THE DISTRIBUTION OF SCROPHULARIACEAE IN THE HOLARCTIC WITH SPECIAL REFERENCE TO THE FLORISTIC RELATIONSHIPS BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA[1]

HONG DE-YUAN[2]

ABSTRACT

Based on a general survey of the distribution of Scrophulariaceae in the Holarctic, eastern Asia is shown to be the richest in members of the family among five regions. Western North America has 53% of the genera (16/30) common to eastern Asia, whereas eastern North America has 48% of the genera (17/35) common to eastern Asia. Among 14 genera (excluding the cosmopolitan and pantropical genera) shared by North America and Eurasia, four distributional patterns are recognized: temperate western North America/Mediterranean disjunction (one genus); temperate Eurasia/North America disjunction (three genera); temperate eastern Asia/eastern North America disjunction (four genera), and continuous distribution through the Bering Strait or Aleutian Islands (six genera). Three phases of plant communication between North America and Eurasia are hypothesized. The origin and migration routes of some taxa are traced. Six genera are suggested to have migrated from eastern Asia to North America and four genera are considered to have migrated in the opposite direction, i.e., from western North America to eastern Asia through Beringia or the Bering Strait.

The floristic affinity between eastern Asia and eastern North America was first noticed by Linnaeus (in a dissertation defended by J. Halenius; see Graham, 1972) as early as 1750 and has been the focus of much attention by plant geographers since Gray's (1840, 1846; reprinted in Graham, 1972) brilliant works. The subject has been extensively discussed over the past century (see Li, 1952; Graham, 1972, for literature). There have been, however, few, if any, discussions on the subject pertaining to individual families, probably due in part to a lack of floristic work on China, the major part of eastern Asia, in the past. This report is intended to be an initial effort in this direction.

The area covered in this work is the Holarctic Kingdom (Takhtajan, 1969) or Melchior's (1964) Kingdom I. To facilitate an analysis of distribution and discussion, the kingdom is divided into five regions, i.e., eastern North America (east of the Rocky Mountains, corresponding basically to Takhtajan's region 4), western North America (Takhtajan's regions 5 plus 9), eastern Asia (Takhtajan's region 3 plus the eastern half of region 2, or Good's (1974) regions 3 plus 2B), western and central Asia (Takhtajan's region 8 or Irano-Turanian Region), and Europe and the Mediterranean together (including the Azores).

GENERAL ASPECT

The Scrophulariaceae are a rather large family, containing 18 tribes, about 200 genera, and 3,000 species. It is highly developed in the Holarctic Kingdom with 14 tribes, 110 genera, and over 2,200 species. The tribes Verbasceae, Paulownieae, Hemiphragmeae, Ellisiophylleae (if included in the family), and Collinsieae are endemic to the area, and the Antirrhineae, Veroniceae, Rhinantheae, and Digitaleae have most of their members here. Of the 110 genera, 72 are endemic. The family, however, also flourishes in the Southern Hemisphere, with the tribes Aptosimeae, Calceolarieae, Hemimerideae, Manuleae, and Aragoeae (Hong & Nilsson, unpubl.) entirely or mainly confined there.

Table 1 shows that of the five regions mentioned above, eastern Asia has the most tribes, the most genera, the most endemic genera, the most species, and the most endemic species. It is the only subregion with endemic tribes (3). The least number of genera occur in western North America and the fewest species (including endemic ones) in eastern North America. North America, as a whole, is comparatively poor in scrophulariaceous plants, having only nine tribes (one endemic), 48 genera (16 endemic), and ca. 630 species (ca. 600 endemic).

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[2] Institute of Botany, Academia Sinica, Beijing, People's Republic of China.

TABLE 1. Taxa in the five regions in North America and Eurasia.

Taxon	Number of Taxa in Eurasia				Number of Taxa in North America		
	E. Asia	W. & C. Asia	Europe & Medit.	Total	E. North America	W. North America	Total
Tribe	11 (3)	8 (0)	8 (0)	12 (4)	8 (0)	8 (0)	9 (1)
Genus	58 (22)	35 (5)	39 (7)	82 (43)	35 (8)	30 (6)	48 (16)
Species	700 (550)	600 (350)	650 (450)	1,750 (1,650)	160 (100)	500 (450)	630 (600)

Western North America/eastern Asia have 16 genera in common; and eastern North America/eastern Asia have 17 genera in common. These paired regions share a greater number of taxa than any of the other paired regions. Thus, in the number of genera shared, the two regions in North America are both closer to eastern Asia than to Europe and Mediterranean together and to western and central Asia. All the large genera in North America have the great majority of their members in the western part of the continent, with few species (*Penstemon, Castilleja,* and *Mimulus*) or only a single species (*Orthocarpus*) extending into the eastern part. It is of interest to note that all four of these genera also occur in eastern Asia. Furthermore, 53% of the genera in western North America are in eastern Asia, whereas 48% of the genera in eastern North America are common to eastern Asia. It is probably reasonable to say that the relationships of the Scrophulariaceae between western North America and eastern Asia are closer than those between eastern North America and eastern Asia.

THE DISTRIBUTIONAL PATTERNS OF THE TAXA SHARED BY NORTH AMERICA AND EURASIA

North America and Eurasia share six tribes (Anthirrhineae, Gerardieae, Gratioleae, Rhinantheae, Scrophularieae, and Veroniceae) and 19 genera (*Antirrhinum, Bacopa, Buchnera, Castilleja, Euphrasia, Gratiola, Lagotis, Limosella, Linaria, Linderia, Melampyrum, Mimulus, Orthocarpus, Pedicularis, Penstemon, Rhinanthus, Scrophularia, Veronica,* and *Veronicastrum*) disjunctly distributed across the Atlantic and/or the Pacific. Since the genera *Bacopa, Gratiola, Limosella, Linderia* (all members of the tribe Gratioleae) and *Buchnera* (Buchnereae) are either cosmopolitan aquatics or pantropical, it is better to omit them for the analysis. The genus *Mimulus,* a widely distributed member of the tribe Gratioleae, is considered because it is best represented in the kingdom, particularly in western North America and shows a special relationship between western North America and eastern Asia.

Different taxonomic ranks are involved in these disjunct distributions. At the tribal level, a number of paired genera are found disjunctly distributed, one member of each pair in North America and the counterpart in Eurasia. In the tribe Veroniceae, *Veronica* on one side and *Synthyris* and *Besseya* together on the other are such a case. *Veronica* is a large and polymorphic genus, with its center from the Pyrenees, along the Alps, north Anatolia, the Caucasus, the Himalayas, and the Pamirs to southwest China and Tienshan, where all eight sections and the majority of species exist. Only a few species (excluding cosmopolitan and weedy ones) mostly belonging to the section *Veronica,* extend into tropical Africa, Australia, and North America. *Synthyris* and *Besseya* together may be its counterpart in North America (Fig. 1). The relationships between *Veronica* and the other two genera are so close that no differences, except for habit and chromosome number, are useful for distinguishing them. *Siphonostegia, Lesquereuxia,* and *Schwalbea* in Rhinantheae provide another example. The first occurs in eastern Asia, the second in Greece and southern Turkey, and the third in eastern North America (Fig. 2). *Siphonostegia* differs from the other two in having pinnatifid leaves and subequal clayx lobes; *Lesquereuxia* is different from *Schwalbea,* mainly in its opposite leaves. The three are closely related (Hedge, 1978).

