D. F. CHAMBERLAIN* & Frank DOLESHY**: Japanese members of *Rhododendron* subsection Pontica: Distribution and classification

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This paper complements Professor Hara's new treatment of *Rhododendron* species in Subsection Pontica. Our specific purposes are to describe the distribution of these plants, explain the factors that appear to account for their distribution, and discuss the relationship between distribution and classification. The first-hand field observations have been the work of one author, Frank Doleshy, together with his wife, Catherine Doleshy. Although the latter did not elect to be listed as coauthor of this paper, she has had much to do with its readability. Together, they have visited Japan six times, in autumn 1965, autumn 1967, spring 1969, spring 1970, autumn 1971, and autumn 1983.

So that readers will not flounder in plant names new to them, we start with the following table showing various sets of names for the *"metternichii"* rhododendrons, together with *R. makinoi*. Professor Hara's names, used in this paper, are at the right, opposite three columns of older names which may include ones the reader finds familiar. For author citations, reference should be made to the recent Hara paper (1986).

Stevenson et al. 1947	Chamberlain 1982	Yamazaki 1964	Hara 1986
	R. japonicum	*R. metternichii*	*R. degronianum*
R. degronianum	var. *pentamerum*	ssp. *pentamerum*	ssp. *degronianum*
R. metternichii	var. *japonicum*	ssp. *metternichii* var. *metternichii* var. *hondoense* var. *kyomaruense* f. *amagianum* (added 1981)	ssp. *heptamerum* var. *heptamerum* var. *hondoense* var. *kyomaruense* f. *amagianum*
	R. yakushimanum	ssp. *yakushimanum*	ssp. *yakushimanum*
R. yakushimanum	ssp. *yakushimanum*	var. *yakushimanum* var. *intermedium*	var. *yakushimanum* var. *intermedium*
R. makinoi	ssp. *makinoi*	*R. makinoi*	*R. makinoi*

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In the following key, we emphasize vegetative rather than floral characteristics. Also, to facilitate the use of this key as a reference list, we augment it with descriptive and geographical statements.

1. Leaf linear-oblanceolate, at least 7 times as long as its own width; undersurface coated with thick beige or brown indumentum. (Honshu: Aichi and Shizuoka Prefectures) ..... *R. makinoi*

1. Leaf broader; indumentum equally thick or less thick.

2. Indumentum thin and appressed or nearly absent; usually with reflective sheen or highlights suggesting a smooth-faced fabric such as satin. Large shrubs, often >3 m tall.

3. Corolla generally 7-lobed. (Throughout various mountain ranges of Shikoku and SW Honshu) ..... *R. degronianum* var. *hondoense*

3. Corolla generally 5(-6) lobed. (Honshu: Izu Peninsula and Akaishi Mtns.) ..... *R. degronianum* var. *kyomaruense*

Forma *amagianum* (described from Izu Peninsula specimen) is distinguished by young leaves with white tomentum.

2. Indumentum thin or thick, with a cottony, velvety, or spongy surface lacking a reflective sheen. Large or small shrubs.

4. Corolla generally 7-lobed, occasionally with more lobes; indumentum varying from thin to velvety. Large shrubs often >2 m tall. (Kyushu, S. Shikoku, Kii Peninsula) ..... *R. degronianum* var. *heptamerum*

4. Corolla generally 5-lobed, with additional lobes fairly common. Indumentum velvety, heavily felted or spongy. Shrubs usually <2 m tall.

5. Indumentum on blade and current-year stem but sparse or absent on mid-rib and year-old stem. Corolla funnel-shape. (Honshu NE of Fossa Magna) ..... *R. degronianum* subsp. *degronianum*

5. Indumentum usually on midrib and year-old stem as well as on blade and current-year stem. Corolla campanulate, with broad base and conspicuously cylindrical tube. (Yaku Island) ..... *R. degronianum* subsp. *yakushimanum*

Var. *intermedium* is distinguished by indumentum composed of short hairs, light-colored or sparse (Author's translation). Described as occurring below 1500 m.

Outside Japan, the distribution and morphological characters of these taxa seem to have been poorly understood. This can be partly attributed to scarcities of herbarium material and translated botanical literature. Also, a significant amount of confusion has evidently stemmed from Siebold's description and dried material of *R. metternichii*. No source locality is given for the 1829 specimen which the Rijksherbarium, Leiden, preserves as the type of this species. However, Siebold in his 1835 discussion stated that it occurs in the alps of northern Japan as well as in Nikko, "where it grows abundantly". Therefore one might suppose the Leiden specimen to be from Nikko (cf. Nitzelius 1961, 152). But Maximowicz (1870, 21) seemed doubtful that Siebold's plant occurs there. In a parenthetical sentence, he raised a question about confusion with *R. brachycarpum*, and he added that Siebold's plant grows plentifully in Kyushu. Likewise, one of the present authors (Doleshy) is not aware that the distribution of this taxon extends north to Nikko; and, when examining the Leiden specimen in 1985, considered it representative of the sourthern var. *heptamerum* (although possibly from a cultivated plant which had been taken to the Nikko area). If thus treated as a southern specimen, it is not a source of confusion.

Rather than discussing the entire Pontica Subsection as a single entity, we find it more productive to group the members as follows for study:

1) The *R. degronianum* taxa and *R. makinoi*.

2) *R. brachycarpum* D. Don and *R. aureum* Georgi, with little resemblance to other Japanese Ponticas, therefore discussed separately in the latter part of this paper.

