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Phylogenetic systematics and biogeography of *Coptis* (Ranunculaceae), an eastern Asian and North American genus

K.-L. Xiang¹, A.S. Erst^{2,3}, T.V. Erst^{3,4}, W. Wang^{1*}

¹ State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing, China; xiangkunli@ibcas.ac.cn, wangwei1127@ibcas.ac.cn

² Central Siberian Botanical Garden, SB RAS, Novosibirsk, Russia; erst_andrew@yahoo.com, tatiana_erst@yahoo.com

³ Tomsk State University, Tomsk, Russia; erst_andrew@yahoo.com

⁴ Institute of Cytology and Genetics SB RAS, Novosibirsk, Russia; tatiana_erst@yahoo.com

Abstract. The goldthread genus *Coptis* includes 15 species disjunctly distributed in eastern Asia and North America. Here, we provide a dated phylogeny for the genus with all 15 species. Our results indicate that *Coptis* contains two strongly supported clades (I and II). Clade I consists of subg. *Coptis* and sect. *Japonocoptis* of subg. *Metacoptis*; clade II composes sect. *Japonocoptis* of subg. *Metacoptis*. Central leaflet base, sepal shape, and petal blade carry a strong phylogenetic signal in *Coptis*, while leaf type, sepal and petal color, and petal shape exhibit relatively higher levels of evolutionary flexibility. Our dating and biogeographic analyses indicate that a vicariance event between Japan-North America occurred in the middle Miocene, resulting in the split of *Coptis* and its sister group. Subsequently, a colonization event occurred at 9.55 Ma from Japan to mainland China. Both vicariance and dispersal events have played important roles in shaping the current distribution and endemism of *Coptis*, likely resulting from eustatic sea-level changes, mountain formation processes and an increasing drier and cooler climate from the middle Miocene onwards.

Keywords: ancestral range evolution, climate change, *Coptis*, eastern Asian, monophyly, phylogenetics, Taiwan, western of North America.

Филогенетическая систематика и биогеография восточноазиатско-североамериканского рода *Coptis* (Ranunculaceae)

К.-Л. Хiang¹, А.С. Эрст^{2,3}, Т.В. Эрст^{3,4}, W. Wang¹

¹ Государственная лаборатория систематики и эволюционной ботаники Института ботаники Китайской академии наук, Пекин, Китай; xiangkunli@ibcas.ac.cn, wangwei1127@ibcas.ac.cn

² Центральный сибирский ботанический сад СО РАН, Новосибирск, Россия; erst_andrew@yahoo.com, tatiana_erst@yahoo.com

³ Томский государственный университет, Томск, Россия; erst_andrew@yahoo.com

⁴ Институт цитологии и генетики СО РАН, Новосибирск, Россия; tatiana_erst@yahoo.com

Аннотация. Род *Coptis* включает 15 видов, разрозненно распространенных в Восточной Азии и Северной Америке. В статье приведена филогения всех 15 видов рода. Наши результаты показывают, что *Coptis* содержит две высоко поддерживаемые клады (I и II). Клада I включает род *Coptis* и секцию *Japonocoptis* подрода *Metacoptis*; клада II состоит из секции *Japonocoptis* подрода *Metacoptis*. Основание центрального листочка, форма чашелистика и лепестка имеют у *Coptis* сильный филогенетический сигнал, тогда как тип листа, цвет чашелистика и лепестка, а также форма лепестка демонстрируют относительно более высокие уровни эволюционной гибкости. Наши датировки и биогеографические анализы показывают, что событие викарии между Японией и Северной Америкой произошло в среднем миоцене, что привело к разделению рода *Coptis* и его сестринской группы. Впоследствии событие колонизации произошло в 9,55 млн лет назад от Японии до материкового Китая. События как колонизации, так и расселения сыграли важную роль в формировании современного распространения и эндемизма *Coptis*, вероятно, в результате эвстатических изменений уровня моря, процессов горообразования и более сухого и прохладного климата, начиная со среднего миоцена.

Ключевые слова: эволюция ареала предков, изменение климата, *Coptis*, Восточная Азия, монофилия, филогенетика, Тайвань, запад Северной Америки.

The goldthread genus *Coptis* (Ranunculaceae) is of pharmaceutical and economical importance and is mainly distributed in the warm temperate to the cold coniferous forests of eastern Asia and North America (Tamura, 1995). Dried rhizomes of *Coptis* plants are utilized for *Rhizoma Coptidis* (RC), a traditional Chinese medicine famous for its functions of clearing heat, dispelling dampness, and purging fire toxins. In marked contrast to the extensive knowledge about the pharmacological properties of *Coptis*, understanding of evolutionary history of the genus is extremely limited. In this study, we first reconstruct a dated phylogeny for *Coptis* based on six DNA markers, using a Bayesian relaxed clock method. Using the resulting dated-phylogenetic framework, we then infer the ancestral range evolution of *Coptis* under the best-fitting biogeographic model.

