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THE DISTRIBUTION OF RHODODENDRON SUBGENUS HYMENANTHES WITH SPECIAL REFERENCE TO YUNNAN (W CHINA)

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ABSTRACT. The distribution patterns of the taxa in *Rhododendron* subgenus *Hymenanthes* are discussed. The main centre of distribution that extends from NW India along the Himalayan Mountain Chain to South and East China is subdivided into 7 major zones and 33 areas. These reflect disjunctions in the distributions of the taxa. Migration routes and climatic differences are suggested as explanations for these discontinuities with special reference to Yunnan Province in West China. A possible link between evolutionary trends within subgen. *Hymenanthes* and the present-day distribution of some of the subsections is proposed.

The distribution patterns of the taxa in the genus *Rhododendron* are important in that they can confirm the relative importance of morphological differences in some instances where there may be doubt. This is particularly important below the level of the species when a geographical subspecies concept is used. Where the differences between two or more recognizable taxa are such that the recognition of separate species is not justified then, if these differences are correlated with at least partial geographical discontinuity, subspecies are used for the taxa. If the taxa occupy the same geographical range they are then considered to be varieties. At the other end of the scale, there are one or two instances where the distribution of individual species may be of assistance in assigning them to a subsection or section.

Distribution patterns may also give useful clues when considering possible migration routes and they may in turn be relevant when considering the affinities of the infra-generic categories. Furthermore, they may also indicate the physical and climatic factors that limit the distributions of the individual species and subspecies.

The genus *Rhododendron* has two major centres of distribution. The first is in tropical SE Asia where perhaps 300 species occur, more than 95% of which belong to sect. *Vireya* in subgen. *Rhododendron*. The second runs along the Himalayan Mountain Chain from NW India to W China and extends eastwards into Sichuan Province and adjoining provinces in C China. This is where the majority of the remaining 165 species of subgen. *Rhododendron* occur and it is also the centre of distribution for the 240 species that comprise subgen. *Hymenanthes*, the subject of this paper. Of the 23 subsections in subgenus *Hymenanthes* only subsect. *Pontica* occurs exclusively outside this centre of distribution. The species of this subsection occur in Japan, Soviet Eastern Asia, the extreme NE part of China, the USA and Caucasia, with an extension into SW Europe. Some species of subsect. *Irrorata* come from SE Asia (Vietnam, Malaya and Indonesia) but otherwise almost all of the remaining species occur within the boundaries of the second centre of distribution which is

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the area under consideration in this paper. The justification for paying special attention to Yunnan Province in Western China are: (1) the rhododendrons of Yunnan are relatively well-known through the extensive collections of herbarium material; (2) Yunnan probably has the richest indigenous flora of any area of comparable size, certainly within the boundaries of China—this being reflected by the large number of species of *Rhododendron* that occur within its confines; (3) our more detailed knowledge of the Yunnan rhododendrons allows us to make a more precise analysis of the distribution patterns than would be possible for any other comparable area.

The Himalayan–Chinese centre of distribution has been divided into 33 areas grouped into 7 zones to facilitate the analysis of the distribution patterns. The area boundaries have been drawn to correspond with common boundaries or areas of minor overlap for a group of taxa. Clearly, the larger the number of taxa with roughly similar distributions, the more significant the area that summarizes those distributions. The 33 areas (as shown in Figs 1 & 2) have been assigned to the zones as follows:

Zone A—W Indo-Himalayas (N India, East to Bengal, Nepal, Sikkim, Bhutan, S Xizang (Tibet); areas 1–3.

Zone B—E Indo-Himalayas (NE India, SE Xizang); areas 4–8, 25 & 26.

Zone C—Sino-Himalayas (W China, from SE Xizang and W Yunnan to SW Sichuan; NE Burma); areas 9–16.

Zone D—W China (SW Sichuan, C Yunnan (Kunming to Cushong); areas 17–19.

