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GEOGRAPHICAL DISTRIBUTION OF THE GENUS *PHRAGMIDIUM* LINK

Key words: *Phragmidium*, *geographical distribution*, *centre of origin*

Abstract

The genus *Phragmidium* (Uredinales) comprises autoecious parasites of the subfamily Rosoideae. More than 150 species names are known but only about 90 species are distinctive. The geographical distribution of the genus clearly reveals its Holarctic and Pacific affinity. By their distribution, species of *Phragmidium* can be divided into 6 groups: 1) East Asian; 2) Central and South Asian; 3) Eurasian; 4) North American; 5) Holarctic; 6) Species distributed in the Southern Hemisphere. In geographical terms a hypothesis could be proposed that the genus originated in the area north-east of the Tethys ocean gap and spread westward and northwards after that gap was closed by collision of India and Arabia with the Asian plate. The westward spread gave rise to species of rather narrow distribution in Western China, the Himalaya, Pakistan, Central Asia and Iran. The northward spread to Northern Eurasia and North America mainly resulted in widespread Holarctic and Eurasian species. The origin of New Zealand and Australian phragmidiums is still unclear.

Introduction

Explaining global patterns of species diversity is one of the most challenging objectives in biology. The genus *Phragmidium* (Uredinales) is a good topic for such investigations: it comprises autoecious parasites of the subfamily Rosoideae which share many common morphological characters. More than 150 species names are known but only about 90 species are distinctive. Unfortunately, information on geographic distribution and systematics of this group is dispersed and far from complete. There is still no monographic treatment of the genus, and recent publications on molecular phylogeny of rusts [4, 8] involved only few representatives of the genus. Given these considerations and the lack of a reliable phylogeny for the genus, it is too early to attempt any cladistic biogeographic analysis in the sense of modern authors [3, 5–7]. At present the distribution of the phragmidiums could be analysed only in terms of dispersal biogeography. So, the aims of the present work are to collate information on the distribution of individual species, identify areas of endemism for the genus and the likely centre of its origin. The compilation

includes distributional data from many publications (a full list of source works is available on request from the author).

Results

Based on their distribution, species of *Phragmidium* can be divided into 6 groups:

I. Twenty three species distributed in East Asia (China, Taiwan, Korea, Japan, Russia— Russian Far East):

Ph. alpinum Hirats. f. on *Rubus* L.: Japan, Russia (Sakhalin); *Ph. arisanense* Hirats. & Hashioka on *Rubus*: China, Taiwan; *Ph. brevipedicellatum* Hirats. f. on *Potentilla* L.: China, Japan, Korea, Russia (Russian Far East); *Ph. formosanum* Hirats. on *Rubus*: China, Taiwan, Japan; *Ph. griseum* Dietel on *Rubus*: China (Heilongjiang, Jilin, Liaoning, Hebei), Taiwan, Korea, Japan, Russia (Maritime Region); *Ph. hashiokai* Hirats. f. on *Rosa* L.: China, Taiwan; *Ph. heterosporum* Dietel on *Rubus*: Taiwan, Japan; *Ph. hiratsukanum* S.X. Wei on *Rubus*: China, Taiwan, Japan; *Ph. itoanum* Hirats. f. on *Potentilla*: Japan, Russia (Kuril Islands); *Ph. miyabeianum* S. Ito & Hirats. f. on *Sieversia* Willd., *Geum* L.: Japan, Russia (Sakhalin); *Ph. miyakeanum* Hirats. on *Rubus*: Japan, Russia (Sakhalin); *Ph. nambuanum* Dietel on *Rubus*: China, Japan; *Ph. octolocularis* Barclay on *Rubus*: Japan; *Ph. okianum* Hara on *Rubus*: Japan, China; *Ph. papillatum* Dietel on *Potentilla*: China, Japan, Russia (Maritime Region), Korea (recorded also for Pakistan); *Ph. paucilocularis* (Dietel) Syd. & P. Syd. on *Rubus*: China, Korea, Japan, Taiwan, Russia (Maritime Region, Kuril Islands); *Ph. rosae-davuricae* Miura on *Rosa*: China (north-eastern part); *Ph. rosae-multiflorae* Dietel on *Rosa*: China, Japan, Taiwan, Korea; Russia (Maritime Region); *Ph. rosae-rugosae* Kasai on *Rosa*: China (Yunnan, Sichuan), Japan, Russia (Kamchatka, Sakhalin, Kuril Islands), Korea (recorded also for Himalaya); *Ph. rubi-japonici* Kasai on *Rubus*: Japan; *Ph. rubi-oldhami* Togashi & Y. Maki on *Rubus*: Japan; *Ph. rubi-thunbergii* Kusano on *Rubus*: China (Zhejiang), Japan; *Ph. yamadanum* Hirats. on *Rubus*: Japan, China.

