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Vicariism in the Geography of the Scrophulariaceae in China[1]

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With six text-figures

In the distribution of plant, a frequently noted phenomenon is the occurrence of closely related species in geographically neighbouring areas. Sometimes the separation is horizontal or geographical; while at other times the difference is mainly altitudinal, a lowland species being substituted by a morphologically similar species at higher elevations. Such vicarious forms are usually morphologically so closely related that their intimate genetic kinship is evident. Phylogenetically, they are descendents from a common ancestral type.

This concept of vicariism or geographical displacement is not necessarily limited to species. It is equally applicable to subspecific categories. When a large series of specimens of a single species are made available, these being collected from various localities of the range of the species, geographical variations are often detectable. These variations, morphological characters based on the criteria of geographical distribution, serve as the basis of classification of subspecific categories.

In a study of the scrophulariaceous flora of China, based on relatively abundant materials, an attempt is made to corelate criteria of geographical distribution with that of morphological characters. It is found that in most of the genera there are some species that are without apparent geographical variations and others with more or less clearcut geographical races or subspecific units. For species that are widely distributed and common, geographical variation appears to be the provalent phenomenon, and it is only because of lack of sufficently extensive material in the herbaria that such a classification of the component races has not been attempted.

Among those species that are normally accepted by plant taxonomists as such, vicarious pairs or sets are found in many of the genera. These pairs or

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sets are closely related species, morphologically essentially similar, and in their distribution occupying neighbouring but mutually exclusive areas. That these allopatric species have apparently descended from a common ancestral species are without any doubt in many cases. Whether they should or should not be considered components of a polytypic species seems to be a problem worthy of careful scrutinization in plant taxonomy.

The following is an account of the more outstanding cases of such vicarious species as observed in the Scrophulariaceae of China. Systematic treatments of the various genera will be published seperately. Not mentioned are such important genera as *Pedicularis* and *Euphrasia*. Because of their extensiveness and complexity, inquiries into their problems of distribution will be attempted separately in the future.

Mazus

In *Mazus*, the widely distributed *Mazus japonicus* (Thunb.) O. Kuntze of the warmer parts of eastern Asia is represented in western China at higher altitudes by the closely related *M. Delavayi* Bonati. *Mazus japonicus* is commonly found in moist places of the lowlands in India, Japan, south to the Philippines and Java. It is a variable plant and is in need of classifying subspecifically. The morphologicaly very similar *M. Delavayi* is also of moist habitat, but it is found at higher altitudes of about 1200–2800 meters in Yunnan and Sikang only. It is also of a more hirsute habit and with more numerous and more decumbent stems and shorter pedicels, all of them characters adapted to higher altitudes.

Verbascum

Verbascum coromendelianum (Vahl) O. Kuntze has a range extending from India and the Himalayas to China. The Chinese plant, originally considered by most authors to be the same as the Indian plant, is recognized by Merbock (in Act. Univ. Lunds n. Ser. 22 (1): 135. 1925) and Handel-Mazzatti (Symb. Sin. 7: 829. 1936) as representing a distinct variety. The Chinese variety, as compared with the Indian one, is taller, more robust and less glabrous, and is technically differentiable in the shorter pedicels, larger calyx, and larger corolla. This variety is thus geographically substituted by the typical form of the species in the Himalayas and India, a contiguous yet exclusive area.

Scrophularia

Most of the species of the genus *Scrophularia* of China are of limited

ranges. One of the most widely distributed species of the genus, *S. nodosa* L. of Europe, Siberia and North America, probably does not exist in China. In China, it is substituted by *S. ningpoensis* Hemsl., a species of fairly wide distribution in southeastern China. Morphologically it is so closely related to *S. nodosa* that Stiefelhagen (in Bot. Jahrb. 44: 461. 1910) reduces it to the synoymy of the latter. However, as Handel-Mazzetti maintains (Symb. Sin. 7: 830. 1936), and evidently with proper justification, the two are actually distinct. When compared with *S. nodosa*, *S. ningpoensis* has longer and more slender pedicels, shorter petioles, and less cordate leaf-bases.

Veronica

In *Veronica*, vicarious pairs of species are readily found in China. *Veronica Fargesii* Franch., a species of western Hupeh and eastern Szechuan, is replaced by the closely related *V. pirolaeformis* Franch. in northwestern Yunnan. The former thrives at an altitude of about 2000 meters while the latter

Fig. 1. A. The northern limit of the range of *Veronica cana*. B. The range of *V. vandelloides*.

has an altitudinal range of from 3600 to 4000 meters. It has thicker and more densely pubescent leaves.