Older and newer elements among the *R. degronianum* taxa and *R. makinoi* The ages of these taxa, on the geologic time scale, are not known with any certainty. However, as a basis for our review of distribution, we establish three hypothetical age groups as follows:

—Long present: These have velvet-like, felt-like, or spongy indumentum maturing to buff or darker colors, together with (usually) 5-lobed flowers, and they are found in geographically more or less peripheral regions of Japan. The taxa are *R. degronianum* subsp. *degronianum* and subsp. *yakushimanum*, together with *R. makinoi*.

—Recent arrivals: These are two varieties of *R. degronianum* subsp. *heptamerum*, as follows: The more widespread is the usually 7-partite var. *hondoense*, of south-central Japan. With comparatively thin indumentum, usually

buff to white, it is analogous with some species in the Argyrophylla and Taliensia Subsections. However, no definite relationships with those taxa have yet been defined. The less widespread is var. *kyomaruense*, distinguished by glabrescent leaf undersurfaces and 5-part corollas but otherwise very similar to var. *hondoense*. This is found at the east end of the var. *hondoense* range, and the two taxa apparently intergrade.

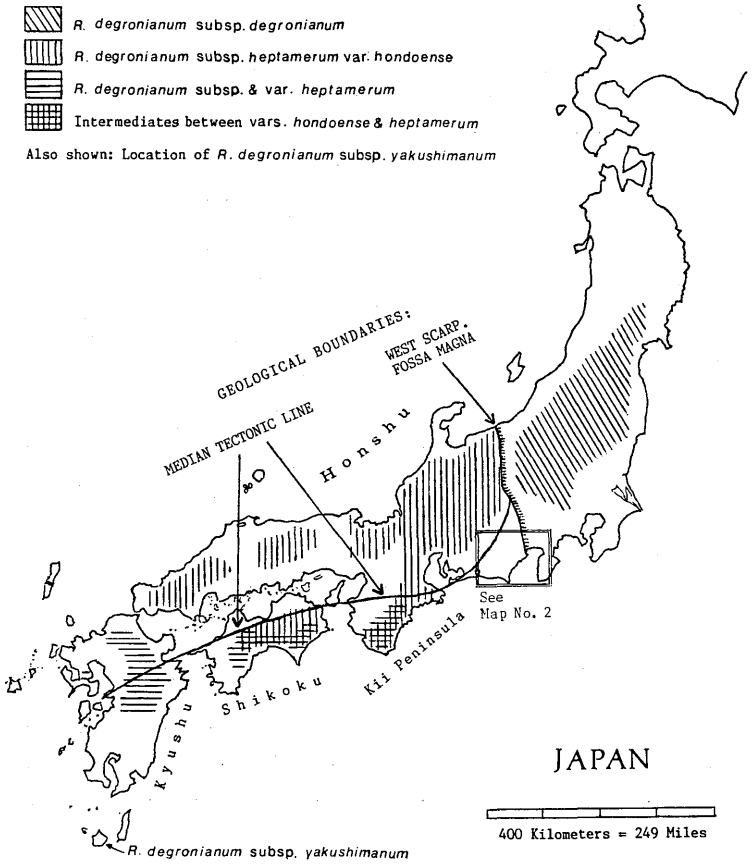

Fig. 1. Generalized distribution, the more widespread members of the *Rhododendron degronianum* group.

—The one with mixed characters: This is *R. degronianum* var. *heptamerum*, found in a band of territory across Kyushu, Shikoku, and southern Honshu (Kii Peninsula). Although the numerous individual stands vary by locality, their characters are in most respects intermediate between those of the apparently older and newer subgroups. However, flower parts are usually 7, as in var. *hondoense*—perhaps reflecting dominance of 7 over 5 parts, together with some competitive advantage conferred by the large number of parts. On the other hand, the thicker leaf indumentum often resembles that of subsp. *degronianum*. Var. *heptamerum* appears to have been the source of the *R. metternichii* type specimen at Leiden.

Corolla and seed capsule parts The general impression is that corollas and capsules consist of 5 parts in subsp. *degronianum*, subsp. *yakushimanum*, and *R. makinoi*; 7 parts in subsp. *heptamerum*, excepting var. *kyomaruense* which is distinguished by its 5-part corollas. Yet our observations, shown below, indicate variation within and between the samples for one taxon, as well as year-to-year differences and perhaps some inconsistency between corolla and seed capsule parts. Moreover, although 7-part capsules could be expected on the above-mentioned Leiden specimen, 8-part capsules are actually present. And on plants grown from far-southern var. *heptamerum* seed collected by one of the authors, both 7-part and 8-part flowers are commonly found, although one of these plants produces 11-part flowers in some years but only 7 or 8-part in other years. Therefore these counts are not infallible as taxonomic guideposts.

Despite these difficulties, our field observations, dried material and photographs indicate that flowers are somewhat less variable than capsules. Also, we have noticed many Subsect. Pontica flowers with a slightly split or slightly doubled corolla lobe, or one weak lobe, and would suggest that these correspond with extra or missing capsule sections. To sum up, the corolla and capsule counts are to be interpreted with caution but are certainly as useful as other rather indefinite taxonomic features. And, when trying to account for present-day distribution, these counts may be useful data.

Several of our more extensive counts are given in the following table, which shows as percentages the frequency of capsules or corollas with 4 parts, 5 parts, etc.