The 14 genera common to the two continents may be grouped into four categories according to their distributional patterns:

1) Disjuncts across the Atlantic (with one part of the area in Europe and the Mediterranean region and the other in North America). Only one genus, *Anthirrhinum,* falls into this category. It consists of 30 species, 17 of them occurring in the western Mediterranean west of Italy; the oth-

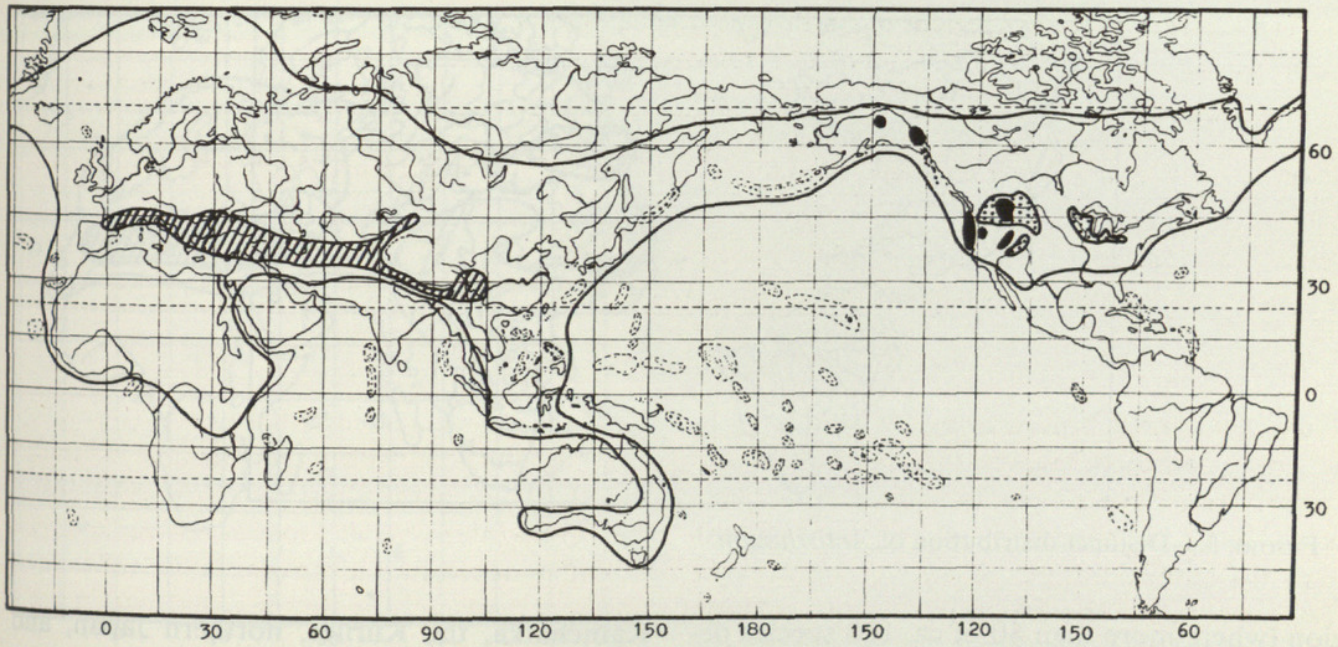

FIGURE 1. Distribution of the genera *Veronica, Synthyris,* and *Besseya.* Although *Veronica* is distributed almost worldwide, the majority of species and all eight sections occur in the southern Holarctic Kingdom (the cosmopolitans are not included in the map). *Synthyris* is totally in western North America and *Besseya* has only one species in eastern North America. *Synthyris* and *Besseya* may be regarded as congeneric. Shaded area—distribution center of *Veronica*; black area—*Synthyris*; dotted area—*Besseya.*

er 13 are restricted to California in the United States (Fig. 3).

2) Genera disjunct across both the Pacific and the Atlantic (that is with one part of the area in temperate Eurasia and the other in temperate North America). In this category are three genera, *Scrophularia, Linaria,* and *Melampyrum,* all centered mainly in southern Europe and the Mediterranean. *Scrophularia* is a large genus with ca. 150 species, of which over 100 grow in the region from the Pyrenees to the Pamirs, and with ca. 20 in a small area in southwest China (Fig. 4). In North America the genus has nine species (or only two species depending on species concept). The situation in *Linaria* appears similar (Fig. 5). It is centered in the Mediterranean re-

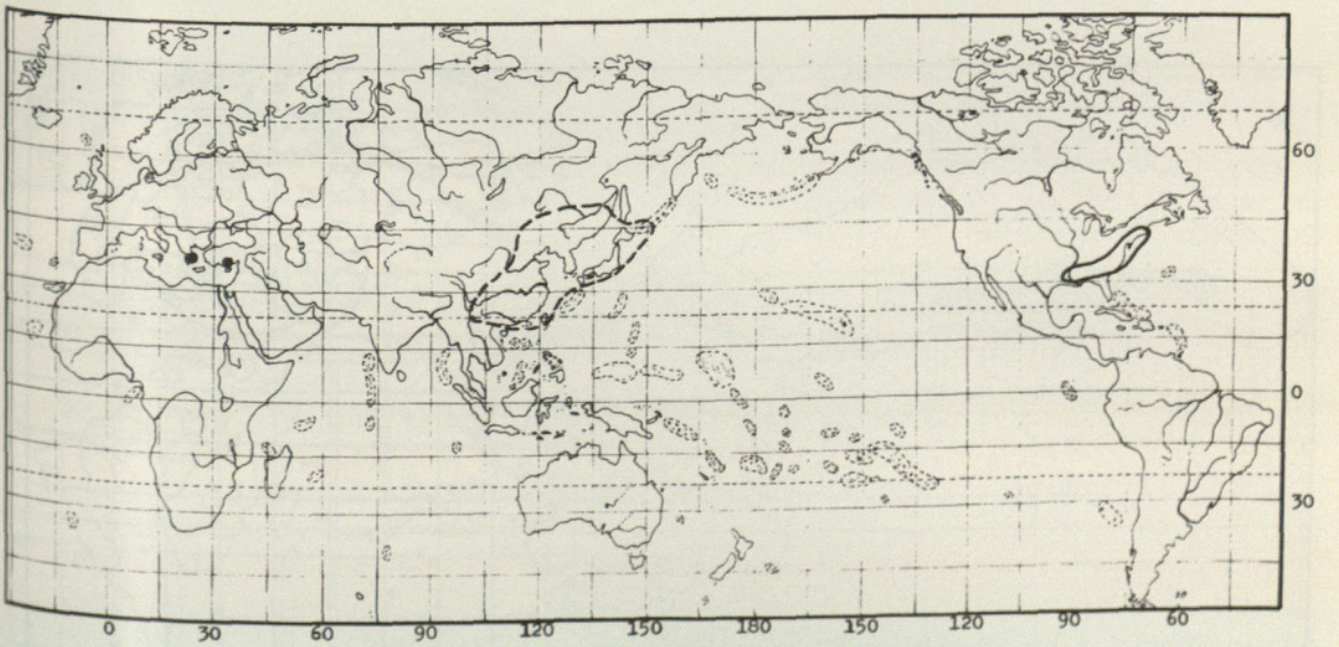

FIGURE 2. Distribution of three very closely related genera, *Schwalbea* (continuous line), *Siphonostegia* (broken line), and *Lesquereuxia* (two black dots).

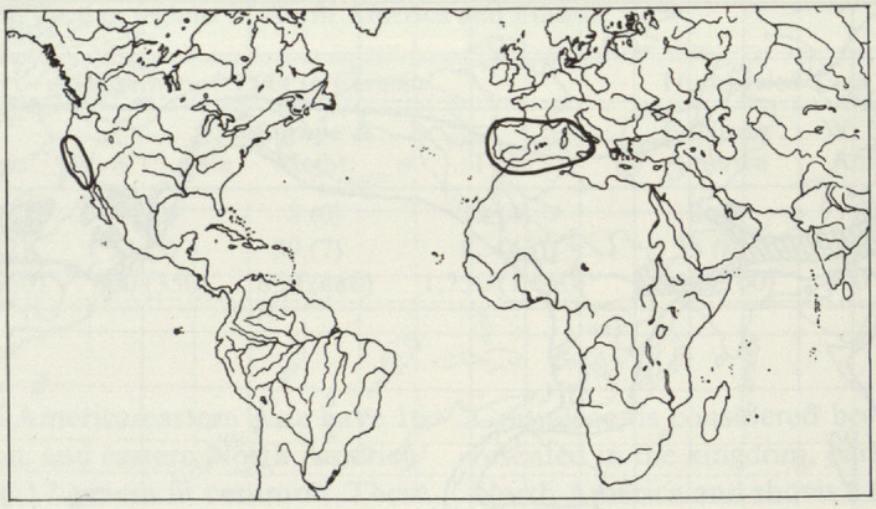

FIGURE 3. Disjunct distribution of *Antirrhinum*.

gion (where more than 80 of ca. 120 species occur), particularly in Portugal and Spain. Only one or two species grow in North America. *Melampyrum* is a much smaller genus with ca. 30 species, two-thirds of which are concentrated in southeast Europe and the Caucasus. Only one polymorphic species, *M. lineare*, occurs in temperate North America (Fig. 6).

