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CITRUS LINCZANGENSIS SP. N., A LEAF FOSSIL OF RUTACEAE FROM THE LATE MIOCENE OF YUNNAN, CHINA

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Premise of research. The origin and phytogeographic history of *Citrus* (Rutaceae) is poorly known, partly because of the very limited fossil record of this genus. Our newly discovered fossil materials confirm the existence of *Citrus* in the late Miocene in Asia.

Methodology. Fossil leaves were collected from the field, carefully exposed in the laboratory, and investigated through comparison of architectural characters with extant leaves.

Pivotal results. A new species, *Citrus linczangensis* sp. n., from the late Miocene of Lincang, Yunnan, China, is characterized by unifoliolate compound leaf morphology, an articulated and broadly winged petiole, and an entire margined leaflet with basal intramarginal veins.

Conclusions. The unique morphological characters of this fossil provide definitive evidence of *Citrus* in the fossil record of Asia and expand the geological history of the genus back to the late Miocene. The new fossil material gives some clues for the origin of modern *Citrus* species and supplements knowledge of the Lincang fossil flora.

Keywords: *Citrus*, Lincang, Miocene, Rutaceae, Yunnan.

Introduction

The Rutaceae, a large angiosperm family in the Sapindales, contains ~155 genera with ~1600 species and is distributed nearly worldwide but mainly in tropical and subtropical areas, especially of southern Africa and Australia (Zhang et al. 2008). Engler (1931) recognized seven subfamilies (Rhabdodendroideae, Aurantioideae, Flindersioideae, Spathelioideae, Dicytomatoideae, Rutoideae, and Toddaloideae) on the basis of gynoecial and fruit characters. Afterward, the subfamilies of Rutaceae have been rearranged several times (Bayer et al. 2009; Schwartz 2011), but most of these groups are still non-monophyletic (Chase et al. 1999; Scott et al. 2000). However, the citrus subfamily, Aurantioideae, is supported to be monophyletic by both morphological characteristics and molecular studies (Penjor et al. 2010; Schwartz 2011; Mou and Zhang 2012). The Aurantioideae, with 33 genera and 203 species, consists of two tribes (Swingle and Reece 1967), Clauseneae (subtribes: Micromelinae, Clauseninae, and Merrillinae) and Citreae (subtribes: Triphasiinae, Citrinae, and Balsamocitriinae). In the tribe Citreae, species are easily distinguished from those of Clauseneae by axillary spines and simple, unifoliolate (or trifoliolate) leaves. Subtribe Citrinae differs from all the

other five subtribes in the Aurantioideae by having pulp vesicles in the fruit and is comprised of three groups: primitive citrus fruit trees, near citrus fruit trees, and true citrus fruit trees (Swingle and Reece 1967). The latter group—including *Fortunella*, *Eremocitrus*, *Poncirus*, *Chymenia*, *Microcitrus*, and *Citrus*—has been supported as a monophyletic clade (Bayer et al. 2009) and is characterized by persistent unifoliolate or simple leaves (except *Poncirus*, which has trifoliolate leaves; Swingle and Reece 1967).

The genus *Citrus*—containing 20–25 species distributed in east, south, and southeast Asia and Australia and the southwest Pacific Islands (Zhang et al. 2008)—has undergone a long history of cultivation, resulting in many edible cultivars. The first mention of *Citrus* fruits in China was reported in the *Book of Odes*, written in the Chou dynasty (1122–240 BC; Dugo and Giacomo 2002). It is difficult to ascertain the center of origin of most *Citrus* species (Mabberley 2004), since they have been subjected to natural hybridization and probably also cultivation for a very long time. The delimitation and classification of *Citrus* (Araújo et al. 2003) has proven particularly difficult as a result of the numerous cultivars and hybrids, including spontaneous mutants. According to Scora (1975) and Mabberley (1997), three species—*Citrus maxima* (Burman) Merrill. (pomelo), *Citrus medica* L. (citron), and *Citrus reticulata* Blanco (mandarin)—are the parent species of all the citrus crops known today. *Citrus maxima* and *C. reticulata* originated in China, and *C. medica* originated in India (Spiegel-Roy and Goldschmidt 1996).

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All other species are believed to be derived from cross-pollination among these three. However, in spite of a long history of cultivation of *Citrus* and its close relatives, the early origin of *Citrus* in geological history is still poorly known because of the lack of fossil record coupled with the discrepancies between morphologically based classifications and molecular-based phylogenetic hypotheses for the Rutaceae.

