely at least, from a single Asiatic

species that came via the Bering bridge, perhaps in late Pliocene. Data from the rusts that attack these plants (Savile, 1967) suggest that diversification from the original immigrant occurred very rapidly under stimulus of the Pleistocene climatic fluctuations and population fragmentation. The more widespread rust, *Puccinia clintonii*, is microcyclic and has variously striate teliospores. It is probably derived from a smoothed-spored Asiatic rust, perhaps much like the Himalayan *Puccinia bhutanensis* (Savile, 1968a). *Puccinia clintonii* occurs in at least seven host-limited varieties with small morphological distinctions, six in North America and one in Ireland and western Scotland. This last variety (*sylvaticae*) is closest to var. *clintonii* on *Ped. canadensis* in eastern North America. Because it is confined to the periphery of the range of its host, *Ped. sylvatica*, var. *sylvaticae* is believed to have diverged from ancestral var. *clintonii* when isolated at the onset of the Würm Wisconsin) glaciation. Unlike any rust reported on Rhinanthoideae, *Puccinia rufescens* produces distinctive aecia (and occasionally pycnia) as well as telia. It has multiple morphological correlations with *Puc. palmeri*, which attacks advanced species of *Penstemon* (Savile, 1967, 1968b). It is clear that *Puccinia rufescens* (the more advanced rust) arose by a jump from *Puc. palmeri*. The requirements for a successful jump (Savile, 1968b, 1971) include: strongly overlapping ecogeographic boundaries of existing and prospective hosts; a rust in its evolutionary youth, and thus with a diverse gene pool; and a prospective host in its evolutionary youth. These circumstances maximize the probability of meeting by compatible host and parasite genomes. Thus the rust from *Penstemon* (an advanced and recently evolved genus centred in the cordilleran region) moved to a very rapidly evolving species complex in *Pedicularis*. This event emphasizes that these *Pedicularis* species are of recent origin. Both rusts cut across the groups and subgroups proposed by Pennell (1951).

It may be noted that such an explosion by an immigrant species is not unique to *Pedicularis*. The same pattern was followed in the cordilleran *Allium* species, all of which have the much rarer of the two Asiatic base chromosome numbers, and almost certainly evolved from a single immigrant. Unfortunately, in *Pedicularis* chromosome numbers are of little help. Although base numbers of 6, 7 and 8 are recorded, 6 and 7 are both rare; and the fact that the cordilleran species have $x = 8$ (and usually $n = 8$) is of minor significance. Thus the rust relationships seem to provide the best evidence for the unity of the group.

FUNCTION OF PINNATE LEAVES

I suspected that the diversity of leaf shapes in the cordilleran *Pedicularis* must reflect ecological pressures, and that such changes must often occur rapidly. This belief was strengthened by the work of Simpson (1973), who demonstrated repeated Pleistocene speciation in a group of *Perezia* (Asteraceae—Mutisieae), the species of which have leaves ranging from entire to pinnately dissected, and inhabit predominantly alpine sites in South America.

Recently Balding and Cunningham (1976) confirmed, from wind-tunnel tests with instrumented leaf models, that pinnately dissected leaves dissipate heat substantially better than entire ones. They pointed out that plants on dry sites exposed to intense insolation may often be subjected to potentially lethal temperatures. The risk must be particularly high in plants with basal rosettes, a growth form that is common on arctic and alpine sites because it protects the winter buds from snow abrasion (Savile, 1972). On mid- to low-latitude dry alpine sites, where great atmospheric clarity allows intense insolation, selection pressure for pinnate leaves must be very strong.

Perezia nutans and *P. prenanthoides* occur in the *Nothofagus* forest (Simpson, 1973). Both species seem to originate from a common ancestor as a result of fragmentation of the population by a Pleistocene glacier; and they have pinnately dissected leaves, which suggest an alpine ancestor, but greatly enlarged leaf segments.