3) Genera disjunct across the Pacific (with one part in North America and the other in east Asia). Four genera (*Penstemon, Mimulus, Veronicastrum*, and *Orthocarpus*) belong to this category. All but *Veronicastrum* have the majority of their members in western North America. *Penstemon* consists of some 220 species, with a great majority concentrated in temperate western North America, but with one species, *P. frutescens*, in Kamchatka, the Kuriles, northern Japan, and Sakhalin (Fig. 7). *Orthocarpus* occurs almost entirely in western North America. Only one species extends eastward into the eastern part of the continent; another isolated species grows in Andean America. A new species, *O. chinensis*, was recently discovered from central China (Hong, 1979). Thus, *Orthocarpus* is actually disjunct between western North America and eastern Asia (Fig. 8). Although the genus *Mimulus* is widely distributed, abundance and center of diversity is again in western North America where over two-thirds of the total number of species (ca. 70/110) grow; the Asian part of the range is a strip from the south Kuriles and Sakhalin to the Himalayas and is distantly disjunct from the Australian and African parts of the range of the genus (Fig. 9).

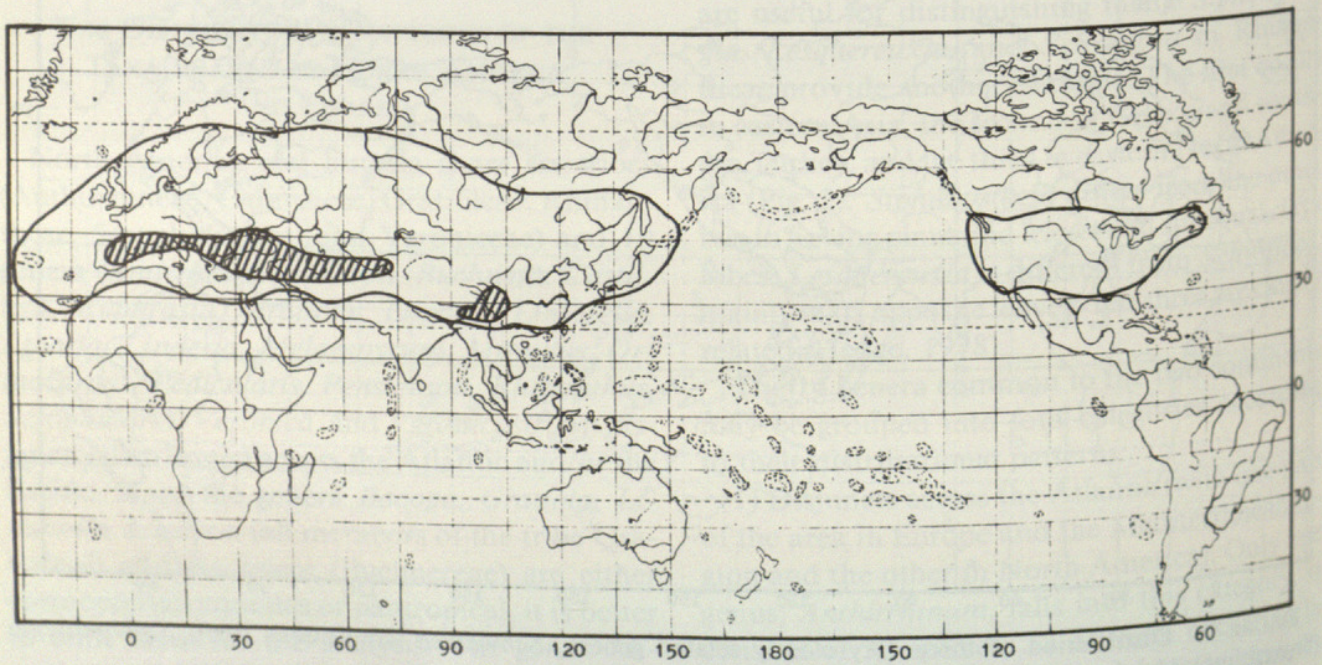

FIGURE 4. Disjunct distribution of *Scrophularia*. The distribution center is shaded.

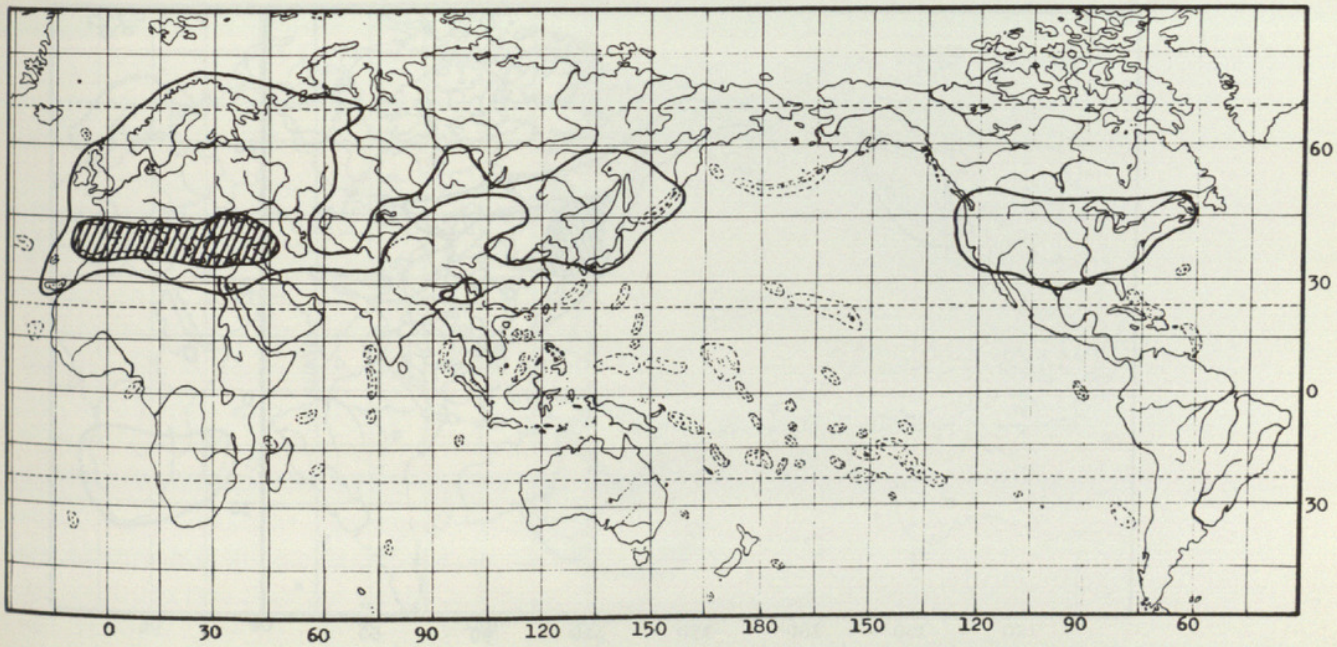

FIGURE 5. Disjunct distribution of *Linaria*. The shaded area indicates the distribution center.

The discontinuous distribution of *Veronicastrum* was noted by Li (1952) in his discussion of floristic relationships between eastern Asia and eastern North America. The genus has 19 species in eastern Asia, from the eastern Himalayas to Sakhalin, and a single species in eastern North America south of 50°N (Fig. 10).