Identity and sample size (Seed capsules unless corollas are indicated):		Sections or lobes 4	5	6	7	8	9 & 10
		%	%	%	%	%	%
R. degronianum subsp. *degronianum*							
Kusatsu-Shirane, N. Honshu, 1965	Sample=75		51	31	17	1	
From same stand, 1971	Sample=100	1	79	19	1		
R. degronianum subsp. *yakushimanum*							
Yaku Island, 1600–1836 m. s. m.	Sample=94	1	72	18	9		
R. degronianum var. *kyomaruense*							
Jokojisan, Honshu	Sample=293		18	46	27	8	1
Near Sumatakyo, Honshu	Sample=130		1	51	34	14	
R. degronianum var. *kyomaruense/hondoense* intermediate							
Tsukiyosawa Pass, Honshu	Sample=52		10	38	40	8	4
R. degronianum var. *hondoense*							
Oki Island	Sample=95			13	86	0	1
Okutsu, Honshu	Sample=23			4.5	91	4.5	
R. degronianum var. *hondoense/heptamerum* intermediate							
Central Kii, Honshu	Sample=100		1	6	84	6	3
Eastern Kii, Honshu	Sample=40		2.5	2.5	95		
R. degronianum var. *heptamerum*							
Shakutake, Kyushu	Sample=166		3	13	83	0	1
Kuju Mtns., Kyushu	Sample=182			18	82		
Shiromizu-taki, Kyushu, cult., 1967	Sample=85				75	25	
Corresponding wild stand, 1967	Sample=134			1.5	94	4.5	
Corresponding wild stand, 1970 Corolla Lobes:	Sample=ca. 50	Approximations:			82.5	17.5	

As shown in this table, variation ranged from slight to moderate in the stands of *R. degronianum* vars. *heptamerum* and *hondoense*. But the results for two stands of var. *kyomaruense* indicated a wider-than-suppsed range of variation, with a preponderance of 6-chambered capsules. Therefore, although this taxon is defined as having 5-part corollas, the underlying tendency toward variation seems strong. We discuss this in a subsequent section on the origins of this taxon.

In stands of *R. degronianum* subsp. *degronianum* and subsp. *yakushimanum*, exceptions to 5-part capsules are at least moderately numerous, and the pattern of variation in these two taxa is roughly the same.

R. degronianum* subsp. *heptamerum*, excluding var. *kyomaruense Fig. 1 shows major geological boundaries and generalized *Rhododendron* distribution, and Fig. 2 shows the details of an area where the geological and the distributional boundaries converge. Correlation between these two kinds of boundaries is readily apparent and, we believe, is the key to a better understanding of relationships among the taxa.

One of the illustrated geological boundaries is the great depression separating northeastern from southwestern Japan. This depression, called the "great trench" or "Fossa Magna", is best defined by its west scarp, i.e., the conspicuous line of cliffs and mountain ridges along that edge. At the foot of the west scarp, the depression is largely a broad lowland, with inactive or active volcanoes (including Fuji) rising from its surface. The depression's east boundary is less distinct because of various topographic irregularities.

Starting from the Fossa Magna and extending southwest, the Median Tectonic Line divides Japan lengthwise into the more northerly "inner zone" and more southerly "outer zone". On geological maps, the distinction between these two zones is conspicuous because the northerly one includes much granite,

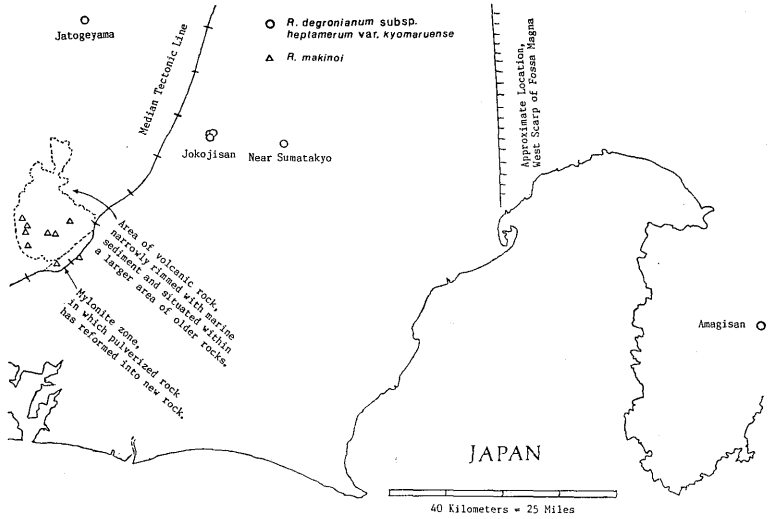

Fig. 2. Detailed distribution of *R. degronianum* subsp. *heptamerum* var. *kyomaruense* and *R. makinoi*.

while the southerly is largely sediment-derived. This has led to a recent hypothesis that the northerly zone is actually a land mass of moderate size that moved out from the Asian coast and became part of Japan. Making this hypothesis credible, the land in question would fit neatly into the Korean-Siberian coastline; moreover its geological formations resemble those of Korea and Siberia more closely than those of the adjacent Japanese territory (See Maekawa 1974, pp. 34-58). While this land mass was moving, additional formations may have accumulated along its leading edge and come to rest beside the Median Tectonic Line.

The move of this land from mainland Asia possibly began during the Upper Jurassic period (ca. 150 million years before present) and was apparently completed no earlier than the close of the Cretaceous (65 m.y.b.p.), or perhaps after the close of the Palaeogene (i.e., somewhat less than 26 m.y.b.p.). Therefore the apparently long-present group—*R. degronianum*, subsp. *degronianum* and subsp. *yakushimanum*, and *R. makinoi* (or their ancestors)—may have occurred in the preexisting lands of Japan. With arrival of the added land, their territory would probably have been pushed apart and outward, with disruptions which could account for the wide gaps in their distribution today.

