

American Rhododendron Society

VALLEY FORGE CHAPTER

14 Northwoods Road, Radnor, PA 19087 Chapter's Website: <u>www.ValleyForgeARS.org</u>

BONUS NEWSLETTER

December 2020

It has been 9 months since we met in person. Each year we normally have 5 newsletters and skip July and December. The newsletter has attempted to be more informative, but decided to have a bonus issue dedicated to a single topic of unusual but general interest. We hope you enjoy and stay safe. *The Editor*

President's Message

I hope everyone continues to do well during the Covid-19 pandemic. As everyone is aware this year has been much different with all the cancellations. And this month we added another cancellation, our November Banquet, which we always use to usher in the Holiday Season. Our District 8 Director, Steve Henning, contacted me and thought this year it would be nice to do something a little different. What follows is a bonus December issue of the Valley Forge Newsletter. As you will discover, the entire issue concentrates on the Genus Rhododendron, where it grows and how it got there. I looked over the paper and it is very interesting. I think every Rhododendron enthusiast will find it an enjoyable and fascinating story.

Everyone, please stay safe. Sincerely, Jerry O'Dell, (610) 608-2018, westdell@verizon.net

Reminder:

Membership Renewals Are Due Dec. 1

Thank you if you renewed already. If not, please support the ARS and send in your dues. Even if we can't meet face to face right now, we hope you enjoy the ARS Journal and our chapter newsletters. We appreciate the many Associate Members from other chapters, too.

Members must renew by December 1 to avoid Journal disruption, so try to renew on time.

The ARS now accepts online renewals for those who prefer to pay by credit card or personal Pay Pal account. To avoid dealing with the mail, check out the ARS Office and click on Membership Services:

https://www.arsoffice.org/

You will need your "membership number" to complete the renewal process which is on your Journal mailing label.

If you didn't receive or misplaced the chapter's dues mailing or you want to be a new member, use the online form at <u>http://valleyforgears.org/join.html</u>. If you have any questions, contact Darlene Henning at 717-735-7116 or <u>mdhenning@earthlink.net</u>.

Why Rhododendrons grow where they do and how they got there.

For the 1989 ARS Victoria convention, Ted Irving, a retired geophysicist and emeritus scientist with the Geological Survey of Canada, and Richard Hebda, a botanist with the Royal British Columbia Museum, presented an excellent program entitled *Concerning The Origin and Distribution of Rhododendrons*. It was subsequently published in JARS in 1993. This is a review of their landmark presentation with new material added. ¹²

Scientists have combined data from earth sciences, plant science and animal sciences to come up with a fairly detailed theory of when the earth was formed and how it developed.

Earth's Geologic Timeline			
Millions of	The Event		
Years Ago			
4,550	Formation of the Earth		
4,527	Formation of the Moon		
circa. 4,000	Heavy Meteor Showers End		
circa. 3,700	Earliest microbial life emerges		
circa. 3,200	Start of Photosynthesis		
circa. 2,300	Oxygen-rich Atmosphere		
760	First creatures: Sea Sponges		
750-635	Snowball Earth (ice covered)		
541-485	Cambrian Explosion: All major		
	animal phyla started appearing		
	in fossil records.		
circa 470	Earliest Land Plants		
circa 380	First Vertebrate Land Animals		
270	First Ginkgo biloba, a living		
	fossil today		
230-66	Non-Avian Dinosaurs Roamed		
	The Earth		
circa. 65	Earliest Ericaceae		
circa. 55	Earliest Rhododendrons		
circa. 25	Beginning of Asian Monsoons		
2	Earliest Hominins		

The theory of plate tectonics and continental drift explains many observations. The original continents Laurasia and Gondwana were together and formed the continent of Pangaea. When they drifted off Laurasia contained what was to be North America and Eurasia, while Gondwana contained what was to be South America, Africa, India, Antarctica, and Australia. During these processes some areas sank and other areas rose from the oceans. But major land masses survived and the plants on them survived.



Plate tectonics and continental drift of plates.