II. Twenty nine species distributed in Central and South Asia (Western and South-Western China, Nepal, India, Sri Lanka, Pakistan, Iran, Central Asia states):

Ph. assamense Syd. & P. Syd. on *Rubus*: China (Shaanxi, Sichuan, Tibet), India; *Ph. barclayi* Dietel on *Rubus*: China, India, Nepal, Pakistan; *Ph. bayatii* Esfand. & Petr. on *Hulthemia* Dumort.: Iran; *Ph. burmanicum* Syd. & P. Syd. on *Rubus*: India; *Ph. butleri* Syd. & P. Syd. on *Rosa*: China (Tibet), India, Pakistan; *Ph. cinnamomeum* Durrieu on *Rosa*: Nepal, China (Sichuan, Tibet); *Ph. circumvallatum* Magnus on *Geum*: Iran, Turkmenistan, Tajikistan, Kirghizia, Kazakhstan (recorded also for Mediterranean); *Ph. coreanum* L. Guo on *Rubus*: China (Hubei); *Ph. devastatrix* Sorokin on *Rosa*: Tajikistan, Kazakhstan, Kirghizia, Uzbekistan; *Ph. egenulum* Syd., P. Syd. & E.J. Butler on *Rosa*: India (Kashmir), Pakistan; *Ph. fragariae-vestitae* D.K. Agarwal on *Potentilla*: India; *Ph. handelii* Petr. on *Rosa*: China (Yunnan); *Ph. himalense* J.Y. Zhuang on *Rubus*: China (Tibet, Yunnan); *Ph. incompletum*

Barklay on *Rubus*: India, Nepal; *Ph. iranicum* Petr. & Esfand. on *Rubus*: Iran; *Ph. mysorensis* (Thurum. & Mundk.) on *Rubus*: India, Pakistan; *Ph. nepalense* Barclay on *Potentilla*: Pakistan; *Ph. orientale* Syd. & P. Syd. on *Rubus*: India; *Ph. quinqueloculare* Barclay on *Rubus*: Nepal, India; *Ph. rosae-lacerantis* Dietel on *Rosa*: Turkmenistan, Uzbekistan, Tadzikistan, Iran; *Ph. rosae-moschatae* Dietel on *Rosa*: India, Pakistan; *Ph. rosae-omeiensis* S.X. Wei on *Rosa*: China (Sichuan); *Ph. rubi-eucalypti* S.X. Wei on *Rubus*: China (Sichuan); *Ph. sarcopoterii* Gjaerum & Bahç. on *Sarcopoterium* Spach.: Turkey (Anatolia); *Ph. shengezeense* M.M. Chen & Chen on *Rubus*: China (Tibet), Nepal; *Ph. shogranense* Petr. on *Rubus*: Pakistan; *Ph. sikangense* Petr. on *Rubus*: China (Sichuan); *Ph. zamonense* M.M. Chen & Chen on *Rubus*: China (Tibet); *Ph. zeylanicum* Petch on *Rubus*: Sri Lanka.