Turning to the apparently newer var. *hondoense*, this taxon could have arrived in Japan either via the hypothesized land movement or else via a more or less temporary land connection. In either case, if the new arrival encountered other rhododendrons already present in Japan—such as subsp. *degronianum*, subsp. *yakushimanum* or *R. makinoi*—genetic mixing would have been likely. Yet the two modes of arrival would probably have left differing evidence behind them. If new plants arrived via a temporary land connection and hybridized with the plants already present, this process could well have left a varying series of hybrids all the way across the new plant's zone of influence. On the other hand, if the incoming plants arrived by land movement, a part of this land might today be occupied by unmixed descendants of the arriving taxon, with hybrids to be found where this taxon spread south into territory beyond the edge of the new land, or where an already-present taxon spread north into the new land.

Arrival by land movement seems more likely, in view of the following distribution (See Fig. 1):

1) Unexceptional stands of var. *hondoense*, with relatively uniform seed capsules, occur in various areas of southwestern Honshu and northern Shikoku, i.e., within the supposedly new land or close to its southern edge. These would seem to be the essentially unmixed descendants of the incoming taxon.

2) A mosaic of var. *hondoense-heptamerum* intermediates is found in, roughly, an east-west zone of Shikoku and the Kii Peninsula. This zone would seem to be an area of encounter, perhaps still unstable, where in many places the characters of the incoming taxon tend to prevail over those of an earlier-present taxon resembling today's subsp. *degronianum* or subsp. *yakushimanum*. Examples can be conveniently seen just east of Mt. Ishizuchi in Shikoku, along a "Skyline Road" which crosses the boundary between the apparently older and newer land.

3) The more or less homogeneous var. *heptamerum* appears to be the end product of the hybridizing process. Yet, even with such an origin, it seems sufficiently stabilized to be treated as a separate entity. It is distributed as follows:

(a) In Shikoku and the Kii Peninsula, some stands are interspersed with those of the intermediates while others are more isolated and usually south or west of the intermediates. Most or all the var. *heptamerum* in these two regions is within the boundary of the apparently older land.

(b) In Kyushu, var. *hondoense* and the intermediates are scarce or absent, and var. *heptamerum* extends up and down the island, crossing the boundary between apparently older and newer land.

The difference between these two modes of distribution can probably be explained by Pliocene and Quaternary (less than 12 m.y.b.p.) volcanic eruptions which covered much of northern Kyushu with lava, killing the existing plants and making way for already established stands of var. *heptamerum* to spread northward from southern Kyushu.

R. degronianum* subsp. *heptamerum* var. *kyomaruense As stated above, var. *kyomaruense* is identified by its glabrescent leaf undersurface and 5-part corolla but is otherwise similar to var. *hondoense*. Of the identifying characters, the 5-part corolla is the more useful, since thin indumentum is also found in some stands of var. *hondoense*. When working in the field, one of the authors has not been able to distinguish the two varieties on the basis of height, growth habit, or leaf size and shape (On the other hand, var. *kyomaruense*, with such

close resemblance to var. *hondoense*, is unlikely to be mistaken for subsp. *degronianum*, even though both are 5-partite).

Geographical distribution, as shown on Figs. 1 and 2, suggests two possible ways to account for var. *kyomaruense*: First, it may be a natural hybrid between var. *hondoense* and subsp. *degronianum* or their ancestors. Second, it may be a variant or relict taxon allied with var. *hondoense*, and it may have accompanied var. *hondoense* as a co-immigrant from the Asian continent.

The first suggestion is appealing because the only obvious barrier separating 5-partite var. *kyomaruense* from its supposed parent, the 5-partite subsp. *degronianum*, is the Fossa Magna depressed area. Yet this structure may be more of a barrier than the distances would indicate. In the south it is filled with Miocene and more recent sediments (Kimura 1659, Takai & Tsuchi in Takai et al. 1963) therefore may be coeval with the supposed arrival of land now to the southwest, and the surface features of these sedimentary deposits may never have been conductive to migration of Subsect. Pontica. To the north, related lowlands may have been equally a barrier.

Also, this first suggestion is subject to the following criticisms:

—Such hybridization seems unlikely to produce stands with a preponderance of 5-lobed corollas, since the late K. Wada, after a lifetime of hybridizing experiments involving Subsection Pontica, reported that 7 lobes are generally dominant over 5 (Personal communication to author). Also, if the 5-lobe character of subsp. *degronianum* had some way become established southwest of the Fossa Magna, it is difficult to see why this character would now be the only visible evidence of subsp. *degronianum* ancestry.

—Across much of Shikoku and Kii, the 7-partite character of var. *hondoense* apparently has transferred into an older, presumably 5-partite taxon, and we are not aware of any reverse transfer. Therefore, in the case of var. *kyomaruense*, a 5-partite-to-7-partite transfer—i.e., from subsp. *degronianum* to var. *hondoense*—seems doubtful.

Turning, then, to the second suggestion, we can try to account for var. *kyomaruense* by examining its connections with var. *hondoense*, and we have the following possibilities to consider:

—First, that var. *kyomarnense* originated as a mutant from of var. *hondoense*, able to survive but with no advantage that has yet enabled it to spread over a wide area.