The dated phylogeny of *Coptis* inferred from the six marker data (cpDNA: *rbcl*, *trnL* intron, *trnL-F* spacers, *trnD-trnT*, and *trnH-psbA*; nrDNA: ITS) is shown in Figure 1. Within *Coptis*, two major clades (I and II) were identified. Clade I consists of subgenus *Coptis* and sect. *Japonocoptis* of subg. *Metacoptis*, supported by sessile central leaflets, elliptic sepals, petals non-concolorous with sepals, and cup-shaped petals.

Clade II consists of sect. *Chrysocoptis* of subg. *Metacoptis*, characterized by petiolate central leaflets, lanceolate to linear sepals, and epeltate petals. Thus, two subgenera of *Coptis* all needs adjustment to attain monophyly.

The split of *Coptis* and *Xanthorrhiza* occurred in the middle Miocene (*ca.* 15.47 Ma; node 1). *Coptis* started their diversification in the early late Miocene (*ca.* 9.55 Ma; node 2). A DIVALIKE was found to be the best-fitting model for *Coptis*. Our ancestral range estimation indicate that a late Miocene vicariance event resulted in the eastern Asian and western North American disjunction in the genus (*ca.* 7.78 Ma; node 3), and within eastern Asia, dispersals from mainland Asia to Japan and from Japan to Taiwan occurred at *ca.* 4.85 Ma (node 4) and at *ca.* 1.34 Ma (node 5), respectively.

The eustatic sea-level changes, mountain formation processes and an increasing drier and cooler climate from the middle Miocene onwards might have been responsible for these biogeographic events. This study shed light on the past floristic exchanges between East Asia and North America, as well as within East Asia.

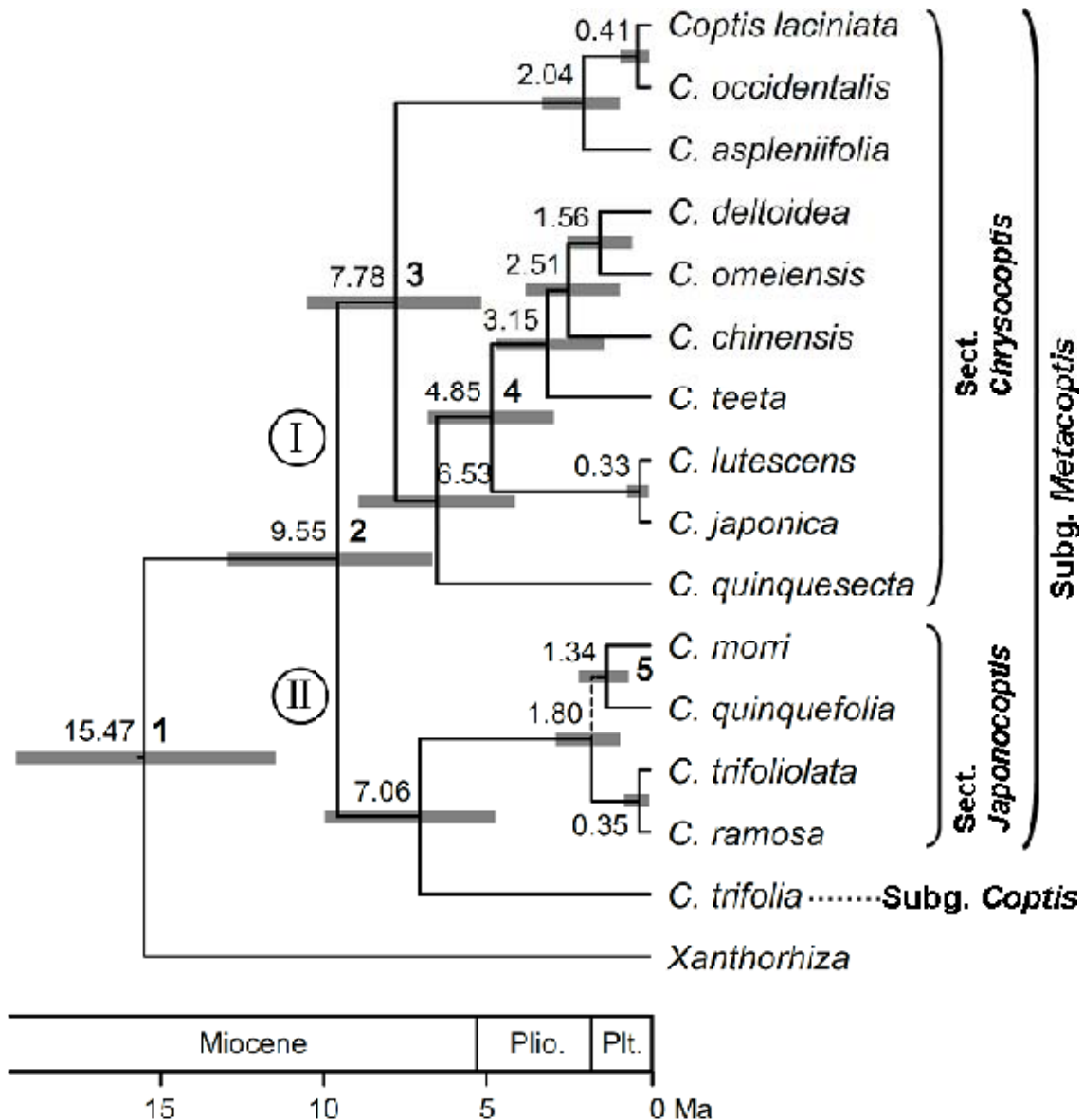


Figure 1. Dated phylogeny of *Coptis* inferred from the six marker data using BEAST
 Gray bars represent 95 % highest posterior density intervals. Nodes of interests were marked as 1–5 in bold