Similarly *V. cana* Wall., a wide-spread species of eastern Asia, is paired with *V. vandelloides* Maxim. The former extends from the eastern Himalayas throagh Yunnan, Szechuan, and Hupeh to Japan. In western China, it grows at altitudes of about 2000–3000 meters. *V. vandelloides*, however, is of a more limited range, occurring only in Sikang and Kansu, north of the range of *V. cana* and growing in alpine regions at 3000–3600 meters. It is also better adpated to the alpine habitat in being a very low plant. (Fig. 1).

Veronica capitata Royle is a montane species of altitudes ranging from 2700 to 4200 meters in the eastern Himalayas, Tibet, and western China. In western China, it occurs in northwestern Yunnan and adjacent southern parts of Sikang and Szechuan respectively. Closely related to this species and morphologically very similar is *V. szechuanica* Royle, a species of about the same altitudes but of a more northerly range in Sikang, northern Szechuan, western

Fig. 2. A. The range of *Veronica capitata*. B. The range of *V. szechuanica*.

Hupeh, southern Shansi, and Kansu. This latter species, being of higher latitudes, is a more or less hairy one. (Fig. 2).

Veronica spuria L., a species of very wide distribution from Europe through continental Asia to Japan, is also widely distributed in China all way from Manchuria and Mongolia southward to Kwangtung. It inhabits various kinds of habitats, such as moist garasslands or thickets, on hills or mountains ranging from 700–3500 meters in altitudes. It is evidently a polymorphic species running into many forms varying in shape and size of the leaves. As yet there is not a sufficiently extensive assemblage of material for the breaking up of the whole complex into specific or subspecific categories. However, material now available indicates that geographical distribution evidently correlates with morphological variation. For instance, specimens from Yunnan have, on the whole, less acute leaves and shorter-pedicelled flowers, then those from other regions.

Centranthera

Centranthera, a genus of about seven species, is mainly of southeastern Asia; one of the species extends also to northern Australia. Among the widespread species, there are three that are often confused with each other taxonomically. However, when their geographical ranges are taken into consideration, their identities, based originally on morphological characters, become apparent and distinct. The three species, *C. nepalensis* D. Don, *C. cochinchinensis* (Lour.) Merr., and *C. hispida* R. Brown, are morphologically very similar. In fact Merrill (in Bull. Torrey Bot. Club 64: 595–596. 1937) treats the three as belonging to one species, *C. cochinchinensis*, with the first and the last as representing two varieties of the species. The name *C. hispida*, has even been applied by many authors to include *C. cochinchinensis* in its scope as a straight synonym, but their difference, whether as species or varieties notwithstanding, is apparent and not to be overlooked.

Centranthera cochinchinensis is distinguished, among other characters, by its yellow corolla. Its range extends from, southeastern China, Formosa, Japan, the Philippine Islands, and Java, to Sumutra. *C. hispida* and *C. nepalensis* both have purple corolla. However, they have widely separated ranges. *C. hispida* is found in eastern and northern Australia and New Guinea, that is, south of the range of *C. cochinchinensis*. *C. nepalensis* occurs from the western through the eastern Himalayas to Yunnan and Hupeh in China, a range entirely in the northwest of *C. cochinchinensis*. The three species, in addition to their

color of the corolla, can also be distiguished from each other by other morphological characters. Their altitudinal ranges are also different. *C. nepalensis*, the northernmost species, is essentially a montane form, occuring at altitudes of about 100–1500 meters. *C. cochinchinensis* is of medium altitudes at about 110–240 meters and *C. hispida* is a lowland species, at abont 10–30 meters, rarely to 400 meters.

The three species are appanently closely related, yet they are sufficiently distinct in their morphological character, geographical ranges, and altitudinal preferences to be recognized as distinct entities taxonomically. It is especially interesting to note that their ranges, though wide in all cases, are close, yet mutually exlcusive.

Melampyrum

The genus *Melampyrum* itself is a natural genus, its species all show very close similarities in habits, leaves, flowers and fruits. However, because of lack of sharp and distinctive characters among the various species in the different parts of the plants, the component species are very difficult to delimit. Consequently various authors have markedly different views on the interpretation of the species, especially with regard to eastern Asiatic ones. As a result, a very complex and burdensome synonymy is accumulated.