—Second, that var. *kyomaruense* consists of relict stands from a period when vars. *honodoense* and *kyomaruense* were identically 5-partite, and that a dominant, advantageous 7-part character later appeared, spreading throughout most stands. —Third, that an invading taxon from the Asian continent (discussed in the preceding section) included both 5-partite and 7-partite forms, which respectively survived as vars. *hondoense* and *kyomaruense*.

While each of these possibilities seems reasonable as a hypothesis, we lack the knowledge necessary for verification. But these hypotheses seem less questionable than the suggested descent of var. *kyomaruense* from subsp. *degronainum*. Therefore the inclusion of var. *kyomaruense* in subsp. *heptamerum* rather than subsp. *degronianum* appears appropriate at this time.

The apparently older taxa As stated just after the introduction, we hypothesize that *R. degronianum*, subsp. *degronianum* and subsp. *yakushimanum*, and *R. makinoi* (or their ancestors) have been present in Japan longer than other members of Subsection Pontica. The basis for this is their present distribution and shared characters, although *R. makinoi* is so distinct that it is recognized as a separate species.

Of these three taxa, only *R. degronianum* subsp. *degronianum* occupies a large region; this is in northern Honshu, apparently delimited on the north by the plant's cold tolerance or snow tolerance and on the south by its inability to cross the broad lowlands of the Fossa Magna. The region within these limits consists of three parallel north-south mountain chains separated by two valley systems, affording opportunities for the plant to migrate higher and lower, or north and south, with cycles of climatic change.

As set forth in the discussion of var. *kyomaruense*, the Fossa Magna has apparently served since Miocene time as a barrier to southwestward diffusion of subsp. *degronianum* characters. Yet an ally may once have inhabited Kii, Shikoku, and Kyushu, where (as discussed above) it eventually may have lost its identity by hybridizing with the arriving var. *hondoense*. Such a once-present ally, together with the ancestors of today's subsp. *degronianum*, subsp. *yakushimanum* and *R. makinoi*, could perhaps be considered an early pan-Japanese taxon.

Subsp. *yakushimanum* occurs only on Yakushima, an island of granite except for its coastal rim of sedimentary rock and Pleistocene deposits. Since the sedimentary rock matches that of southern Kyushu, southern Shikoku, and

southern Kii, Yakushima may formerly have been connected to those areas and may have shared a common flora. However, any such connection was apparently broken so early that subsp. *yakushimanum* escaped the introgression of var. *hondoense* characters that evidently occurred in the other southern areas.

Subsp. *yakushimanum* var. *intermedium* is distinguished by an indumentum of short hairs, sparse or light-colored. Sugimoto established this variety in 1961 and included it in his 1978 New Keys (p. 381), giving 1000–1500 m as its elevation range, compared with 1500–1900 m for the typical variety. One of the present authors, however, has recorded somewhat different observations as follows:

—At 1220 m, subsp. *yakushimanum* leaves were large and nearly flat, with thin, pale indumentum, i.e., the plants were clearly var. *intermedium*.

—Plants from ca. 1375 m to ca. 1500 m were a mixed assortment, some with thinner, lighter-colored indumentum and some with thicker, deeper-colored indumentum (occasionally spongy and with pits).

—At higher elevations, thick indumentum was more general but did not entirely replace the thinner. For example, on a large plant at ca. 1700 m, the leaves were 15–20 cm long, with thin, nearly white indumentum.

—Contrasting with these observations, a Yakushima resident's photograph showed a compact, "summit-form" plant which, he stated, was growing at an elevation of only 900 m.

Besides having varied indumentum, the plants within a particular environmental niche were often seen to vary in growth habit, leaf size and shape, and flower color. This variability, we think, is perpetuated by the frequently violent weather, capable of dispersing seed and pollen for unusual distances. In these circumstances, a plant's seed must compete with assorted blown-in or washed-in seed, and a plant found in a favorable niche might or might not be succeeded by a similar plant. Therefore we suggest that the *intermedium* taxon can only loosely be considered a variety.

Compared with subsp. *yakushimanum*, *R. makinoi* seems almost as insular. It is found in Honshu, on or very near two adjoining geologic formations just north of the Median Tectonic Line and, together, ca. 15 km in diameter. (See Fig. 2; also see Kyoto 1 : 500,000 sheet, Geol. Survey of Japan). The larger formation, to the northwest, consists of volcanic rock mostly rimmed with marine sedimentary rock, both being early to middle Miocene (ca. 20 m. y. b. p.).

The smaller formation, to the southeast, is a 1.5-to-2-km-wide band of mylonite, i.e., pulverized rock reformed into new rock. Specifically, the latter is Kashio Mylonite, of the early Cretaceous (ca. 130 m.y.b.p.). The sediment-rimmed volcanic formation is not only younger than the mylonite; it is also younger than the formations surrounding it on other sides.

This situation suggests that the volcanic formation may have been a drifting fragment of land which carried *R. makinoi* and was pushed south from some point in the Japan Sea by the land mass thought to have moved from the Asian coast. Alternatively, *R. makinoi* may have been present earlier on the mylonite, then colonized the volcanic rook after it arrived (or perhaps after it originated from local, underwater eruption). The first of these possibilities, i.e., the drift of a land fragment, is interesting, since the taxon appears to be of Japanese origin, but its late flowering and very late production of new leaves indicate that it reached its present range via a place with much different climate.

In its minute present range, this taxon is common and vigorous, and any spreading or introgression has apparently been prevented by low elevations of the surrounding terrain, also perhaps by unfavorable soils.