Fossil records indicate the Ericaceae emerged about 68 million years ago. Rhododendrons were found in fossils in North America and Eurasia. ^{16, 17}

Rhododendrons have been in existence for at least 55 million years, but not before 68 million years ago. This is significant because the regions of north Burma, southwest China, and New Guinea that we think of as the centers of rhododendron diversity did not exist 55 million years ago. Since fossils are usually found in lowlands, the lack of numerous fossil records of rhododendrons indicates they were more prevalent in upland habitats much as they are today. Fossil records of rhododendrons were present in North America and Eurasia dated soon after their origin. Alaska and Asia were connected by Beringia, a land mass, in what is now the Bering Strait. ^{16, 17}

The following sections illustrate several stages in the paleogeographic evolution of rhododendrons proposed by Irving and Hebda. Except for the evergreen azaleas (Tsutsusi) which may always have been fairly restricted, rhododendrons were spread widely across the northern continents during the climatically-mild interval 60 to 40 million years ago. Although widespread and abundant, they were not necessarily represented by many species since they were not strongly diversified. ¹³

55 Million Years Ago

55 million years ago, the Beringia land bridge connected North America with Asia. The high mountains of south Asia hadn't been formed because the India subcontinent was only approaching Asia. Also, at this time, South America was only approaching North America. Also significant is the fact that Mixed Northern Hardwood Forest connected the northern regions of North America and Asia even extending to Europe. Hence, whether rhododendrons originated in North America, Beringia, or Asia, they could freely spread both directions during the next 15 to 25 million years. Most of the world was tropical except the temperate polar region. ^{12, 16}

During the early history of rhododendrons 60 to 40 million years ago, North America and Eurasia were close to or north of the positions they occupy today; they were squarely lodged between 30 and 60°N latitude, with large areas north of 60°N. The climate, however, was warmer and more stable, and forests grew at much higher latitudes, because the Earth was then in a non-glacial stage. As a consequence, there apparently were only about four major vegetational zones, compared to about three times that number today. These were respectively, from south to north, "tropical" rain forest ("tropical" placed in quotes because such forest extended well outside the tropics), para-tropical rain forest, broadleaved evergreen forest, and polar deciduous forest. These ancient forests can only be compared to modern forests in a general way because many modern forest trees had not yet evolved. For example, the dominant coniferous trees were not the spruces, pines and firs of today, but instead were, for the most part, members of the bald cypress family (Taxodiaceae), which includes such trees as the dawn redwoods, the redwoods and the bald cypress, whose range is fragmented now and restricted to small areas. 7, 16

The polar deciduous forest, which included deciduous hardwoods and conifers such as the dawn redwood, occurred in northern North American and northern Siberia well inside the Arctic Circle. In and just south of the Arctic Circle there was a belt of broad-leaved evergreen forest which included palms, followed by a belt of warm para-tropical rain forest. Both belts probably extended into lower latitudes in upland areas, and both probably provided an environment suitable for rhododendrons. "Tropical" rain forests were the dominant vegetation, which,

55 MILLION YEARS AGO



Continent & Plant Distribution 55 Million Years Age ¹³

apparently, covered most low-lying regions in latitudes lower than about 45°. Most areas suitable for rhododendrons were likely to have occurred only in upland regions, but these could have been widespread.

It seems probable on geographic, climatic, and ecological grounds that rhododendrons, during their early history, could have extended more or less continuously from North America to Greenland and Europe, and eastward into China and northeastern Asia. It is probable that they moved freely between North America and Europe across the narrow gulfs of the emerging North Atlantic Ocean as well as across Beringia. The early populations of rhododendrons may not have been composed of very many species. ¹⁶

40 Million Years Ago

40 million years ago the temperate region was expanding southward. North America was developing its Coniferous Forest and Asia was developing a Broad-Leaved Evergreen Forest. There was still Beringia, the land connection between North America and Asia, and plants could easily migrate within the temperate region. ^{7, 20}