4) Genera continuously distributed across the northern Pacific. In this category are six genera, *Veronica, Lagotis, Pedicularis, Euphrasia, Rhinanthus,* and *Castilleja.* As mentioned above, *Veronica* is a large genus with the majority of its species in temperate Eurasia, but with 13 species native to North America (excluding the cosmopolitan species). Seven are endemic, three (*V. alpina, V. fruticans,* and *V. scutellata*) are circumpolar, and *V. stelleri* occurs from the Chang-Bai Mountain in northeast China to southern Alaska across the Aleutians (Fig. 11). *Lagotis* is mainly an eastern Asian genus centered in southwestern China; only two species extend into northeastern Europe and one into the Caucasus. *Lagotis glauca,* however, reaches Alaska and the Yukon in the northwestern corner of Canada (Fig. 12). *Pedicularis,* the largest genus in the Scrophulariaceae, with ca. 500 species, is typical of the

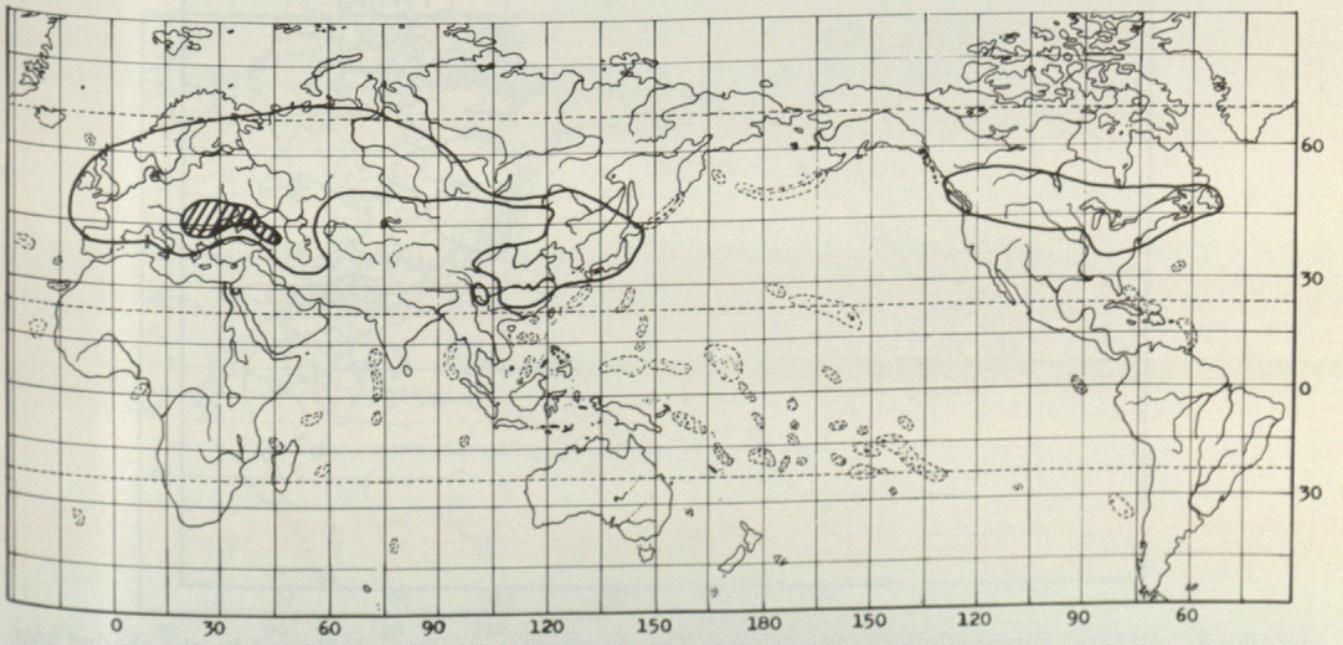

FIGURE 6. Disjunct distribution of *Melampyrum.* The distribution center is indicated by the shaded area.

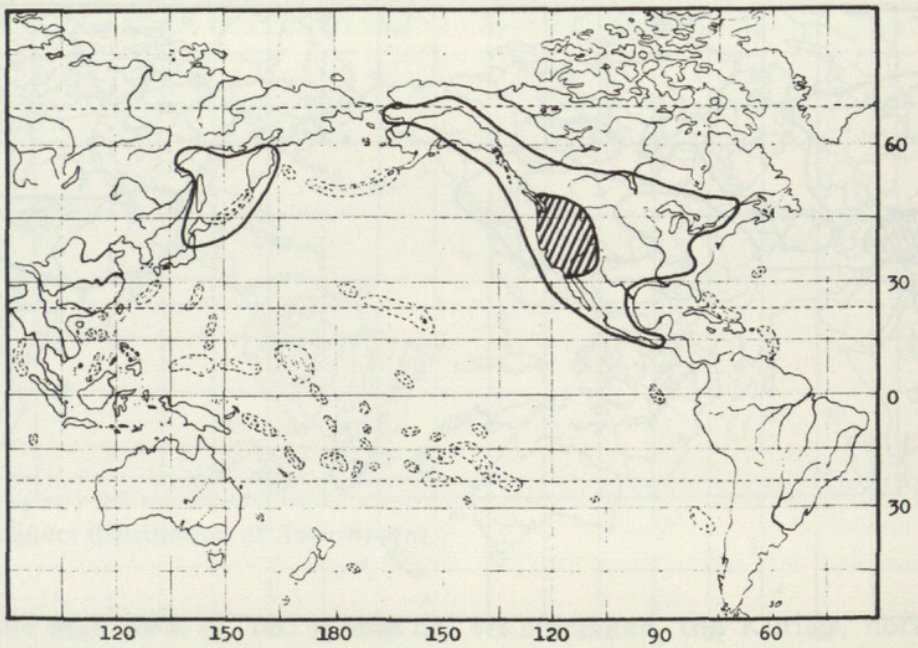

FIGURE 7. Disjunct distribution of *Penstemon*. Shaded area indicates distribution center. Only one species, *P. frutescens,* occurs in eastern Asia.

Holarctic Kingdom. Over 300 species are concentrated in a small area in the eastern Himalayas, western Sichuan, and northwestern Yunnan. Among the 32 species native to North America, 12 are common to eastern Asia and eight are common to Europe (Fig. 13). Although *Euphrasia* is widespread, section *Euphrasia,* consisting of annuals, is totally within the Holarctic Kingdom with the greatest number of species in Europe. Native to North America are seven species, four endemic to the eastern part; two are also in northern Europe and one is also in eastern Asia (Fig. 14). *Rhinanthus* is to some extent similar to *Euphrasia* section *Euphrasia,* but there are two gaps in the continental part of the range in the Far East and Kamchatka and only a single species, *R. borealis,* occurs in North America (Fig. 15). *Castilleja* is different from the genera mentioned above in that it extends to South America and is centered in western North

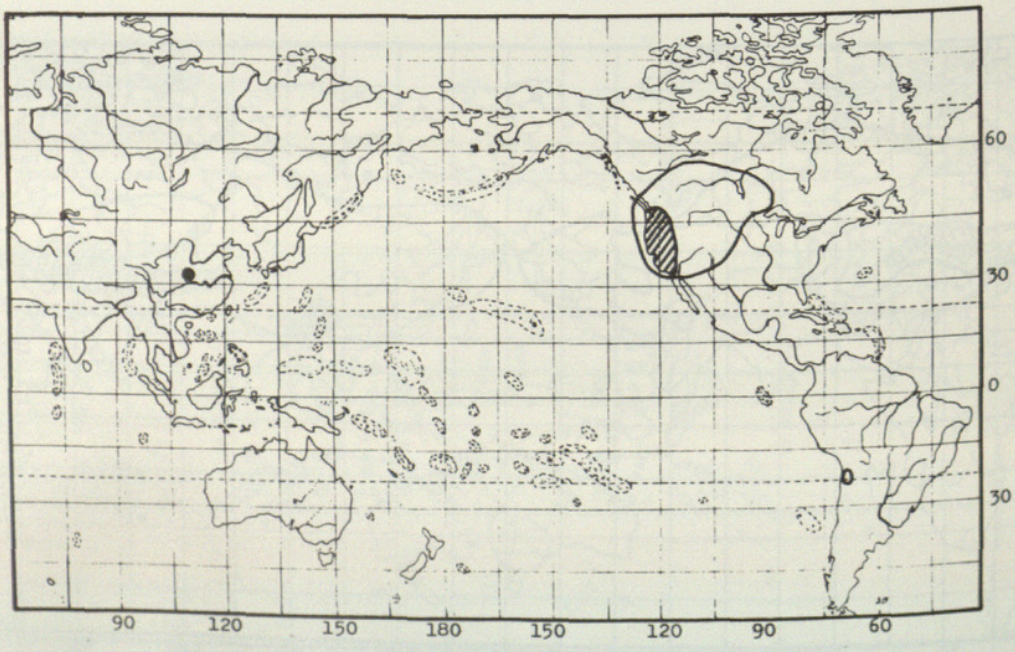

FIGURE 8. Disjunct distribution of *Orthocarpus.* The distribution center is indicated by the shaded area. Black dot—one single Asian species, *O. chinensis* Hong.