The genus has been monographed by Beauverd in 1916 (in Mem. Soc. Phys. Hist. Nat. Geneve 38: 291–657, f. 1–31. 1916) and again by Soo in 1925–26 (in Rep. Sp. Nov. 23: 159–176, 1926, 385–397. 1927, 24: 127–193, pl. 39–41. 1927). The latter author also treats especially the eastern Asiatic species in a separate paper (in Journ. Bot. Brit. & For. 65: 138–145. 1927). Handel-Mazzetti's treatment of the Chinese species in 1936 is the latest (Symb. Sin. 7: 843–848. 1936). These three authors differ considerably in their interpretation of the various species and their limits. Handel-Mazzetti's treatment, however, is more satisfactory, and this is especially true when we analyze the various characters of the plants in association with their geographical distribution.

Handel-Mazzetti recognizes four species in China. He notes, however, intermediate forms between the species are very frequent. Of the four species, *M. obtusifolium* Bonati is known from the original collection only. The type is from Hupeh. Its identity as a distinct species is somewhat doutful and it may prove to be identical with *M. Esquirolii* (Lev. & Vant.) Hand.-Mazz. *M. Klebelsbergianum* Soo is distinguished by its nearly entire bracts and narrower and smaller leaves. This is a species confined to southwestern China in

northern Yunnan and ajacents parts of Sikang and Kweichow. It grows at altitudes of about 2800 to 3600 meters, of higher elevations than other Chinese species. The species is most abundant in northwestern Yunnan, and becoming less common in the outer ranges. Also the plants from northwestern Yunnan are more distinct and readily recognized, while those from Kweichow, in the eastern part of the range of the species and closer to the ranges of the other species, exhibit intermediate characters between this and the other species.

Melampyrum Esquirolii and *M. roseum* Maxim. differ from the former in the usually many awn-dentate bracts and broader, larger leaves. *M. Esquirolii* is of central, eastern, and southern China, occupying an area more or less in between the other two species; while *M. roseum* is of easternand northwestern China, farthest from *M. Klebelsbergianum*. The bracts of *M. Esquirolii* has shorter awns, and those of *M. Klebelsbergianum* has longer ones. Thus geographically, this relatively important diagnostic character among the species shows parallel and gradual manisfestation from the southwest toward the northeast.

Among the three species, *M. Esquirolii* is of the widest distribution. It is found all over northern, eastern, central and southern China at altitudes of 500–1800 meters. It has been collected in Shansi and Hopei in the north, Hupeh, Hunan, and Kiangsi in central China, Shangtung, Anhwei, and Chekiang in the east, and Fukien, Kwangtung, and Kwangsi in the south. Intergrading forms between this and other species appear to be common especially in central China. In some plants the awns on the bracts are either very few or may even absent, approaching closely the condition in *M. Klebelsbergianum*. But these plants can still be distinguished from the latter by their larger and broader leaves and bracts.

Melampyrum roseum occurs at slightly lower elevations, at 100–1500 meters. It is found in Manchuria and southward to Honan in central China, and Anhwei and Chekiang in eastern China. The plants from Manchuria are distinct, while transitional forms to *M. Esquirolii* are found only in eastern and central China. Some of these plants are of equal propriety to be placed in *M. Esquirolii* taxonomically.

The Chinese species of *Melampyrum*, therefore, in spite of their fluid taxonomic characters, can be assembled into separate units by correlating morphological characters with geographical ranges. Before we have data regarding their reproduction and hybridity, it is largely a matter of opinion whether these should be entitled specific rank or be relegated into subspecies or varieties of

subspecies as Beauverd does. It is clear, however, that there are three groups that occur at different parts of the country, their ranges distinct or at places overlapping, and their intergrading forms appearing only near the margins of their ranges or in overlapping areas. (Fig. 3).