By 40 million years ago, there were about five global vegetational zones. "Tropical" rain forest occupied a smaller area than before. Polar deciduous forests persisted, and there was a notable development of a northern evergreen coniferous forest composed typically of members of the family Taxodiaceae. The belts of warm para-tropical rain forest and broad-leaved evergreen forest moved southwards and expanded. Except for high mountain regions of SE Asia and it high-island archipelago, both of which had not yet taken shape, the ranges of these two zones embrace the present-day distribution of rhododendrons, including that of the cold-climate R. lapponicum. It appears that in and between the places where rhododendrons are found nowadays, there existed habitats suitable for them. Rhododendrons are still more or less where they always have been. 7, 15, 20

40 MILLION YEARS AGO



Continent & Plant Distribution 40 Million Years Ago¹³

20 Million Years Ago

About 20 million years ago, the mild climate in middle and high latitudes began to deteriorate and as the North Atlantic opened, suitable environments were restricted and rhododendrons became confined to isolated pockets. At about this time, small founder populations of the subgenera Rhododendron (lepidote) and Hymenanthes (elepidote) colonized what is now high mountain regions of SE Asia as Tibet began to be uplifted, and the deep valleys on its southeastern border were eroded. These founder populations proceeded to speciate, especially during the past few million years. ⁶

We see that the temperate region extended throughout North America and Eurasia. There was still a land connection between North America and Asia and plants could easily migrate within the temperate region.

By 20 million years ago "tropical" rain forests were further restricted, and cooling in middle and high latitudes had begun. These changes culminated in the glacial periods of the past few million years. Variable continental climates and grasslands began to develop, and there was a further increase in the number of major vegetational zones from about six about 20 million years ago, to about eight today, twice the number present when rhododendrons began. In the north, extensive coniferous forest dominated by the pine family (Pinaceae), came into existence. Its present-day descendant is the boreal forest of northern North America and northern Eurasia. Mixed hardwood and coniferous forest for the first time occupied large areas of Eurasia and North America, but the great broad-leaved evergreen forests were much diminished, becoming restricted as they are today to southeastern China and the southeastern United States. The mixed hardwood and broad-leaved evergreen forests provided the habitats best suited to rhododendrons.

Between 20 million years ago and today, and especially in the last few million years, the climate in middle and high latitudes became much cooler than when rhododendrons first made their appearance. Large areas of desert, semi-desert and grassland developed in central and southwestern North America, across Africa and into Asia. This expansion of arid environments eliminated vast tracts of rhododendron habitat. During the past 2 to 3 million years, vegetational zones fluctuated greatly in response to glacial advances and retreats. This disrupted the climate of lands bordering glaciated areas. There was a broad circumpolar belt of tundra and ice, and "tropical" rain forests shrank to a remnant of their former extent.



High Mountain Region



Great shear faults which define the river valleys in the high mountain regions of SE Asia.²

One of the most spectacular events in Earth's history is the long drawn-out collision of India with Asia which began about 40 million years ago and continues today. This collision set in motion the chain of events which lead to the creation of the high mountain regions of SE Asia and to conditions highly favorable to the development of a rich rhododendron flora.^{12, 22}

Prior to 120 million years ago, India formed part of

the giant southern supercontinent, Gondwana, Gondwana fragmented in piecemeal fashion. In its northward travel. India relentlessly pushed northward, deforming much of southeastern Asia as it went. Immediately north of the zone of contact, the Earth's crust was doubled in thickness and was lifted up forming the Tibetan Plateau. South of the plateau, debris piled up forming the Himalayas. Together the Tibetan Plateau and the Himalayas form a vast region of high elevation unique on Earth. It is the only region where two continents are colliding with one another today. ¹²

The most recent estimates are that the rapid uplift began about 20 million years ago, and that the plateau reached approximately its present elevation about 8 million years ago. The assembly of a landmass as large as Asia and the uplift of the Himalayas and Tibet profoundly affected climate. ¹²