Zone E—China (NE Yunnan, C Sichuan); areas 20–23 & 27.

Zone F—China (N Sichuan, Gansu, E Qinghai, Shaansi, Hubei); areas 28 & 29.

Zone G—S & E China including SE Yunnan; areas 30–33.

It is noted that area 24 has been deleted in line with the treatment in the monograph on subgenus *Hymenanthes* (Chamberlain, 1982).

The zones and areas are not of equal size and tend to be smaller where the larger concentration of taxa occur. The significance of these zones may be illustrated by some of the taxa that are endemic to individual zones. For distribution maps of these taxa see Chamberlain (1982).

R. barbatum and *R. campanulatum* are largely restricted to area 1. A greater concentration of species is however restricted to areas 2 & 3, a region extending from C & E Nepal through Sikkim and N Bengal to Bhutan. *R. fulgens* is a good example of a species with this distribution. *R. arboreum* subsp. *arboreum* and subsp. *cinnamomeum* have a similar distribution. *R. niveum* and *R. succothii* are further examples of species limited to these two areas though both have more restricted distributions.

The richest region in zone B is the area in S Xizang around the gorges on the Tsangpo River (Zangbo Jiang) and several species have their centres of distribution in this region; e.g. *R. hirtipes* and *R. venator,* both well-known in cultivation. *R. cerasinum* has an essentially similar distribution but there are scattered records to the east in NE India and Upper Burma. Several of the endemics of zone B have very restricted distributions as, for instance, *R. subansiriense* which is known only from the Subansiri District of Arunachal Pradesh in NE India, and *R. macabeanum* from S Assam. Zone C includes the greater part of W

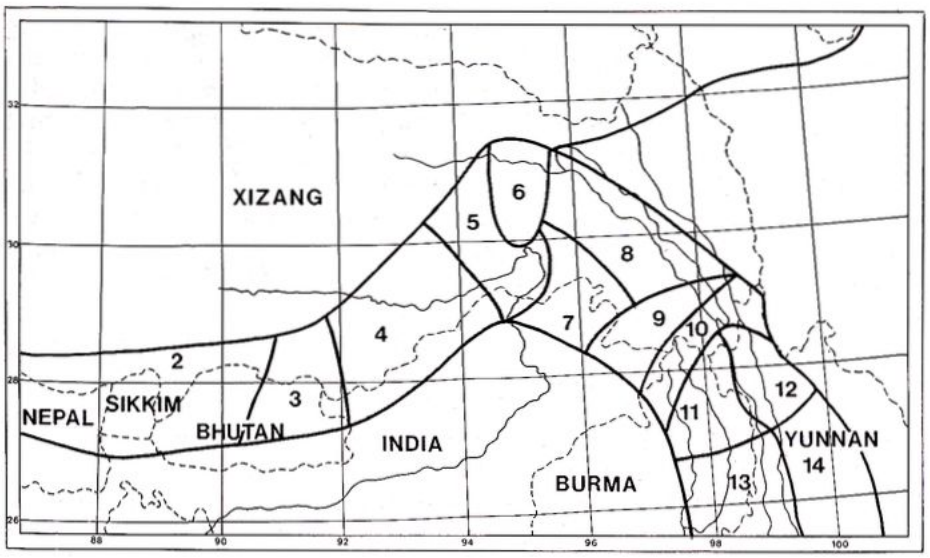

FIG. 1. Map covering the region from C Nepal to W Yunnan to show the Areas used to summarize the distributions of *Rhododendron* subgen. *Hymenanthes*.