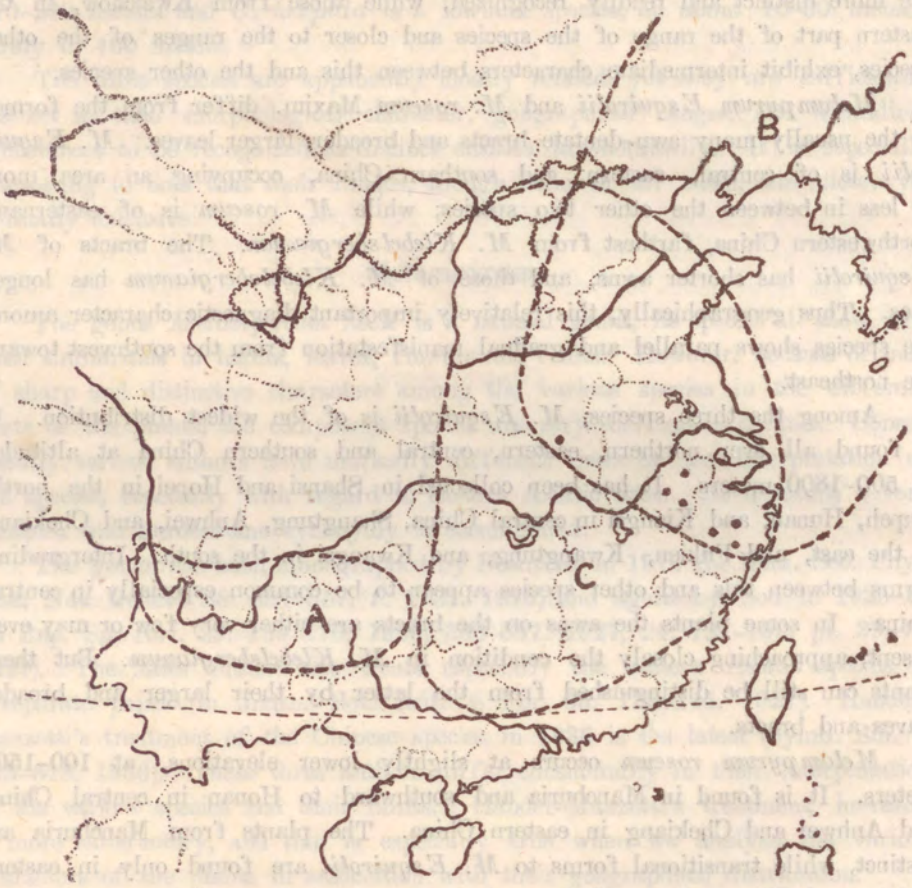

Fig. 3. The ranges of (A) *Melampyrum Klebelsbergianum*, (B) *M. roseum* and (C) *M. Esquirolii* Dots indicate intergading forms.

Phtheirospermum

The genus *Phtheirospermum* is composed of four species, two in the Himalayas and two in China, one of the last two extending also to Japan. One of the Chinese species, *Ph. chinense* Bunge, a species with pinnatifid leaves,

red corolla, and glabrous anthers, is widely distributed in eastern Asia. It occurs from Shensi, Shansi, Hopei, and Manchuria in the north to Japan in the east, Kwangtung in the south, and Szechuan, Sikang, and Yunan in the west. In the latter regions, it may ascend to altitudes of 1600 to 3000 meters, but there it is not as abundant as and is apparently gradually replaced by *Ph. tenuisectum* Bureau & Franch. The latter has more dissected leaves, a yellow corolla, and densely anthers. It is found on mountain slopes at altitudes of 2500 to 3000 meters from the eastern Himalayas in the Chumbi Valley and southern Tibet to northern Yunnan and eastern Sikang. In northern Yunnan and eastern Sikang, its range overlaps with that of *Ph. chinense*, but the latter