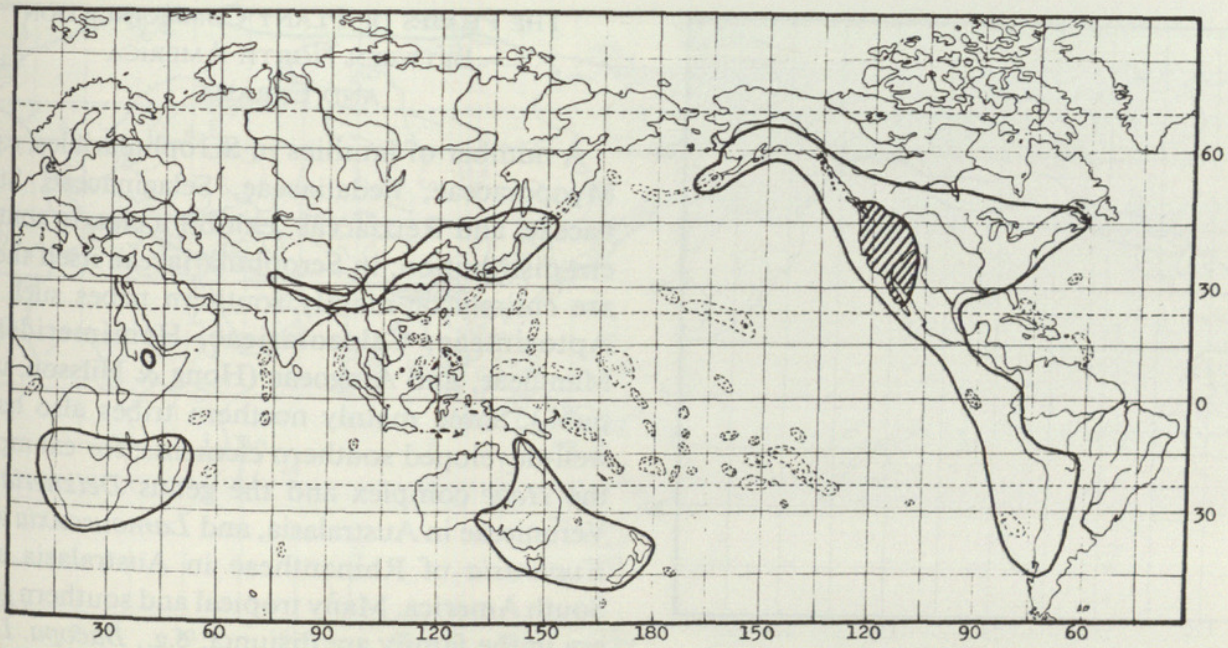

FIGURE 9. Distribution of *Mimulus*. The distribution center is indicated by the shaded area. All the Asian species but *M. strictus*, which is conspecific with the African plants, belong to the section *Paradanthus*, also centered in the Pacific Coast states.

America, with only three species in northern Eurasia (Fig. 16).

In summary, in the Holarctic Kingdom the Scrophulariaceae have six tribes disjunctly distributed in Eurasia/North America. Four of them, the Antirrhineae, Rhinantheae, Scrophularieae, and Veroniceae, are typically or mostly northern tribes. The Antirrhineae are mainly in the Mediterranean region where there are eight genera (including three endemic or nearly endemic ones); the Rhinantheae is best developed in eastern Asia where there are 14 genera (seven endemic); the Scrophularieae is almost equally developed in Eurasia and North America; the Veroniceae have 13 genera in Eurasia, particularly in the southern part, and four genera in North America. Between North America and Eurasia there is also a genus-pair distributional pattern, *Schwalbea/Siphonostegia-Lesquereuxia*. Among 14 northern genera common to North America and Eurasia (five additional pantropical or worldwide genera are out of our consideration) one falls into a Mediter-

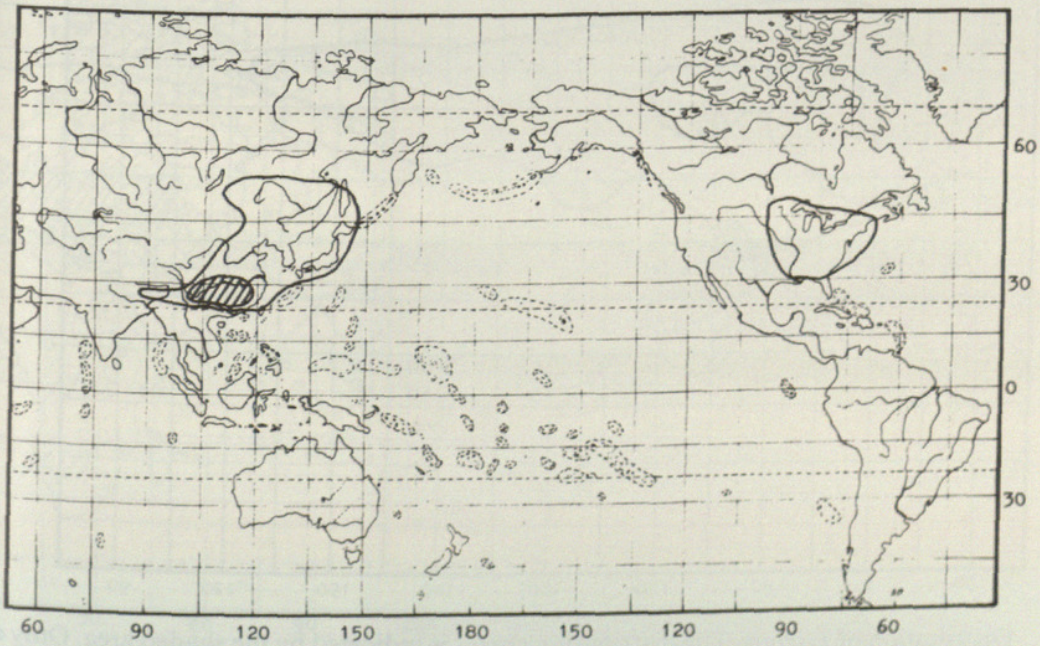

FIGURE 10. Disjunct distribution of *Veronicastrum*. Shaded area indicates the distribution center.