Note: *R. makinoi* has also been reported from Akiwa-san, ca. 16 km east of its known range. However, Mr. Hideo Suzuki, after referring this matter to Dr. Yamazaki, advises by letter that the taxon probably is not found there. In addition, one of the authors searched unsuccessfully for it near Sumatakyo, in the mountains of the Oi River basin—ca. 41 km northeast of its known range. And, searching the margins of its known range with the expert guidance of Mr. Kenji Matsushita, the author found no stands more than 2 km outside the volcanic rock or mylonite where it is abundant.

Taxonomic implications For the plants in the *R. degronianum–R. makinoi* complex, the taxonomic implications of their geographical distribution may be summarized as follows:

1) The Fossa Magna appears to have been an effective barrier to migration or introgression involving subsp. *degronianum*. Hence the distinction between subsp. *degronianum* and subsp. *heptamerum* appears more substantial than any distinctions among the taxa within subsp. *heptamerum*. The classification of *degronianum* as distinct at the level of a subspecies therefore appears appropriate.

2) In southwestern Honshu and Kyushu, the Median Tectonic Line (or the parallel Butsuzo Line) is the division between differing *Rhododendrom* arrays.

North of the line are large stands of var. *hondoense*, thought to be a new arrival or its more or less unchanged derivative. There, this appears to be unmixed with other taxa except where it meets var. *kyomaruense*. South of the line are additional stands of var. *hondoense*, also (a) intermediates between var. *hondoense* and var. *heptamerum*, and (b) var. *heptamrum* itself. This suggests that var. *hondoense* has migrated south across the line and has produced var. *heptamerum* by hybridizing with an indigenous taxon, no longer present in this territory but surviving in the form of scattered present-day derivatives, namely subsp. *yakushimanum*, subsp. *degronianum*, and *R. makinoi*.

3) As discussed above, var. *kyomaruense* appears allied with var. *hondoense*.

4) In Kyushu, Pliocene and more recent volcanic activity has formed extensive lava beds, colonized by relatively uniform stands of var. *heptamerum*. Since its characters are thus stabilized, the taxon can appropriately be treated as a variety rather than a hybrid.

5) Although apparently of Japanese origin, *R. makinoi* may have reached its present range via a place with much different climate. Apparently it has since remained isolated from other taxa by land contours or soils.

Classification and nomenclature The classification and nomenclature of both *Rhododendron aureum* and *R. brachycarpum* present no particular problems and are discussed below in a separate section. On the other hand, the nomenclature of the *R. degronianum-R. metternichii* complex is beset with illegitimately published and problematical names, which have in turn aggravated the classification difficulties. The earliest name in the '*metternichii*' complex is *Hymenanthes japonica* Blume (1826), the basionym for *R. japonicum* (Blume) Schneider (1909). This name applies to the plant that has been called *R. metternichii* Sieb. & Zucc. Unfortunately, there is an earlier combination, *R. japonicum* (A. Gray) Suringar (1908), based on *Azalea japonica* Gray (1858) and it is in this sense that the name *Rhododendron japonicum* has been applied for most of this century.

In the monograph on Subgenus Hymenanthes (Chamberlain 1982) it was assumed that *R. japonicum* (A. Gray) Suringar was an invalid combination. And, with respect to the Hymenanthes taxon, a proposal to reject the combination *R. japonicum* (Blume) Schneider in line with common practice (Taxon **30**: 665, 1981) was *not* accepted by the International Committee for Botanical Nomenclature. This committee also confirmed that *R. japonicum* (A. Gray) Suringar was indeed not valid. After this ruling, the conservation of *R. japo-*

nicum (A. Gray) Suringar against *R. japonicum* (Blume) Schneider was proposed on the grounds, firstly of common usage, and secondly because of the commercial importance of the azalea to which the name applied. Recently, the Nomenclature Committee have reconsidered the status of the Suringar combination and now agree with Sleumer (1939) that it is legitimate. The name *R. japonicum* therefore now applies to the azalea, no doubt much to the relief of rhododendron fanciers.

Unfortunately, *R. metternichii* Sieb. & Zucc. is illegitimate, since the type description cites an earlier valid specific epithet, *Hymenanthes japonica* Blume, in synonymy. This leaves *R. degronianum* as the earliest valid name at specific rank.

As indicated in our discussion of plant origins, there are good grounds for treating *'R. metternichii'* as a subspecies of *R. degronianum*, and in this we agree with Hara's treatment. It is perhaps unfortunate that the epithet *'metternichii'* has been lost. We do however accept the substitution of the name subsp. *heptamerum* for this taxon, since a new description is not required.

The distinction between *'heptamerum'* and *'hondoense'* are not as clear-cut as those between *'heptamerum'* and subsp. *degronianum*, either with respect to morphology or to distribution. We therefore accept Hara's treatment of var. *hondoense* under subsp. *heptamerum*. We consider that var. *hondoense* is the older taxon in a geological sense, and could well be the parent of var. *heptamerum*. However, for nomenclatural reasons, the name *'heptamerum'* has precedence over *'hondoense'*.

The position of var. *kyomaruense*, with f. *amagianum*, remains problematical though we note the obvious similarities in vegetative characters between them and var. *hondoense*.

One of the present authors (Chamberlain 1982) proposed that *R. makinoi* should be a subspecies of *R. yakushimanum*. Now that much more material has been seen he agrees with Hara that *R. makinoi* is distinct enough to be treated as a separate species. While we see merit in maintaining *'yakushimanum'* with its variety *intermedium* as a species distinct from *R. degronianum*, we are prepared to accept Hara's treatment of it as a subspecies of *R. degronianum* because of its obvious affinities with subsp. *degronianum*.