III. Eight species distributed in holarctic Eurasia (Europe, holarctic Asia):

Ph. acuminatum (Fr.) Cooke on *Rubus*: Iceland, UK, Norway, Finland, Denmark, Germany, Lithuania, Estonia, Austria, Czech Republic, Slovakia, Romania, Bulgaria, Ukraine, Turkey, Russia (European part, Siberia, Russian Far East), Kirghizia, Kazakhstan, China; *Ph. bulbosum* (Fr.) Schldl. on *Rubus*: Ireland, UK, Norway, Sweden, Finland, Estonia, Latvia, Lithuania, Denmark, France, Germany, Poland, Switzerland, Austria, Czech Republic, Slovakia, Hungary, Romania, Bulgaria, Spain, Morocco, Italy (Sicilia), Greece, Ukraine, Russia (European part, Siberia, Russian Far East), Armenia, Azerbaijan, Georgia, Turkey, Pakistan, Iraq, Turkmenistan, Kirghizia, Tajikistan, China; *Ph. candicantium* (Vleugel) Dietel on *Rubus*: Norway, Sweden, Germany, Austria, Czech Republic, Slovakia, Hungary, Portugal, Spain, Ukraine; *Ph. fragariae* G. Winter on *Potentilla*: Ireland, UK, Norway, Sweden, Denmark, France, Germany, Poland, Austria, Czech Republic, Slovakia, Hungary, former Yugoslavia, Romania, Bulgaria, Spain, Italy, Greece, Ukraine, Turkmenistan, China; *Ph. kamschatkae* (Anders) Arthur & Cummins on *Rosa*: Finland, Russia (European part, West and East Siberia, Russian Far East), Japan, Taiwan, China (Xinjiang), India, Pakistan, Afghanistan, Turkmenistan, Tajikistan, Kirghizia, Kazakhstan, Georgia; *Ph. sanguisorbae* (DC.) J. Schröt. on *Poterium* L.: Ireland, UK, Norway, Denmark, France, Germany, Poland, Lithuania, Switzerland, Austria, Czech Republic, Slovakia, Hungary, former Yugoslavia, Romania, Bulgaria, Portugal, Spain, Libia, Italy, Greece, Ukraine, Armenia, Azerbaijan, Georgia, Turkey, Iran, Iraq, Pakistan, Turkmenistan, Uzbekistan, Tajikistan, Kirghizia, Kazakhstan; *Ph. tuberculatum* Jul. Møll. on *Rosa*: Ireland, UK, Norway, Sweden, Finland, Estonia, Latvia, Lithuania, Denmark, France, Germany, Poland, Switzerland, Austria, Czech Republic, Slovakia, Hungary, Romania, former Yugoslavia, Bulgaria, Portugal, Spain, Italy, Greece, Ukraine, Russia (European part, Siberia, Russian Far East), Armenia, Azerbaijan, Georgia, Turkey, Turkmenistan, Tajikistan, Kazakhstan, Pakistan, China (introduced to Australia and New Zealand); *Ph. violaceum* (Schultz) G. Winter on *Rubus*: Ireland, UK, Sweden, Denmark, France, Belgium, Germany, Switzerland, Austria, Czech Republic, Slovakia, Hungary, Albania, former Yugoslavia, Romania, Bulgaria,

Portugal, Spain, Italy, Greece, Ukraine, Armenia, Azerbaijan, Georgia, China, (introduced world-wide).

IV. Fourteen species distributed in North America:

Ph. alaskanum (Arthur) P. Syd. & Syd. on *Rubus*: USA (Alaska), Russia (Bering Island); *Ph. americanum* (Peck) Dietel on *Rosa*: USA (eastern and central parts); *Ph. biloculare* Dietel & Holw. on *Potentilla*: USA (Idaho, Washington); *Ph. guatemalense* Cummins on *Potentilla*: Guatemala; *Ph. horkeliae* Garrett on *Horkelia* Cham. & Schldl.: USA (Utah); *Ph. ivesiae* Syd. & P. Syd. on *Acaena*, *Horkelia*, *Ivesia* Torrey & A. Gray, *Potentilla*: USA (western and central parts), Canada (Saskatchewan, Alberta); *Phragmidium jonesii* Dietel on *Ivesia*, *Sanguisorba* L.: USA (Oregon, Nevada); *Ph. occidentale* Arthur on *Rubus*: Mexico, USA (western and central parts), Canada (western part); *Ph. peckianum* Arthur on *Rubus*: USA (western part); *Ph. rosae-arkansanae* Dietel on *Rosa*: USA (central part), Canada (Alberta); *Ph. rosae-californicae* Dietel on *Rosa*: USA (western part), Canada (British Columbia); *Ph. rosicola* (Ellis & Everh.) Arthur on *Rosa*: USA (Colorado, Montana, Nebraska), Mexico; *Ph. rubi-odorati* Dietel on *Rubus*: USA (eastern part), Canada (Ontario); *Ph. speciosum* (Fr.) Burrill on *Rosa*: USA (eastern and central parts), Canada (eastern and central parts).