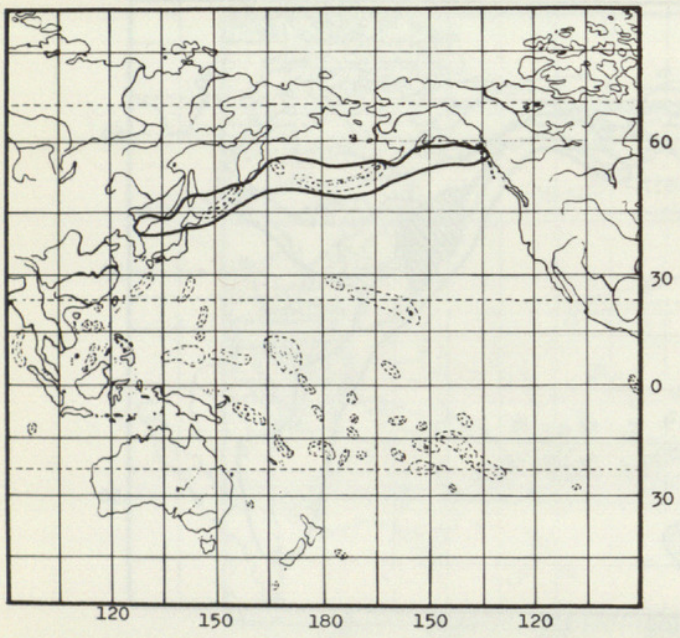

FIGURE 11. Distribution of *Veronica stelleri.*

ranean/western North America pattern; three into a temperate Eurasia/North America pattern; four into a temperate eastern Asia/North America pattern (three are of an eastern Asia/western North America pattern; one is of an eastern Asia/eastern North America pattern). The remaining six are more or less continuously distributed, with small gaps in the Bering Strait or Aleutian regions. One of these is primarily an American genus; five are Eurasian ones (three with eastern Asia as their distributional center).

THE PHASES OF PLANT COMMUNICATION BETWEEN NORTH AMERICA AND EURASIA

A number of families in Scrophulariales, e.g., Myoporaceae, Pedaliaceae, Selaginaceae, Stilbaceae, and Retziaceae, exhibit a clearly southern distribution; in Scrophulariaceae itself there are entirely or mainly southern tribes such as Aptosimeae, Calceolarieae, Hemimerideae, Manuleae, and Aragoeae (Hong & Nilsson, unpubl.). Some mainly northern tribes also have well-developed southern elements; for example, the *Hebe* complex and the genus *Detzneria* of Veroniceae in Australasia, and *Lamourouxia* and *Euphrasia* of Rhinantheae in Australasia and South America. Many tropical and southern genera in the family are disjunct, e.g., *Bacopa, Linderia, Gratiola, Stemodia,* and *Buchnera* in Africa, Asia, Australia, and America; *Striga* and *Limnophila* in Africa, Asia, and Australasia; and *Hebe* and *Jovellacea* in Australasia and South America. On the basis of this distribution, it is reasonable to suggest that the Scrophulariaceae originated and differentiated rather early, probably when Pangaea was still extant or at least before Gondwana had broken up. As to North American/eastern Asian distributional pattern, shown by the genera *Penstemon, Orthocarpus, Mimulus,* and *Veronicastrum,* it is quite plausible that they migrated from North America to Asia or vice versa through Beringia before the

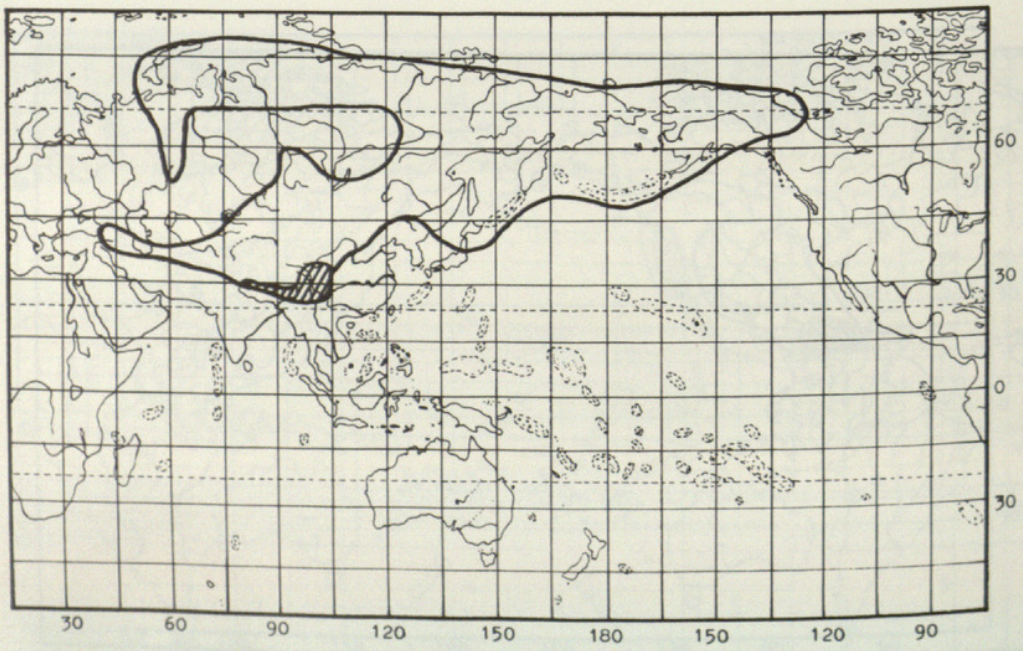

FIGURE 12. Distribution of *Lagotis.* The distribution center is indicated by the shaded area. Only one species, *L. glauca,* extends into North America.

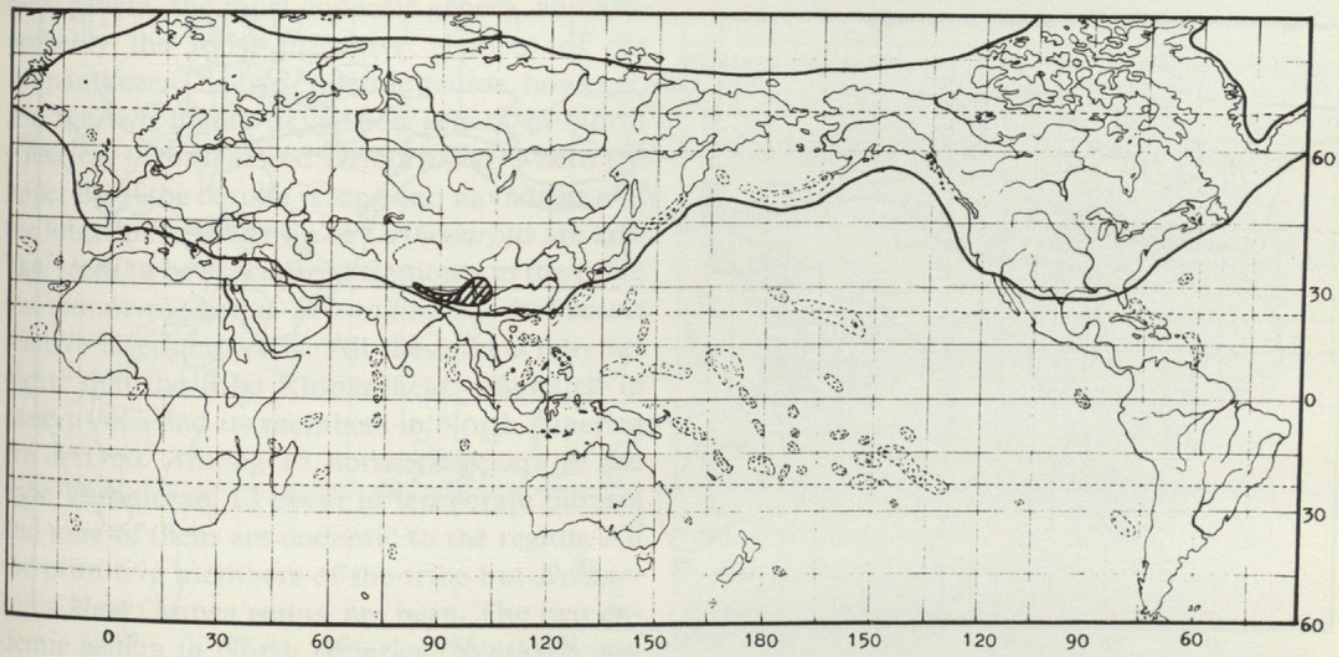

FIGURE 13. Distribution of *Pedicularis*. The majority of species (ca. 300 out of 500) grow in the area shaded.

end of the Miocene, i.e., some 12 million years ago, when the climate there was temperate or cool-temperate (Wolfe, 1972). In pattern 4, represented by genera with a more or less continuous distribution through the Bering Strait and the Aleutians, migration via these two routes during the Quaternary can hardly be doubted.