We therefore accept Hara's treatment as itemised on page one. For complete synonymy reference should be made to his paper (Hara 1986).

R. brachycarpum* and *R. aureum *R. brachycarpum* is easily distinguished from the *R. degronianum* subgroup by its relatively broad leaves with rounded or obtuse bases. Also, when working in the field or with fresh material, the yellow (or occasionally pale green) buds, petioles and midribs are a conspicuous identifying feature.

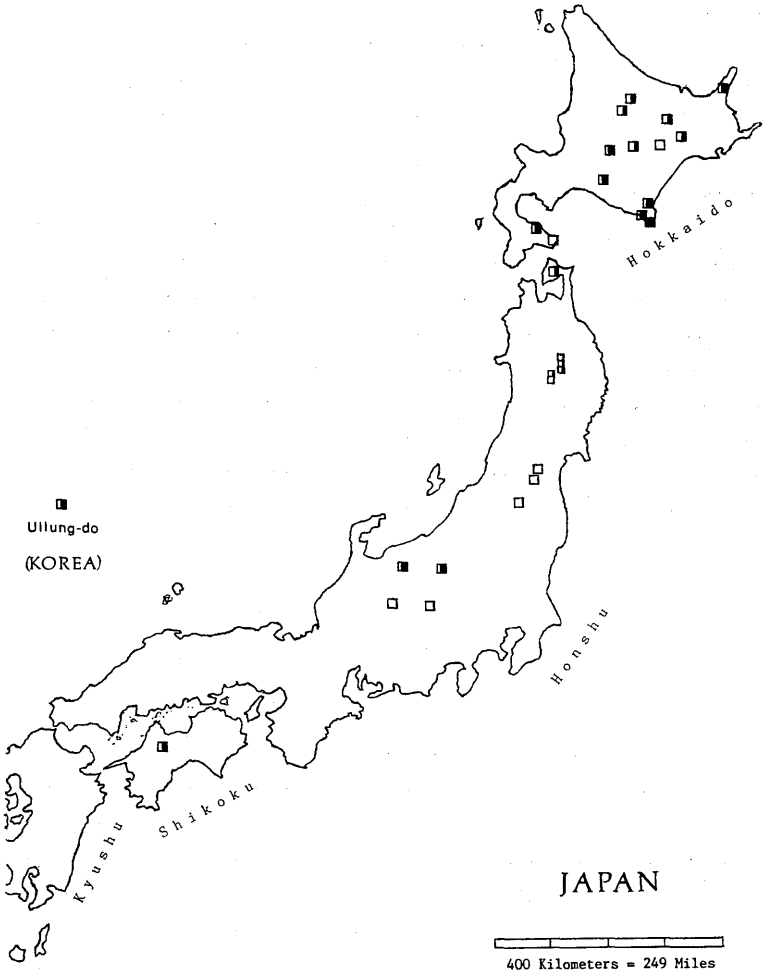

Fig. 3. *Rhododendron brachycarpum.* Shading in each square indicates amount of indumentum.

Various authors have split this taxon into two species, two subspecies, or two varieties, depending on presence or absence of leaf indumentum. To evaluate these separations, we have prepared Fig. 3, showing the geographical variations in the amount of indumentum. On this map, the square for each point of collection, or point of observation, is shaded to indicate the amount of indumentum. And, if indumentum varies with elevation, this is indicated by stacked squares. Our data sources are:

—Dried specimens collected by one of the authors at 13 known locations, in some cases at two or more elevations. Also, if available, leaves of plants grown from seed collected with these specimens.

—Field observations where specimens could not be taken.

—Information furnished by Prof. Tsujii, Curator of Hokkaido University Botanic Garden. This is a Hokkaido Forest Experiment Station study (Nakauchi 1973) containing extensive data on 13 *R. brachycarpum* populations. Their sites duplicated some of ours, and in these cases we found that their observations matched ours.

—In one case, examination of cultivated material only, grown by one of the authors from seed collected at a specified location by persons of known reliability.

This information indicates that indumentum (or lack thereof) is not a regional phenomenon but instead is distributed more or less at random. Therefore it is difficult to justify the separation of *R. brachycarpum* into subspecies. *R. brachycarpum* in the strict sense includes those forms with a leaf indumentum and *R. fauriei* those forms without (Chamberlain 1982, p. 307). The plants without a leaf indumentum could be treated as a distinct forma or variety of *R. brachycarpum*. However, if they are treated as a variety, then var. *fauriei* is not necessarily the correct name as there may be an earlier valid name at varietal rank under *R. brachycarpum*.

R. aureum, a low-growing yellow-flowered mountain plant, may consist of two distinct varieties, but only the var. *aureum* appears to be present in Japan.