V. Nine species distributed in Holarctic (Eurasia and North America):

Ph. andersonii Shear on *Potentilla*: Norway, Sweden, Latvia, Estonia, Russia (European part, Siberia), Kirghizia, China, Canada, USA; on *Cowanina* D. Don ex Tilloch & Taylor, *Dasiphora* Raf.: Russia (Russian Far East), USA; *Ph. arcticum* Lagerh. on *Rubus*: Norway, Sweden, Finland, Estonia, Lithuania, Russia (European part, Siberia, Russian Far East), China, Japan, Canada; *Ph. boreale* Tranzschel on *Potentilla*: Russia (Arctic Siberia), USA (western part), Canada (British Columbia); *Ph. fusiforme* J. Schrut. on *Rosa*: UK, Norway, Finland, Estonia, Denmark, France, Germany, Poland, Switzerland, Austria, Czech Republic, Slovakia, Hungary, former Yugoslavia, Romania, Bulgaria, Spain, Italy, Ukraine, Russia (Siberia, Russian Far East), China, Japan, USA, Canada; *Ph. montivagum* Arthur on *Rosa*: China, Korea, Japan, Russia (Siberia, Kamchatka, Sakhalin, Kuril Islands), North America (western part); *Ph. mucronatum* (Pers.) Schldl. on *Rosa*: introduced world-wide; *Ph. potentillae* (Pers.) P. Karst. on *Acaena*: Australia (introduced); on *Comarum*: Poland; on *Dasiphora*: China; on *Duchesnea* Sm.: China; on *Potentilla*: Ireland, UK, Norway, Sweden, Finland, Denmark, France, Germany, Poland, Lithuania, Latvia, Estonia, Switzerland, Austria, Czech Republic, Slovakia, Hungary, Romania, Bulgaria, Spain, Italy, Greece, Ukraine, Russia (European part, Siberia, Russian Far East), Armenia, Azerbaijan, Georgia, Turkey, Iran, Turkmenistan, Uzbekistan, Tajikistan, Kazakhstan, Kirghizia, China, Japan, Korea, USA, Mexico; *Ph. rosae-pimpinellifoliae* Dietel on *Rosa*: Ireland, UK, Norway, Sweden, Finland, Estonia, Denmark, France, Germany, Poland, Austria, Czech Republic, Slovakia, Hungary, former Yugoslavia, Romania, Bulgaria, Spain, Ukraine, Russia (European part),

Armenia, Azerbaijan, Georgia, Iran, Kirghizia, USA; *Ph. rubi-idaei* (DC.) P. Karst. on *Rubus*: Ireland, UK, Norway, Sweden, Finland, Estonia, Latvia, Lithuania, Denmark, France, Germany, Poland, Switzerland, Austria, Czech Republic, Slovakia, Hungary, Romania, Bulgaria, Portugal, Spain, Italy, Ukraine, Russia (European part, Siberia, Kuril Islands, Kamchatka, Sakhalin), Armenia, Azerbaijan, Georgia, Kazakhstan, Kirghizia, China, Korea, Japan, USA, Canada (introduced to Australia and New Zealand).

VI. Six species distributed in the Southern Hemisphere:

Ph. acaenae G. Cunn. on *Acaena* Mutis ex L.: New Zealand; *Ph. acaenincola* Petr. on *Acaena*: Australia; *Ph. barnardii* Plowr. & G. Winter on *Rubus*: Australia; *Ph. constrictosporum* G.F. Laundon on *Acaena*: New Zealand; *Ph. novae-zelandiae* G. Cunn. on *Acaena*: New Zealand; *Ph. subsimile* G. Cunn. on *Acaena*: New Zealand.