From the foregoing, floristic migration between Eurasia and North America may have taken place in three phases. The exact time of the earliest one is still vague, either when Laurasia was still extant, or later, but when the climate around Beringia was warm-temperate or temperate (probably before Early Miocene); the time and route of the second one is rather certain, i.e., through the Beringian region when it was temperate or cool-temperate; the third is even more certain, through the Bering Strait or the Aleutians in the Quaternary.

MIGRATIONAL DIRECTION

Despite the difficulty in answering the question of migrational direction, I would, nevertheless, like to speculate about it and suggest hypotheses. There is not enough information available for

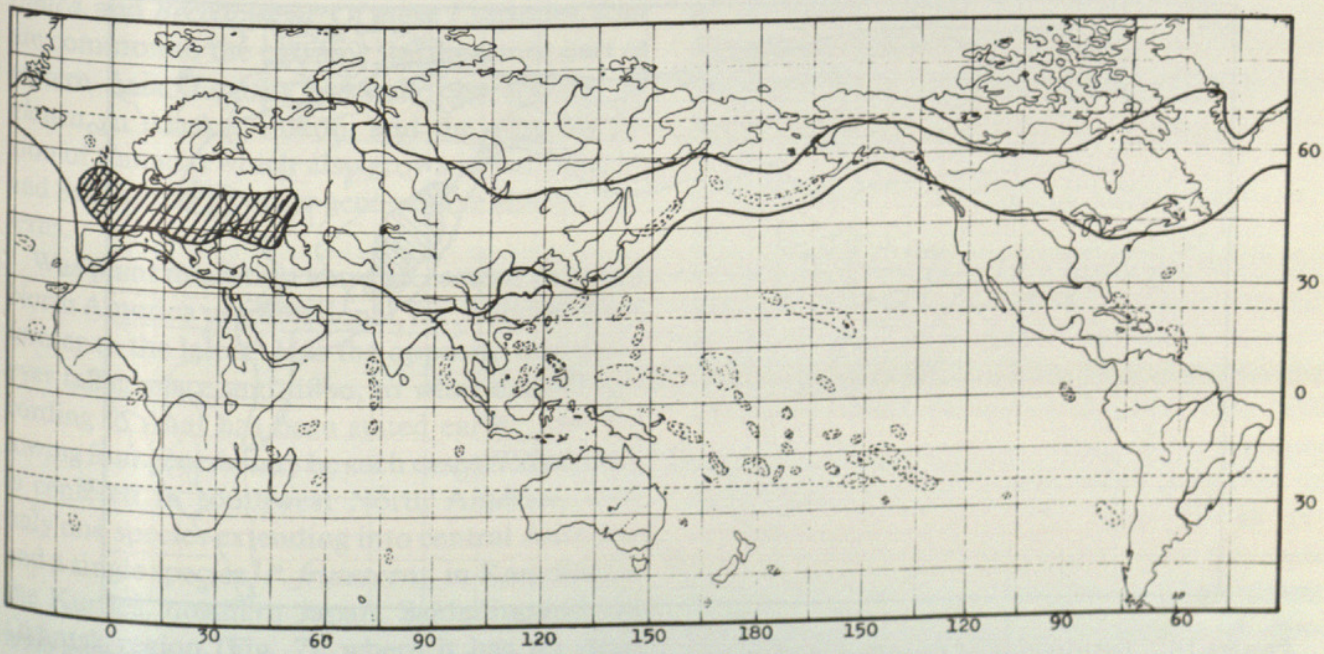

FIGURE 14. Distribution of *Euphrasia* section *Euphrasia*. Shaded area indicates the distribution center.

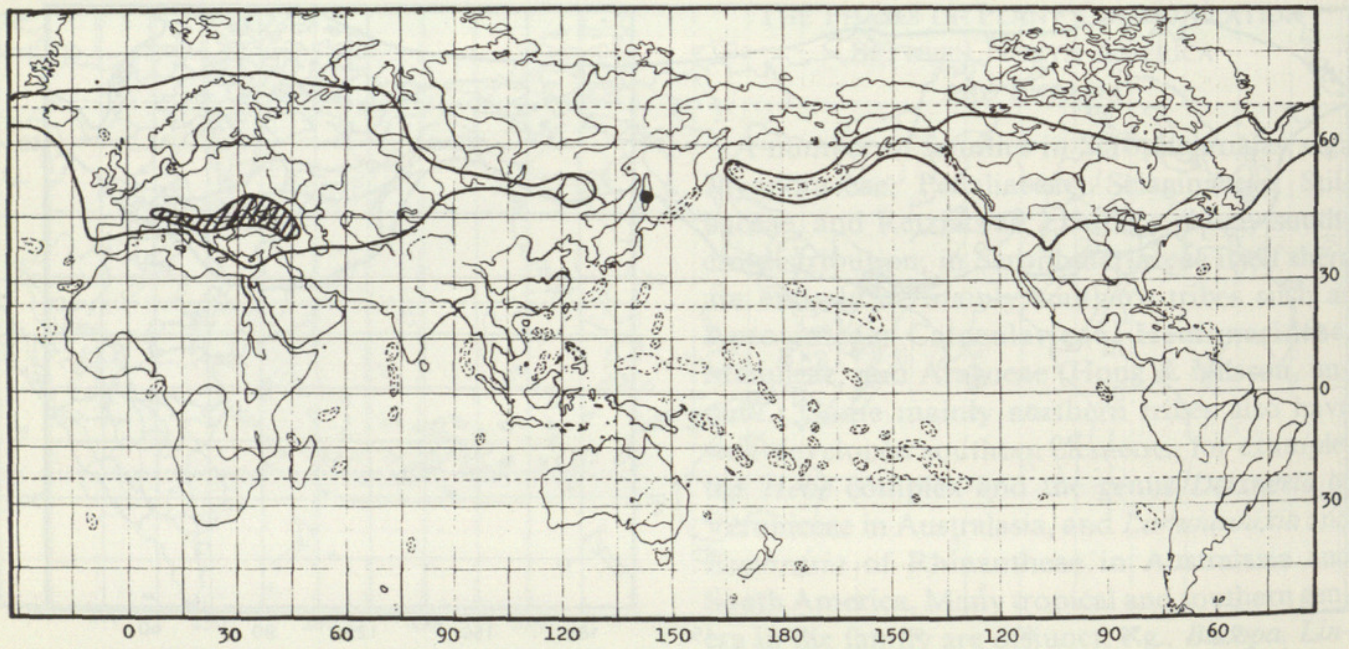

FIGURE 15. Distribution of *Rhinanthus*. The distribution center is indicated by the shaded area.

determining the center of origin and direction of migration of the tribes Scrophularieae and Antirrhineae, but I can say something about the Veroniceae and Rhinantheae. Of the 24 genera of Rhinantheae, eastern Asia has 14, of which seven are endemic. There are also 14 genera in the tribe in Europe and the Mediterranean region, but only three are endemic. In western and central Asia occur ten genera of the tribe, only one of which is endemic. In North America as a whole there are only eight genera, two of which are endemic, and the two other are concentrated there.