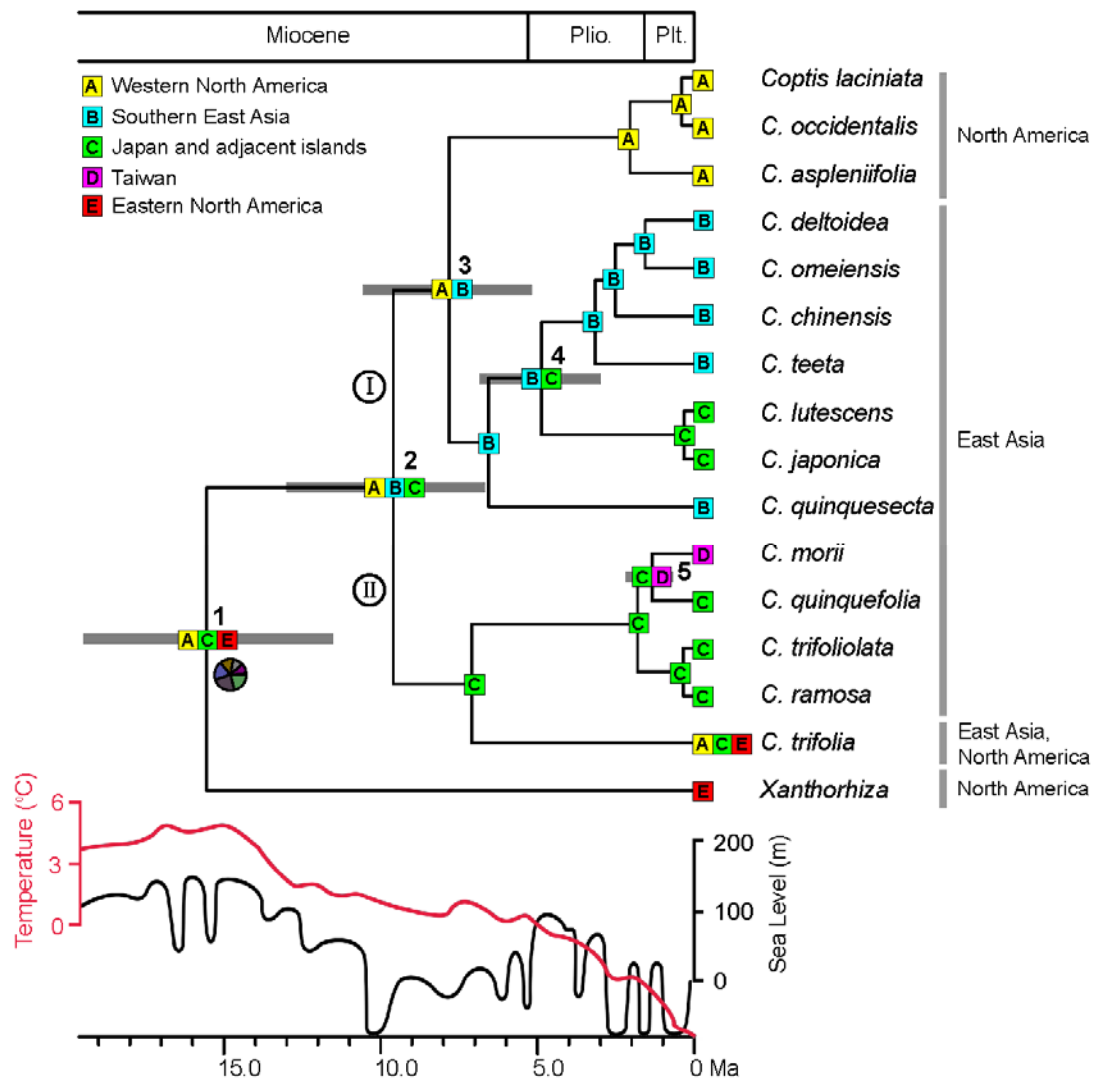


Figure 2. Ancestral range estimation for *Copits* using BioGeoBEARS under the DIVALIKE model

Labeled nodes (1 to 5, as referred to Figure 1), with 95% highest posterior densities (grey bars). The estimated ancestral ranges with the highest ML probability are shown by boxes on each node. A pie is placed in this figure at the root with the highest probability less than 50%. The depictions of temperature (in red) and sea level (in black) changes are modified from Zachos et al. (2001) and Haq et al. (1985), respectively.

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