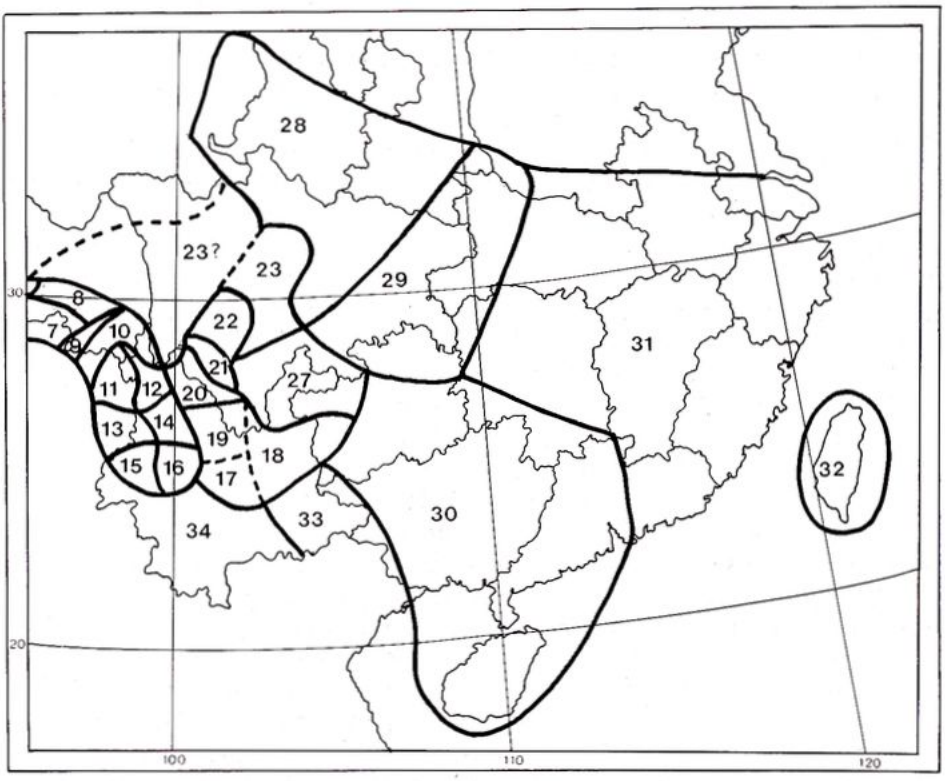

FIG. 2. Map covering China/NE Burma to show the Areas (bold lines) used to summarize the distribution of *Rhododendron* subgen. *Hymenanthes*.

Yunnan and will be discussed more fully later. Zone D is the least clearly defined of the zones and has obvious links with zones C & E. Of the species endemic to zone D, *R. aberconwayi* is probably the best known. The endemic species of *Rhododendron* from zone E include several that are centred on Mt Emei and adjacent mountains in W Sichuan Province. Of these, *R. hemsleyanum* and *R. williamsianum* are apparently the most restricted; the former is known only from Mt Emei. The species endemic to zone E are however usually more widespread and occur in a region extending from WC Sichuan to NE Yunnan. *R. davidii, R. calophytum* and *R. strigillosum* are examples of species with this distribution.

Species endemic to area 28 in zone F include *R. rufum. R. przewalskii* is also centred here. A larger group of species, including *R. auriculatum* and *R. praevernum* occur only in area 29 (E Sichuan and W. Hubei).

Zone G stretches across S & E China; *R. simiarum* illustrates one of the species endemic to this area. There is also a group of species endemic to Taiwan, of which *R. morii, R. pachysanthum* and *R. pseudochrysanthum* are examples.

Just over 75% of the taxa that have been mapped as separate entities are either totally or almost totally restricted to a single zone. The 25% that occur in two or more zones are interesting in that their distributions may indicate migration routes. This will be discussed briefly later.

The distribution patterns of the rhododendrons of Yunnan are important and instructive because that province includes parts of four zones (zones C, D, E & G). This undoubtedly reflects the diversity of topography and the wide range in climatic conditions. The richest region in numbers of species includes areas 10, 11 & 12 (NW Yunnan). If the adjacent parts of NE Burma and SE Xizang are included, then there are no less than 35 taxa that are endemic to the region. *R. crinigerum, R. citriniflorum* and *R. eclecteum* are three of these. A number of species occurring in this region, for example *R. proteoides,* have a wider distribution extending eastwards into zone E in SW Sichuan, in particular to the region around Muli (areas 20–22).