Recently, a new genus of Rhinantheae, *Pseudobartsia,* was described from Yunnan, southwest China (Hong, 1979). A certain number of primitive characters are retained in this genus. The upper lip of the corolla, for example, is almost straight with the two lobes only half-coherent, and has not developed into a definite galea. The seeds are ellipsoidal with a reticulate seed-coat. Therefore, eastern Asia possesses the

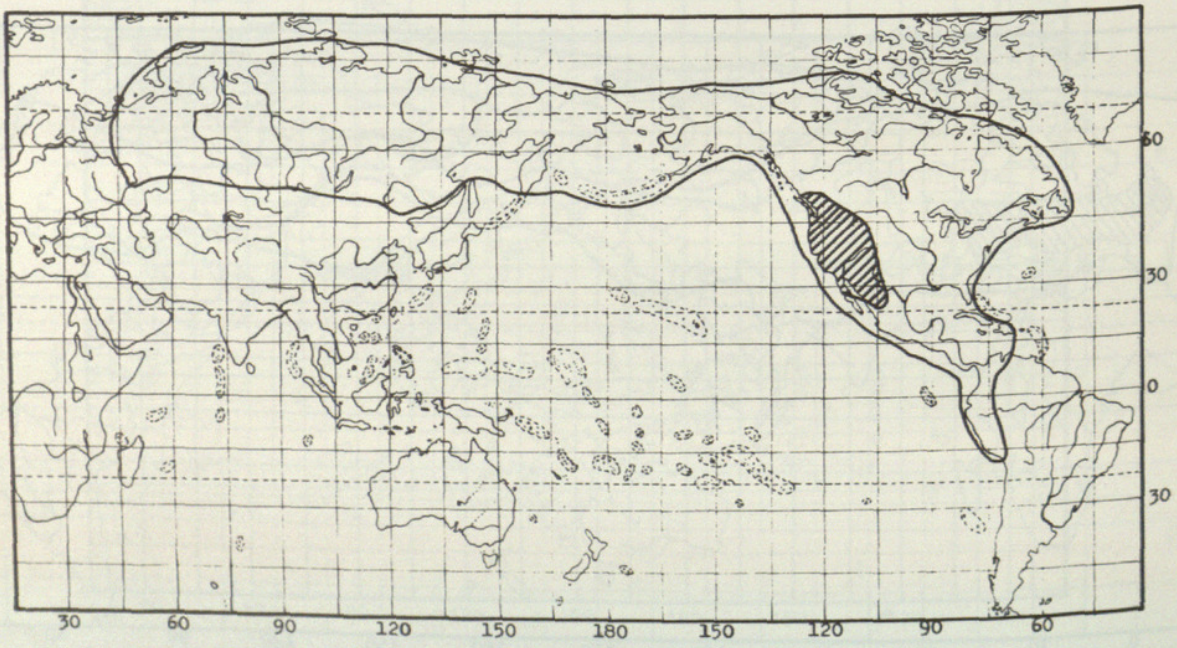

FIGURE 16. Distribution of *Castilleja,* with the center indicated by the shaded area. Only three species occur in northern Asia and northeastern Europe.

most genera, the most endemic genera, and also probably the most primitive element of the Rhinantheae. The two endemic genera, however, and the two highly developed genera in North America, *Castilleja* and *Orthocarpus,* where the upper lip of the corolla is long and navicular, and the lobe tips of lower lip in *Orthocarpus* are sac-like, seem to be specialized elements in the tribe; the monotypic genus *Schwalbea* has its closest relative in eastern Asia. All these facts may indicate that the tribe Rhinantheae originated in eastern Asia and its members in North America are derived. Among 15 northern genera of the tribe Veroniceae, 13 occur in temperate Eurasia and nine of them are endemic to the region. All the primitive members of the tribe but *Detzneria,* a New Guinea genus, are here. The two endemic genera in North America, *Synthyris* and *Besseya* are, however, closely allied to *Veronica* and are apparently derived (Hong, 1984). Figure 17 shows the distribution of the genus *Veronicastrum* as an example of migration of scrophulariaceous plants from eastern Asia to North America.

The migration during glaciation from eastern Asia to North America through the Bering Strait of *Pedicularis, Euphrasia, Lagotis, Veronica,* and *Rhinanthus* is almost certain. All eight sections and most of the species of *Veronica* occur in temperate Eurasia, especially in the southwestern part of eastern Asia. All 13 native species, apart from the cosmopolitan species, of the genus in North America are those adapted to cool or mountainous conditions and belong to three rather advanced sections, *Veronicastrum, Veronica,* and *Beccabunga.* Of these 13 species, four are common to the extreme northeastern part of eastern Asia. *Lagotis* has only one species, *L. glauca,* in Alaska, Yukon, and the adjacent region of Canada, which also grows in Kamchatka and Sakhalin. The other genera have similar patterns.

Was plant migration between eastern Asia and North America unidirectional, i.e., only from the former to the latter? Has the opposite migration ever taken place and, if so, to what extent? According to what has been stated earlier, the following four genera may be such cases. *Penstemon* is centered in southwest North America, with only one species extending into central America, and a single species, *P. frutescens,* in Kamchatka, the Kuriles, northern Japan, Sakhalin, and the Okhotsk region (Fig. 7), where it has no close relatives. The disjunct occurrence may be the result of migration from western North America through Beringia before the Late Miocene, when the Bering Strait had not opened (Durham & MacNeil, 1967) and the climate there was temperate or cool-temperate. *Orthocarpus,* which is centered in the Pacific Coast states, may represent another example of the migration from western North America to eastern Asia. The only Asian species of the genus, *O. chinensis,* was described recently from a single specimen collected half a century ago from central China. No additional collections have been made. The migration from western North America to eastern Asia of *Castilleja,* which also has western North America as its distributional center and has only three species in northern Eurasia, is also presumed by Yurtsev (1972). The case of *Mimulus* is more difficult to explain. In spite of its wide distribution in tropical Africa, Australasia, eastern Asia, and America, it is best developed in western North America, where nine of the ten sections and over two-thirds of the species occur. All seven species in eastern Asia except *M. strictus* (in northern India and northern Pakistan and conspecific with African plants, and may well indicate another source) belong to the section *Paradanthus,* which is also highly centered in western North America. The Asian species, except *M. strictus,* are very closely related to each other and also to those of the Pacific Coast states; for example, *M. sessilifolius* in Japan to *M. dentatus* on the Pacific Coast, and the Asian *M.*

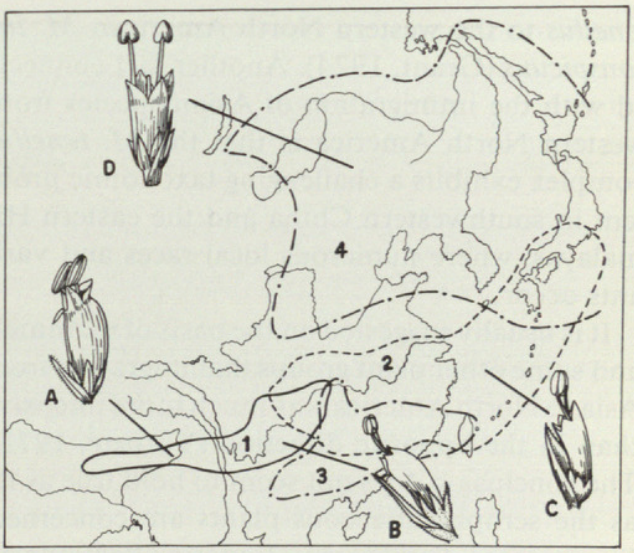

FIGURE 17. Distribution of the sections of *Veronicastrum,* showing the plausible relationship between migration and corolla evolution. 1. Section *Calorhabdos* (Benth.) Hong. 2. Section *Plagiostachys* (Franch.) Yamazaki. 3. Section *Pterocaulon* Yamazaki. 4. Section *Veronicastrum.*

tenellus to the western North American *M. inconspicuus* (Grant, 1924). Another fact connected with the immigration of Asian species from western North America is that the *M. tenellus* complex exhibits a challenging taxonomic problem in southwestern China and the eastern Himalayas, where numerous local races and variants occur.

It is usually suggested on the basis of mammals and some other plant groups that migration from Asia to North America was much more intensive than in the opposite direction (Yurtsev, 1972). The conclusion does not seem to hold true as far as the scrophulariaceous plants are concerned. Six genera, *Euphrasia, Lagotis, Pedicularis, Rhinanthus, Veronica,* and *Veronicastrum,* are suggested to have migrated from eastern Asia to North America, but four genera, *Castilleja, Mimulus, Orthocarpus,* and *Penstemon,* may have migrated in the opposite direction. Although *Linaria, Melampyrum,* and *Scrophularia* may have migrated from Eurasia to North America, it is doubtful if the event took place from eastern Asia to North America through Beringia. *Antirrhinum* presents an even more difficult case in this respect.

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