Monsoons

About this time the monsoons began. They caused major changes in geography and climate. Monsoons started when India had collided with Asia creating the high mountain region in south Asia. Very low atmospheric pressure centered over Pakistan and stretching northeast to Mongolia developed in summer, drawing wet tropical air from across the equator, and causing heavy rainfall along the southeastern border of Tibet and the Himalayas. As uplift continued, river systems grew, their valleys were deeply etched along large faults in the Earth's crust that had been developed as India pushed its way into Asia. It is this close fan-shaped network of faults along the southeast border of the Tibetan Plateau that accounts for the geometry and bunching together of the deep valleys. The fault-controlled alignment of valleys provides ready access to rainbearing prevailing winds ensuring that the slopes of the high mountain regions of SE Asia are well watered. Through time, a landscape evolved which became home to a wide variety of habitats - subtropical valley bottoms, temperate slopes, and alpine peaks all very close together. 15, 18, 21, 22

The monsoons altered the climate creating a rainy season and a dry season. The monsoons altered the geography by creating deep river gorges. ²¹

Founder Populations

Speciation occurs more readily in small reproductively isolated populations of plants and animals. In a small population, genetic drift is more likely to cause changes in a population's characteristics. Such small reproductively isolated populations that undergo rapid diversification are referred to as "founder populations." ^{6, 11, 14}

As already explained, it is possible that during the period from about 60 to 40 million years ago, rhododendrons ranged more or less continuously across North America and Eurasia because suitable climates and topographies occurred there over a much wider area than at present. Although rhododendrons may have been widespread and abundant, the uniformity of conditions may not have led to the evolution of many species. As Asia was enlarged by the addition of India, and as the Tibet-Himalaya region was uplifted, new habitats ideal for rhododendrons came into being. Representatives of both lepidote (subgenus Rhododendron) and elepidote (subgenus Hymenanthes) rhododendrons, but not azaleas, expanded into these newly established favorable habitats and became founder populations. The mixed hardwood, coniferous and broad-leaved evergreen forests of eastern Asia 20 million years ago are their most likely habitat. 6, 12

Present

Fast-forward to the present and the connection between North America and Eurasia is gone. The temperate regions are larger and cold polar regions formed at both poles. The far northern climate is no longer hospitable to the more temperate rhododendrons. The region with temperate rhododendrons has now split with parts in western North America, eastern North America, Europe, and southern and Western Asia. The vireyas, an offshoot from the high mountain regions of SE Asia , were a late development which colonized the recently formed high-island archipelago. ²²

Today there are broad belts of desert and semideserts in tropical and mid-latitudes which are bordered by broad expanses of tropical and temperate grasslands, something quite unknown 50 million or more years ago when rhododendrons first appeared. The region of broad-leaved evergreens and mixed hardwood and coniferous forest is confined to eastern and southeastern North America, Europe and Asia.

Global Climatic Change

Of course, it is not sufficient to say that because there is a suitably hilly landscape that rhododendrons would actually have grown there. A suitable climate is needed also, and the Earth's climate is known to have changed drastically since rhododendrons first appeared.



Today there is a year-round ice cap at both poles, the difference in mean surface temperature between pole and equator is over 40°C, and at latitudes above about 55° the mean surface temperature is below freezing. Earth is said to be in a "glacial period". Earth has been in a glacial period for the past 2 to 3 million years, during which there have been large oscillations roughly every 50,000 years. ⁸



Variation of Mean Sea-Level Temperature at Mid-Lattitudes

This much simplified graph shows the variation with time of mean surface temperature in middle latitudes. During the early history of ericaceous plants, the Earth had a stable non-glacial climate. This was followed by a long slow decline to about 3 million years ago when the present glacial period commenced, although there is evidence of glacial ice in Antarctica as long ago as 15 million years.

During ice ages glaciers have extended down into intermediate latitudes. Between ice ages, during interglacial periods, glaciers have diminished to about their present extent with glaciers at sea level only near the poles. For the past 10,000 years glaciers have been generally in recession. However, from 100 to 40 million years ago it was much warmer in high latitudes and the pole-to-equator temperature difference was only 10 or 15°C, three times less than at present. There appears to have been no ice at sea level, and everywhere the mean surface temperature exceeded freezing (0°C). These are the characteristics of a "non-glacial period" and define Earth's normal climatic regime. Today, climatically speaking, we live in exceptional times.