Within zone E there appears to be a sharp dividing line along or near the Yalong River in SW Sichuan that divides areas 23 & 27. Several species occur to the east of this boundary and some of these reach the NE tip of Yunnan. Of these the distribution of *R. davidii* has already been mentioned. A further example may be seen in the two closely allied species *R. denudatum* and *R. floribundum.* Thus it may be seen that the rhododendron flora of NE Yunnan has more in common with that of WC Sichuan, in particular with the region around Mt Emei, than it does with NW Yunnan. Along the western border of Yunnan where it adjoins NE Burma there is another group of species with a relatively narrow distribution. These are more or less restricted to areas 13 & 15 in zone C and include *R. araiophyllum* and *R. meddianum. R. tanastylum* has a similar distribution but may also occur in area 9 of zone B. A few species with a distribution centred in W Yunnan also occur to the east in the region around Cangshan near Dali, as is illustrated by *R. dichroanthum.* It will be seen that this species has differentiated into recognizable subspecies as it has apparently migrated along a line running north/south along the valleys of the Mekong, the Salween and perhaps the N'Maikha

Rivers. This same migration route may also be implied from the distribution of *R. callimorphum* and *R. haematodes*.

The region around the Cangshan is interesting as the mountains are more or less isolated from the Sino-Himalayan Chain and it is apparently the meeting place for several different assemblages of species showing markedly different distributions. There are a few species that are practically endemic to Cangshan, e.g. *R. cyanocarpum*. The connections with W Yunnan have already been demonstrated. There are also two taxa, *R. balfourianum* and *R. roxieanum* var. *cucullatum*, that are centred in NW Yunnan and SW Sichuan but just reach Cangshan. Otherwise, their nearest stations are around Lichiang in the bend of the Junsha Jiang (River Yangtse). *R. lacteum*, a species with its centre of distribution on the Cangshan, but also with an extension in range to the North-West, also occurs in N Yunnan (Wumeng Mountains). This distribution implies that there have been migration routes in the past across N Yunnan for a plant that does not now occur below 3500m. Perhaps the most remarkable distribution is that of *R. irroratum* with three intergrading subspecies that extend from NW Yunnan through the Cangshan and N & E Yunnan to Indo-China and Sumatra.

Zone D is not noted for its endemics though one species, *R. aberconwayi*, apparently has a very restricted distribution around Luo Xue and Fuming in N Yunnan, within the boundaries of this area. Its closest ally appears to be *R. annae*, a species that is largely confined to W Yunnan though with one surprising outlying station in SW Guizhou.

There is a small group of species that are restricted to S Yunnan and adjacent parts of Vietnam. One of these, *R. mengtszense*, has affinities with *R. brevinerve*, a species from S China. *R. sinofalconeri* is another example. These distributions seem to fit better with those for species from S & E China and for this reason we have included this part of S Yunnan in zone G.

So far the distribution pattern of individual species and subspecies have been discussed. It is however instructive to investigate the distributions of whole subsections, though, as might be expected, the results are not as clear-cut. These are summarized in the *Hymenanthes* monograph (Chamberlain, 1982, pp. 465, 466 & 477). From this analysis it may be seen that subsects *Campanulata, Lanata* and *Fulgensia* are exclusively Indo-Himalayan groups. In contrast, subsect. *Maculifera* is restricted to C & E China. Subsect. *Argyrophylla* is also similarly restricted, apart from *R. coryanum* (a species from NW Yunnan) which is unique in this subsection in having a glabrous ovary. Indeed, it may be more closely allied to *R. uvarifolium* in subsect. *Fulva*, a species that occurs in zones B & C and with which there is a better fit when the distributions are considered. Similarly, the placing of the anomalous *R. griffithianum*, a species restricted to zones A & B, in subsect. *Fortunea*, a subsection that is otherwise only known further east, should perhaps be also questioned.