CORRELATION OF LEAF FORM AND HABITAT

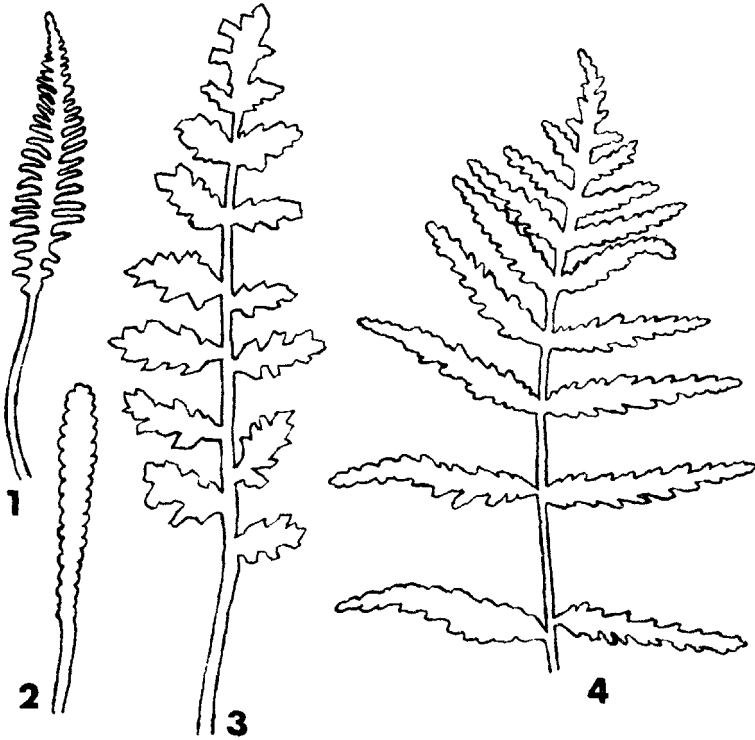
Now let us return to the North American *Pedicularis* species. All the typically cordilleran species that are wholly or partly alpine have leaves with a more or less perfectly pinnately dissected lamina, having linear and often pointed segments—*Ped. atollens*, *Ped. contorta*, *Ped. groenlandica* (Fig. 1), *Ped. ornithorhyncha* (p.p.), *Ped. parryi*, *Ped. pulchella*, and *Ped. rainierensis*. A few arctic species spread sparingly southward to alpine sites, and one such species—*Ped. langsdorfii*—has serrate leaves; but, at its southern limit of 49°30'N lat., it is confined to north slopes where it escapes serious heat stress. Most arctic *Pedicularis* do have strongly pinnatifid leaves, probably not because they need them but because they are derived from mid-latitude alpine plants, and the dissected leaves are not disadvantageous on open sites in the arctic.

The leaves of *Pedicularis dudleyi* (Fig. 3), a species of the redwood forests in coastal California, are fully dissected, but the segments have large and irregularly angular lobes almost exactly like those of *Perezia prenanthoides* in the *Nothofagus* forest. The leaves of *Ped. semibarbata*, a species of dry pine forests from southern Oregon to southern California and adjacent Nevada, closely approach the same form. *Ped. ornithorhyncha* is a coastal plant of moist, cloudy sites ranging from near sea level to low alpine; and it has leaves that vary from simply pinnatifid to nearly the type found in *Ped. dudleyi*. It is evident that these irregularly lobed pinnae represent an early stage of readaptation from dry alpine to forested or at least cloudy sites in which an increase in photosynthetic surface is beneficial.

In *Pedicularis cystopteridifolia*, a subalpine to low-alpine species, some leaf segments are also somewhat enlarged. Above treeline this species, sometimes, at least, grows on north-facing slopes, on which neither aridity nor insolation can be as severe as on level sites.

Pennell (1951) described *pedicularis crenulata* (Fig. 2), with leaves only shallowly crenulate-dentate, as occurring on Upper Sonoran meadows. However,

Weber (1976) gives the habitat as montane or subalpine wet meadows; and all the sheets in DAO are also from high and generally wet mesic sites, much above the desert valleys. Thus this species is never exposed to severe insolation.



FIGS. 1-4.

One other adaptation to moist and often shady habitats, which has apparently not been paralleled in *Perezia*, is seen in *Pedicularis bracteosa* (Fig. 4) and in its various localized segregates, which, as Cronquist (1959) concluded, are probably not specifically distinct. In these plants, rather than the leaves being elliptic in outline, the lower segments become progressively elongate. The leaf blade thus becomes broadly triangular, its form being reminiscent of the fronds of some ferns such as *Dryopteris phegopteris*.

These ecologically correlated leaf forms may not allow a full elucidation of the evolutionary patterns in the North American species of *Pedicularis*; but an understanding of the functions of the different forms helps us to appreciate how quickly the transformation from one form to another may occur. Such an appreciation also further undermines Pennell's attempt to use degree of leaf dissection in establishing supposedly natural groupings in these plants.

ACKNOWLEDGEMENTS

I thank Dr John McNeill for his careful review of the manuscript and Dr M. J. Thirumalachar for helpful suggestions.

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EXPLANATION TO FIGURES

FIGS. 1-4. Representative leaves of North American *Pedicularis*, reproduced at ca. $\frac{1}{4}$ natural size. 1, *P. groenlandica* (alpine). 2, *P. crenulata* (cool, moist meadows). 3, *P. dudleyi* (coastal redwood forest). 4, *P. bracteosa* ssp. *bracteosa* (mesic woodlands, moist grassy slopes, subalpine meadows); from plant of deciduous forest, 1110 m.s.m., southern British Columbia; leaves of subalpine plants generally smaller and with markedly narrower pinnae.