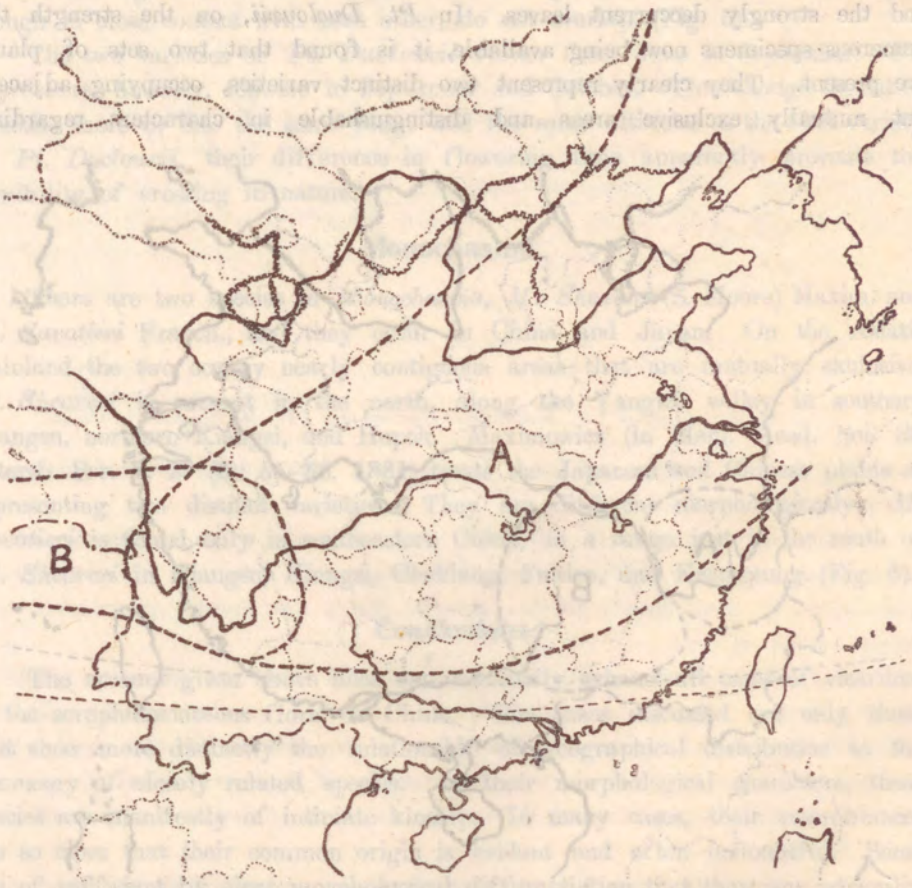

Fig. 4. The ranges of (A) *Phtheirospermum chinense* and (B) *Ph. tenuisectum*.

is much less abundant. This widely distributed species of eastern Asia is thus gradually replaced by the more successful montane species *Ph. tenuisectum* in the Sino-Himalayan and eastern Himalayan regions. (Fig. 4).

Pterygiella

In *Pterygiella* there are two species, *Pt. nigrescens* Oliv. and *Pt. Duclouxii* Franch. The former is a finely puberulous species, located only in Yunnan and adjacent southern Sikang, at an altitude of about 2100 meters. The latter is a glabrous or glabrescent to sparsely pubescent species, and is technically distinguishable from the former by the filaments which are pubescent at base and the strongly decurrent leaves. In *Pt. Duclouxii*, on the strength the numerous specimens now being available, it is found that two sets of plants are present. They clearly represent two distinct varieties, occupying adjacent but mutually exclusive areas and distinguishable in characters regarding

Fig. 5. The vicarious areas of the two varieties of *Ptorgiella Duclouxii*.

pubescence, leaf-shape, and leaf-size. The typical form of the species, a glabrous plant with long linear-lanceolate leaves, which are 2–5 cm. in length and with long acuminate apices and glabrous calyx, has a range approximately corresponds with that of *Pt. nigrescens*. It is found in northwestern Yunnan and southern Sikang on mountain slopes at altitudes of 1400–2800 meters. Another variety has a sparsely pubescent habit, with shorter linear leaves of about 1–2 cm. long and with short-acuminate apices and sparsely pubescent calyx, and is found at comparative but slightly lower altitudes in an area that is immediately to the east of the former, in eastern Yunnan, Kweichow, and western Kwangsi. Both varieties are of the high altitudes, but their ranges, though in close contact with each other, do not overlap. (Fig. 5).

The two varieties of *Pt. Duclouxii* flower from June to September. *Pt. nigrescens*, however, flowers in September and October. Thus though the latter inhabits more or less the same range and the same altitudes as the first variety of *Pt. Duclouxii*, their difference in flowering time apparently prevents the possibility of crossing in nature.

Monochasma

There are two species in *Monochasma*, *M. Sheareri* (S. Moore) Maxim. and *M. Savatieri* Franch., and they occur in China and Japan. On the Asiatic mainland the two occupy nearly contiguous areas that are mutually exclusive. *M. Sheareri* is present in the north, along the Yangtze valley in southern Kiangsu, northern Kiangsi, and Hupeh. Maximowicz (in Mem. Acad. Sci. St. Petersb. Ser. 7. 29 (3): 55–58. 1881) treats the Japanese and Chinese plants as representing two distinct varieties. They are different morphologically. *M. Savatieri* is found only in southeastern China, in a range just in the south of *M. Sheareri* in Kiangsu, Kiangsi, Chekiang, Fukien, and Kwangtung. (Fig. 6).