Seventy-five per cent of the taxa that make up the extremely rich rhododendron flora of NW Yunnan belong to just three subsections. Subsects. *Neriiflora* and *Selensia* are centred in this region, while subsect. *Taliensia* has a second centre of distribution in WC & E Sichuan. The Sichuan species of the last mentioned are generally more dissimilar from

one-another and more well-defined than those from NW Yunnan. Furthermore, this pattern also seems to be true for species in other subsections. This may imply that the process of speciation has been more recent in NW Yunnan but it may also be an artifact due to the greater number of specimens that are available from NW Yunnan. On a smaller scale there is a restricted area around Weixi in NW Yunnan where there is some evidence that hybrid swarms exist involving several species. *R.* ×*erythrocalyx* (a hybrid of *R. wardii* and *R. selense*), hybrids of *R. campylocarpum* and possibly also of *R. semnoides* and *R. fulvum* all occur in this area. The implication is that there is recent hybridization in an area that is to the taxonomist a zone of confusion as the species' boundaries appear to be less distinct. It is difficult to predict whether hybridization is an important factor in the process of speciation in rhododendrons but it obviously has some part to play.

It is perhaps unjustified to speculate as to which of the subsections are primitive and which are advanced, particularly as it is not always clear how the subsections are related to one-another. However, subsect. *Maculifera* does have several features that might be considered primitive, especially in the form of its indumentum. In particular, two hair types, the folioliferous and the stellate hair, which have a relatively simple form, are found in this subsection which has a centre of distribution in C & S China and Taiwan and is not represented at all in W Yunnan or the Indo-Himalayas. In contrast, the subsections with the more complex fasciculate or ramiform hairs, including subsects. *Taliensia, Neriiflora, Fulgensia* and *Campanulata,* are almost entirely restricted to, or are at least well represented in W Yunnan or the Indo-Himalayas. Subsects. *Fortunea* and *Auriculata* also have a centre of distribution in C & S China but, since the majority of the species are entirely glabrous, it is less certain whether they should be treated as advanced or primitive. For a further discussion of the hair types in subgen. *Hymenanthes* reference should be made to Cowan (1950) and Chamberlain (1982, p. 215). From this evidence it is tentatively suggested that there is an area of diversity in at least some of the primitive subsections of subgen. *Hymenanthes* in C & S China at the present time. It will be noted that this region is outside the Himalayan Range.

The species of subgen. *Hymenanthes* are for the most part restricted to the cool temperate montane regions, and many have a relatively narrow altitudinal range. Indeed, altitude is a more important limiting factor than gross climatic differences. Apart from the obvious correlation between the distribution of certain species and the occurrence of suitably high mountains, the geographical distribution patterns that have been discussed do not reflect altitudinal zonation. Mountains can markedly influence climate on a very local scale, quite apart from the influence of altitude. They can therefore be expected to distort macro-climatic patterns. Even so, certain climatic trends do have a bearing on the distribution patterns. For instance, the colder winters and lower rainfall of zone F correlate reasonably well with the distribution of the endemic species. At the other extreme, the warmer winters and higher rainfall are almost certainly factors influencing the boundary between areas 13 & 15 and 14 & 16.

SUMMARY

1. It is possible to divide the main area of distribution of *Rhododendron* subgenus *Hymenanthes* into areas and zones.

2. The boundaries of the zones are somewhat imprecise though over 75% of the taxa are endemic to a single zone.

3. In some instances the boundaries appear to be the result of climatic differences. However, the species are largely montane and significant local climatic variation is to be expected in mountainous regions. This will tend to obscure possible correlations between species' distributions and large scale differences in climate.