Discussion

The geographical distribution of *Phragmidium* clearly reveals its Holarctic and Pacific (mainly East-Asian) affinity. No indigenous species of this genus has so far been recorded from Africa (except from its Mediterranean part) or South America. The spread of some economically important species (*Ph. mucronatum*, *Ph. rubi-idaei*, etc.) to regions outside Holarctic is definitely the result of human activity. East Asia is a very special region biogeographically, being regarded as the centre of origin for many temperate angiosperms [9] and placental mammals [2] in the Northern Hemisphere. Powdery mildews (Erysiphales) are apparently also of East Asia origin [1]. In geographic terms the *Phragmidium* species follow this pattern. There are four easily identifiable centres of endemism: 1) East Asia, 2) South and Central Asia, 3) Western North America, and 4) New Zealand. The first two regions rival each other in their numbers of endemic species but East Asia might be regarded as even more significant, being more temperate and providing a better fit for the typical ecological requirements of *Phragmidium*. Two species — *Ph. zeylanicum* and *Ph. guatemalense* mark the southernmost limits of the range of *Phragmidium* in Asia and North America respectively. *Ph. alaskanum*, *Ph. boreale* and *Ph. montivagum* evidently follow the Beringian track of floristic exchange between East Asia and North America. As a result, a hypothesis can be proposed that the genus *Phragmidium* originated in the area northeast of the Tethys ocean gap and, after that gap was closed by collision of India and Arabia with the Asian plate, the genus spread westwards (which gave rise to species of rather narrow distribution in Western China, Himalaya, Pakistan, Central Asia and Iran) and northwards to Northern Eurasia and North America (mainly resulted in widespread Holarctic and Eurasian species). Almost all phragmidiums which occur in Europe are wide-ranged Eurasian and Holarctic rusts. Only *Ph. candicantium* could be regarded as the species with European distribution. The origin of New Zealand and Australian representatives is still unclear. The range of *Acaena* includes Australia, New Zealand, some

subantarctic islands, Andean part of South and Central America, California and Hawaii but members of *Phragmidium* parasitizing plants of this genus are restricted to New Zealand and Australia. Future molecular phylogenetic investigations might answer the question of whether South Hemisphere species of *Phragmidium* are closer to their North American or Asian relatives. The historical scale for the main dispersal and vicariance events in the evolution of the *Phragmidium* can be framed only tentatively, but it seems possible that the Central and South Asian group is not older than the time of closing of the Tethys gap (Oligocene — Miocene boundary, about 23 million years ago).

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ГЕОГРАФІЧНЕ ПОШИРЕННЯ РОДУ *PHRAGMIDIUM* LINK

Рід *Phragmidium* (Uredinales) об'єднує одногосподарних паразитів під родини Rosoideae. Відомо понад 150 видових назв, але визнаними є лише близько 90 видів. У географічному поширенні роду чітко виявляються його голарктичні та тихоокеанські зв'язки. Згідно з ними види *Phragmidium* можна розподілити на шість груп: 1) східноазіатські; 2) центральні та південноазіатські; 3) євразіатські; 4) північноамериканські; 5) голарктичні;

б) види, поширені у південній півкулі. З точки зору географії може бути запропонована гіпотеза щодо виникнення роду в регіоні на північний схід від океану Тетис і його поширення на захід та північ після зіткнення Індії та Аравії з азіатською плитою і закриття Тетису. Поширення на захід призвело до виникнення видів з досить обмеженими ареалами у Західному Китаї, Гімалаях, Пакистані, Середній Азії та Ірані. Поширення на північ до Північної Євразії та Північної Америки головним чином дало початок голарктичним та євразійським видам з широкими ареалами. Походження новозеландських та австралійських видів роду *Phragmidium* залишається нез'ясованим.

Ключові слова: *Phragmidium*, географічне поширення, центр походження

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ГЕОГРАФИЧЕСКОЕ РАСПРОСТРАНЕНИЕ РОДА *PHRAGMIDIUM* LINK

Род *Phragmidium* (Uredinales) объединяет однохозяйных паразитов подсемейства *Rosoideae*. Известно более 150 видовых названий, но признаны лишь около 90 видов. В географическом распространении рода четко проявляются его голарктические и тихоокеанские связи. Виды *Phragmidium* согласно их распространению можно распределить на шесть групп: 1) восточноазиатские; 2) центрально- и южноазиатские; 3) евразийские; 4) североамериканские; 5) голарктические; 6) виды, распространенные в южном полушарии. С точки зрения географии может быть предложена гипотеза о возникновении рода в регионе на северо-восток от океана Тетис и распространении его на запад и север после столкновения Индии и Аравии с азиатской плитой и закрытия Тетиса. Распространение на запад привело к возникновению видов с довольно узкими ареалами в Западном Китае, Гималаях, Пакистане, Средней Азии и Иране. Распространение на север в Северную Евразию и Северную Америку главным образом дало начало голарктическим и евразийским видам с широкими ареалами. Происхождение новозеландских и австралийских видов рода *Phragmidium* остается невыясненным.

Ключевые слова: *Phragmidium*, географическое распространение, центр происхождения