References

Chamberlain, D. F. 1982. Revision of *Rhododendron* II. Subgenus Hymenanthes. Notes RBG Edinb. **39**(2) : 209–486. Doleshy, F. L. Accounts of field observations given in: Otr. Bul. Am. Rhod. Soc. **20**: 3–9, 76–86, 147–58 (1966) ; **22**: 2–5, 145–59 (1968) ; **24**: 68–79, 147–53 (1970) ; **25**: 31–38, 84–91 (1971) ; **26**:

20-22, 102-4, 193-5 (1972) ; J. Am. Rhod. Soc. **38**: 2-5, 29-31 (1984). Geological Survey of Japan 1968 and later eds. Geological map of Japan, Volcanoes of Japan, Tectonic map of Japan. Scales from 1 : 500,000 to 1 : 5,000,000. Pub. by the Geolog. Survey, Kawasaki. —— 1982. 1 : 500,000 Geological Map. Sheet 11, Kyoto. Pub. as above. Hara, H. 1948. Occurrence and distribution of rhododendrons in Japan. Rhod. Yr. Bk. **3**: 112-27. —— 1986. Scientific names of the *Rhododendron Degronianum* group. Journ. Jap. Bot. **61**: 245-7. (Japanese with nomenclature in Latin and English). Kimura, T. 1959. A sharp bent of the Median tectonic line and its relation to the Akaishi tectonic line. Jap. Jour. Geol. Geog. **30**: 215-32. Maximowicz, C. J. 1870. Rhododendreae Asiae orientalis. Mem. Acad. Sci. St.-Pétersbourg, Ser. 7, **16**(9) : 1-53. Maekawa, F. 1974. Geographical background to Japan's flora and vegetation : General geography of Japan and its relationship to the flora, pp. 2-20. Also, Origin and characteristics of Japan's flora, pp. 33-86. *In* M. Numata (ed.) : The flora and vegetation of Japan. Kodansha, Tokyo. Nakauchi, T., S. Saito & T. Hirakimoto 1973. A study on a indigenous rhododendron (*Rhododendron fauriae* Franch.) in Hokkaido. Bull. Hokkaido Forest Exp. St. **11**: 45-54. (Japanese). Nitzelius, T. G. 1961. Notes on some Japanese species of the genus *Rhododendron*. Acta Horti Gotoburg. **24**: 135-74. Sleumer, H. 1939. Kritische Bemerkungen zu K. A. Reiter "*Azalea mollis* und *Azalea japonica*". Jahrb. Deutsch. Rhod. Ges., Bremen, pp. 95-96. Stevenson, J. B. (ed.) 1947. The species of *Rhododendron*. 2nd ed. The Rhod. Soc., London. Sugimoto, J. 1978. New keys to woody plants of Japan. Inoue Book Co., Tokyo. (Japanese). Takai, F., T. Matsumoto & R. Toriyama (eds.) 1963. Geology of Japan. Univ. of Tokyo Press, Tokyo. Wada, K. The cited comments were given one of the authors verbally in various conversations. Yamazaki, T. 1964. A new variety of *Rhododendrou metternichii* and its alliance. Journ. Jap. Bot. **39**: 13-18. (Japanese with Latin & English summary).

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日本のシャクナゲ類の分類についてはいくつかの見解がある。学名の点でも混乱が生じている。著者のひとり Chamberlain は1982年にレンゲツツジに広く用いられてきた *Rhododendron japonicum* という学名をツクシシャクナゲに使用し国際的な議論を呼んだのは記憶に新しい。IAPT の種子植物命名委員会の結論を踏まえて昨年 (1986) 原寛博士は，本誌に新しいシャクナゲ類の分類説を発表した (**61**: 245-247)。本稿は，基本

的にはこの原博士の説を補足することを目的としたもので，日本のシャクナゲ類について自生地あるいは栽培下で主として著者のひとりDoleshyがこれまでに行なった観察結果を報告し，併せてアズマシャクナゲの種内分類群ならびにエンシュウシャクナゲの分化を地史との関連で推論し，最後に学名について見解を述べたものである。本稿では，分化の年代に関連して地理分布から3つの群を設定した。それらは，1)古くから存在する群 (Long present)，2)新しく展開した群 (Recent arrival) ならびに 3)複合的な性質をもつ群 (the group with mixed characters) であり，アズマシャクナゲとヤクシマシャクナゲならびにエンシュウシャクナゲは (1) に，ホンシャクナゲとキョウマルシャクナゲは(2)に，ツクシシャクナゲは(3)に該当するとした。アズマシャクナゲの各種内分類群について4数性から10数性に至る花の員数の変異を調べその頻度分布を求め，本種においては員数の変異幅が広いが種内分類群毎に特定の変異の幅と傾向を示すことを明らかにした。

□木村陽二郎：**生物学史論集** 431 pp. 1987. 八坂書房，東京．¥12,000. 著者がこれまでに発表した生物学史関係論文の集成である。Ⅰヨーロッパ，Ⅱ日本，Ⅲ本，Ⅳ人と分けてまとめてあるが，どこから読んでもかまわない。現代生物学の基礎をつくった人やできごとが興味深く書かれている。後記は著者自身の学問の履歴を述べたものである。
(金井弘夫)

□Gustafson, J.P., G.L. Stebbins & F.J. Ayala (eds.)：**Genetics, development, and evolution** 361 pp. 1986. Plenum Press, New York. $49.50. 本書は1985年ミズリー大学で開催された第17回 Stadler Genetics Symposium の講演を編集したものである。DNA にコードされている情報が個体発生を通して種の形態，生理，行動等の特性として表現される。この基本的な関係の中で遺伝と進化に関連する多くの解明すべき問題があり，その研究には発生学や遺伝学に加えて，近年分子生物学，細胞生物学，生化学などの知識と研究方法が積極的に取り入れられている。本書は遺伝学分野から，これらの問題に関する真核多細胞生物を対象とした論文を15篇集めている。各論文には多数の文献が引用されている。植物を材料とした論文には G.L. Stebbins による「遺伝子の行動と形態形成」や E.J. Klekowski Jr. et al. による「突然変異，頂端分裂組織および発生上の選択」などが含まれている。
(大橋広好)