4. The patterns of distribution of the rhododendrons of Yunnan Province in W China are particularly complex. Certain migration routes may be postulated from these distributions. The concentration of taxa in NW Yunnan is probably the result of recent speciation in just three subsections.

5. It is suggested that the taxa in NW Yunnan intergrade with one another to a greater extent than do those from India and other regions of China. While this may reflect more intensive collecting, it is possible that NW Yunnan is an area of active speciation.

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QUESTIONS

W. R. Philipson: Subsect. *Lapponica* (subgen. *Rhododendron*) is certainly centred in W & NW Yunnan and has spread along the Himalayas while one or two species have escaped northwards into Siberia and around the Arctic. We generally had no difficulties in defining geographical or species' limits for the species of this subsection; we treated about 3% of the specimens as hybrids. However, in the area around Weixi in NW Yunnan, precisely that defined by Chamberlain as a zone of confusion, there were three species that seemed to blend into one another. It was the only area that we came across where there was a hybrid swarm.

With regard to the primitive type in subgen. *Hymenanthes* I hope to present evidence in my paper to show that both subgen. *Rhododendron* and *Hymenanthes* are groups derived from one or other of the subgenera in the so-called 'Azalea Complex'.

Chamberlain: On the last point I am not proposing that the elepidotes come from the lepidotes, only that if there is a common origin then one of the possibly primitive subsections, such as subsect. *Fortunea*, is closer to it.

F. E. Bump: Have you considered the effect of soil pH on distribution patterns?

Chamberlain: This is not straightforward. I have seen *R. fastigiatum* growing in magnesian limestone-based soil at pH 8.5. It is reported that rhododendrons can tolerate a relatively high pH so long as the magnesium level is relatively high. I have not considered distributions with respect to soil type. In an area of perhaps 2000 by 300 miles it would be impossible to make correlations between distribution and soil type. However, I agree that there may be limiting factors that are edaphic.

Stevens: I have two questions: (1) do you have a general age for subgen. *Hymenanthes?*; (2) do you find the most closely related species in a single area, in adjacent areas or in areas that are not adjacent?
Chamberlain: On the first point I do not wish to comment. On the second, there is evidence in certain subsections that they are speciating locally. For instance 90% of the species in subsect. *Neriiflora* occur in a very restricted area in zone C. Again, subsect. *Argyrophylla* is almost entirely restricted to an area outside the main centre of distribution for subgen. *Hymenanthes*. In subsect. *Taliensia* the taxonomically critical groups of species occur in N & NW Yunnan which may indicate a group of closely related species evolving locally.
Kores: To what extent are the distributions of rhododendrons influenced by man in China?
Chamberlain: Not yet. There is devastation on a local scale; in the Cangshan Range there is perhaps 10% of the natural vegetation left. The Chinese are aware of the problem and are trying to solve them before it is too late.
M. Paton: Would we expect migration to proceed with the flow down river complexes?
Chamberlain: We are looking at species that may be 1000m above the river levels but they could have been much lower during a colder phase or higher during a warmer phase. Migration up and down the sides of the river valleys during the climatic cycles associated with the Ice Ages may have brought species together with consequential hybridization. This may be just as important a factor. Water movement probably has little to do with migration.
G. Ring: What have you done to tie up the age of the species with topographical evolution?
Chamberlain: Nothing. The pollen is uniform. Therefore pollen analysis is not helpful. We have virtually no fossil evidence available.
de Spoelberch: Could the Chinese raise some of the species artificially to find what are the factors limiting their distribution?
Chamberlain: This may become a practical proposition. The Kunming Botanical Institute are planning to establish a high-level garden for this sort of study.
Stevens: Do we have evidence for distributions during the quaternary period?
Chamberlain: There is virtually nothing.
R. Shaw: Are the temperature and rainfall patterns based on accurate information?
Chamberlain: I guess that the information is relatively accurate.