PRESENT HPRI HPR HIPR Subspecies: TROPICAL' BAINFOREST H=Elepidotes PARATROPICAL RAINFOREST R=Lepidotes P=Deciduous Az GRASSLAND AND SAVANNAH T=Evergreen Az BROAD-LEAVED EVERGREEN FOREST MIXED NORTHERN HARDWOOD FOREST EVERGREEN WOODLAND (MEDITERRANEAN) DESERT, SEMI-DESERT, SCRUB CONIFEROUS FOREST

Continent & Plant Distribution at the Present¹³

It is of vital significance for rhododendron evolution that the rapid uplift of the Tibetan Plateau was occurring at a time when global climate was cooling. As Earth entered a glacial period, ice advances and retreats occurred repeatedly every 50 to 100 thousand years.

Speciation in high mountain regions

In the high mountain regions of SE Asia, as an ice age commenced and harsh conditions at high altitudes expanded, species ranges would be displaced downward to lower elevations. Populations in valley bottoms, previously separated by unfavorable condition, could mix with populations from adjacent slopes and valleys, and species could cross after long intervals of separation to generate new hybrids, the potential progenitors of new species. Populations at higher elevations would become separated temporarily from one another by intervening glaciers or unfavorable alpine habitat. These now-separated populations would reproduce in isolation and, over time, diverge from each other by genetic drift following their own evolutionary path. During interglacial intervals, populations at higher elevation could migrate upward over ridges and opportunities for species to mix and separate repeatedly. The large vertical range of valleys and ranges meant that species distributions could be displaced rapidly upward and downward without annihilation, despite major climate shifts, because the actual distances travelled would be short. Consequently, fragmentation and coalescing of rhododendron habitats could have occurred repeatedly as a consequence of glaciation and deglaciation, so producing the present-day diverse flora. 14, 22



Habitat Variation with Climate Cycling

In essence, mountains and deep valleys each act as islands of habitat which repeatedly join and separate as climatic zones and plant populations ascend and descend. These joining-separating cycles occur at about the right interval for them to serve as a forcing process for speciation. A period of 50 to 100 thousand years is generally considered sufficient for a small, physically isolated population to undergo changes great enough to ensure reproductive isolation. These separations and rejoinings would provide repeated opportunities for formerly isolated populations to intermingle. ¹³

The end result would be a very large number of closely related species many of which would retain the ability to hybridize. It was precisely this combination of very high mountains situated in tropical latitudes, and cycles of glaciation and deglaciation, that provided the dynamic conditions for the extraordinary speciation of lepidote and elepidote rhododendrons in the high mountain regions of SE Asia . According to this view, most of the speciation has happened in the last 3 million years during the current glacial period. ²²

Lowland areas or mountains of modest size provide fewer opportunities for populations to separate and then rejoin (the hallmark of the above speciation mechanism). They provide no refuge in times of severe climate. In shallow valleys rhododendron populations would be eliminated or greatly reduced as climate deteriorated; as temperature fell and valleys become occupied by unfavorable habitats or even filled with ice, there would be no possibility of downward migration; as rainfall diminished during warmer interglacial periods, there would be no nearby higher wetter slopes on which to find refuge.

Much of northern North America was covered by ice during major glaciations, whereas to the south relatively dry climate prevailed. There were few suitable habitats nearby, and during ice ages the local rhododendron population must have suffered severely. In the high mountain regions of SE Asia the correct balance appears to have been struck, so that although climatic changes were great, the tropical latitudes and the great depth of the valleys ensured that safe havens were nearby. In such a physical environment, latitudinally well-placed, climate change acts not as an agent of destruction, but as an incentive to diversification. Nowadays, because of its unique elevation, the high mountain regions of SE Asia is isolated botanically from the rest of the Asian land mass of which it is a part. Moreover, the region itself is a vast intricate honeycomb of valleys whose degree of isolation changes as ice ages wax and wane and as continuing uplift and erosion modify their configurations.²²

Azaleas

Azaleas differ from other rhododendrons in that azaleas only have about one tenth the number of species, and they are absent from the high mountain regions of SE Asia .