Conclusions

The account given above does not necessarily exhaust all cases of vicariism in the scrophulariaceous flora of China. The cases discussed are only those that show more distinctly the relationship of geographical distribution to the taxonomy of closely related species. In their morphological characters, these species are manifestly of intimate kinship. In many cases, their resemblances are so close that their common origin is evident and often undoubtful. Some are of sufficient by clear morphological differentiation that they are generally recognized as distinct species. Others, of less marked differences, are reckoned,

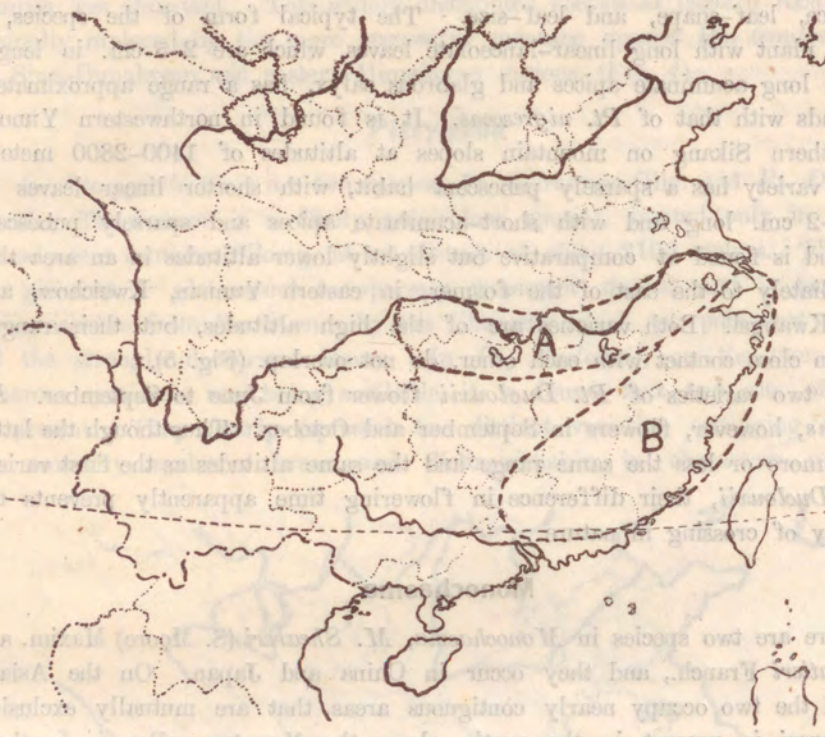

Fig. 6. The ranges of (A) *Monochasma Shearei* and (B) *M. Savatieri* in China.

according to the practice of most taxonomists, into subspecific categories, as subspecios or varieties.

It is not the purpose of this paper to go into the concept of species or the relative merits of the diffrent subspecific categories. But from the geographical distribution of these closely related species, there are several phenomena that seems worthy of note.

Some of the forms occupy wider ranges, and these are generally plants of lower altitudes. A closely related form, the other member of the vicarious pair, often occurs at higher altitudes either in the west or in the north. The northern or higher altitudinal form is generally of a mere limited range, and aside from other morphological differences, is often of lower stature or of more hairy habit.

Those vicarious forms that are taxonomically recognized as species by most authors generally occupy distinct and adjacent but at times partially overlapping

ranges. Whenever intergrading forms do occur these are usually present in these overlapping areas or toward that part of the periphery of their respective ranges that comes into contact with the ranges of other related forms.

In species that can be differentiated into subspecific categories, the different components of a species nearly always occupy contiguous but mutually exlcusive areas. Intergrading forms are frequently observed, and these also occur near the periphery of their ranges in continuation with the areas of the other forms of the same species.

The above study serves to show that in the geographical distribution of the scrophulariaceous plants of China, vicariism seems to be a common phenomenon. A species may be substituted or represented by a closely related species in an adjacent but usually mutually exclusive area. Also species, those of polymorphic nature, can often be subjected to subspecific differentiation on a geographical basis. These geographical races are usually distinguishable by morphological differences. Thus the advantage of making taxonomic studies of plants by means of a geographical approach is clearly indicated. The classification of plants will greatly benifit by the adoption of a geographical approach to the interpretation of interspecific and intraspecific relationships.

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