Deciduous azaleas occur mainly in southeastern USA and in southeastern Asia and Japan, with scattered representatives in southern Europe, Asia Minor, southwestern Asia, and western North America. This pattern indicates that, as has happened with the subgenera Hymenanthes and Rhododendron, they were more generally distributed over the northern hemisphere, and that their range has since been reduced and fragmented by climatic deterioration and by the widening of the North Atlantic, which increasingly presented a barrier to dispersal.

Evergreen azaleas are found only in southeastern China and Japan, and it is possible that they have always remained confined to warm temperate broadleaved evergreen forests. They may never have ventured far beyond their original ecological niches, and their range has, in consequence, shrunk along with that of broad-leaved evergreen forests.

The azaleas are not plants of the high mountain regions of SE Asia although they live close by. Presumably, because of their genetic make-up and historical circumstances, they were unable to take advantage of the dynamic environment of the high mountain regions of SE Asia . Although well positioned to act as founder populations, they failed to do so. In this respect, the paleogeo-graphical evolution of azaleas appears therefore to have been very different from that of other rhododendrons. ⁶

Vireyas

The Indo-Malaysian region has an abundance of species from section Vireya of the subgenus Rhododendron. Other representatives of the genus are rare (the evergreen azalea R. subsessile grows in the Philippine Islands). Vireyas are also found, but in much fewer numbers, in the high mountain regions of SE Asia , in the mountain ranges of Indochina and Malaya, and in adjacent areas of southeastern China and Taiwan. In contrast to many other sections, such as the section Ponticum (of the sub-genus Hymenanthes) which has representatives in North America, Europe, and southeastern Asia and a markedly discontinuous distribution, the vireyas are concentrated in one essentially

continuous region. This suggests that they have originated comparatively recently, more recently, for example, than the section Ponticum. The terrains in which the majority of vireyas are found today are of recent origin indicating that the abundance and diversity of vireyas is also a recent phenomenon. Many of the mountain ranges of the high-island archipelago, have been created by volcanic activity as the Indian and Pacific Plates pushed the Eurasian Plate up. The highlands of New Guinea, which exceed 4000 meters in relief and began to be uplifted about 4 million years ago. Because the region is near the equator, vegetational zones vary from tropical forest at sea level to alpine grassland with glaciers on the peaks, and they may have fallen as much as 1000 meters during ice ages. Hence, a mechanism for speciation similar to that proposed for the high mountain regions of SE Asia may also be operative here. The founder populations of the section Vireya most likely originated in the high mountain regions of SE Asia within the past few million years. From there they have spread swiftly down the Malay Peninsula into the high-island archipelago where they speciated rapidly. One species has even reached Australia, where it occurs in the tropical rain forest of the Atherton Tableland. 6, 8, 10, 12, 22

Summary

Rhododendrons originated over 55 million years ago and were more-or-less continuously distributed across North America and Eurasia. The climate was mild and change was slow. Their range became much reduced as a result of worsening of the global climate caused by the formation of high mountains. This worsening began about 25 million years ago, was clearly marked by about 15 million years ago, and became extreme with the onset of the current glacial period about 3 million years ago. Small founder populations of the sub-genera Hymenanthes and Rhododendron (but not azaleas) situated marginal to their main range were able to enter and retain a foothold in the newly developing high mountain regions on the southeastern fringe of the Tibet-Himalayan region. It was from there that the vireyas spread into the mountains of the high-island archipelago. By taking advantage of special newly developing conditions, these small, originally peripheral populations have become now the most numerous and diverse. The place of origin of rhododendrons is not known, but it was not the high mountain regions of SE Asia where nowadays they are most diverse and abundant. That region did not

exist then. These conclusions are based on the fossil record of rhododendrons and are based upon the observations of many scientists. They provide reasonable explanations of the present remarkable distribution of rhododendrons and of their differing abilities to cross and recross.²²

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NEWSLETTER December 2020



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