The Rutaceae is well represented in the Cenozoic of the Northern Hemisphere, on the basis of seeds and fruits (Gregor 1989) of both extinct (Manchester and Zastawniak 2007) and extant (Call and Dilcher 1995) genera. Rutaceous seeds are reported from the Eocene to Miocene of Europe (e.g., Tiffney 1981; Collinson and Gregor 1988; Collinson et al. 2012), North America (e.g., Tiffney 1980), and Asia (e.g., Li et al. 2013). Leaves (WG CPC 1978; Pan 2010; Guo 2011) and woods (Gregory et al. 2009) of Rutaceae are also reported from the Cenozoic of Europe, Asia, and Africa. On the basis of samaras, Call and Dilcher (1995) revised the Miocene records of *Ptelea* (subfamily Toddalioidae), and Manchester and O'Leary (2010) expanded the fossil history of that genus back to the middle Eocene. So far, the fossils reported have mostly been assigned to the subfamilies Rutoideae and Toddalioidae; however, records of the Aurantioideae are less well known. A fossil leaf assigned to *Citrus meletensis* from the Pliocene of Italy (Fischer and Butzmann 1998) indicates that *Citrus* occurred outside of its modern native geographic distribution in the geologic past. Otherwise, the fossil record of *Citrus* is scant, and no definitive examples have been documented in Asia.

In this article, we describe a new species of *Citrus* from the late Miocene strata of the Bangmai Formation of Lincang, Yunnan, southwestern China, and discuss its importance for understanding the evolutionary history and distribution of this economically important genus. This occurrence augments our knowledge of fossil history of the family Rutaceae and especially the subfamily Aurantioideae.

Material and Methods

The fossil leaf specimens were collected in February 2009 and December 2011 from coal-bearing strata of the Bangmai Formation from an open-cast coal mine (23°54'N, 100°0'E) of Bangmai Village, about 10 km northwest of Lincang City, Yunnan, China. The Bangmai Formation contains abundant fossil plants and is considered to be of late Miocene age, on the basis of floristic and stratigraphic correlations (Zhang 1996; Ge and Li 1999; Hu et al. 2009). The flora of this formation was initially studied by Tao and Chen (1983); subsequent lists of the fossil plant species from the site were published by Guo and Chen (1989) and Ge and Li (1999). Recently, Guo (2011) presented a comprehensive investigation based on previously collected fossils. However, *Citrus* fossils were unknown from previous investigations of the Bangmai Formation.

The fossils were recovered by fracturing the weakly consolidated rocks with hammer and spade. Two *Citrus* leaf specimens were collected, each represented by part and counterpart impressions in siltstone. They were photographed with a Sony T70 digital camera and described using standard terminology (Ellis et al. 2009).

Extant *Citrus* material of about 16 species from the Kunming Institute of Botany, Chinese Academy of Science (KUN),

China, and the Florida Museum of Natural History (FLAS) was examined and compared with the fossils. The fossil specimens are housed at the Institute of Palaeontology and Stratigraphy, Lanzhou University, Gansu Province, China.

Systematics

Family—Rutaceae Juss., 1789

Subfamily—Aurantioideae Swingle and Reece 1967

Genus—*Citrus* L. 1753

Species—*Citrus linczangensis* sp. n. (Fig. 1)

Specific diagnosis. Unifoliolate compound leaf, leaflet (i.e., the apical part of the leaf) entire margined, symmetrical, ovate, with round base, length : width ratio ~1.5 : 1; leaflet venation pinnate; secondary veins camptodromous, joining to form an intramarginal vein; intersecondary veins common; petiole conspicuously winged, articulated with base of leaflet; petiole wing (i.e., the basal part of the leaf) entire margined, symmetrical, basally acute with cordiform apex, and with pinnate venation with secondary veins merging into an intramarginal vein.

Holotype. LUMCD090206-022A&B, Institute of Palaeontology and Stratigraphy, Lanzhou University, China, here designated (fig. 1A, 1B, 1D, 1E).

Type locality. Bangmai Village (23°54'N, 100°0'E), Lincang City, Yunnan Province, China.

Paratype. LUMCD090225-012A&B, Institute of Palaeontology and Stratigraphy, Lanzhou University, China, here designated (fig. 1C, 1F, 1G).

Horizon and age. Bangmai Formation, late Miocene.

Etymology. The specific epithet refers to Lincang City, where the fossil specimens were collected.

Description. Unifoliolate compound leaf. Leaf length ~7 cm, maximum width 3.3 cm (fig. 1A). Leaflet ovate, symmetrical, entire margined, length at least 5 cm, maximum width 3.3 cm (fig. 1A); venation pinnate, with at least 11 pairs of secondary veins arising decurrently from the midvein angles of 56°–76°; secondary veins camptodromous, joining to form an intramarginal vein 0.5–1.1 mm from the leaf margin in the basal part of the leaf; some secondary veins dichotomizing in apical portion of the leaf, about one-third of the distance from margin; intersecondary veins common, extending more than half the length of subjacent secondary. Tertiary veins reticulate, arising horizontally from secondary veins and joining to subjacent secondary veins; higher-order veins obscure (fig. 1B). Petiole up to 9 mm long, conspicuously winged, articulated with base of leaflet (fig. 1C, 1D); wing cordiform, decurrent on the petiole, entire margined, about 1.6–2.4 cm wide and 1.5–2.3 cm long (1.5–2.3 × 1.6–2.4 cm), symmetrical, basally acute with retuse apex (fig. 1E, 1F), and has pinnate venation including an intramarginal vein (fig. 1G).

Discussion

Systematic Considerations

This leaf morphotype is characterized by the unusual feature of the winged petiole and a single leaflet indicating unifoliolate

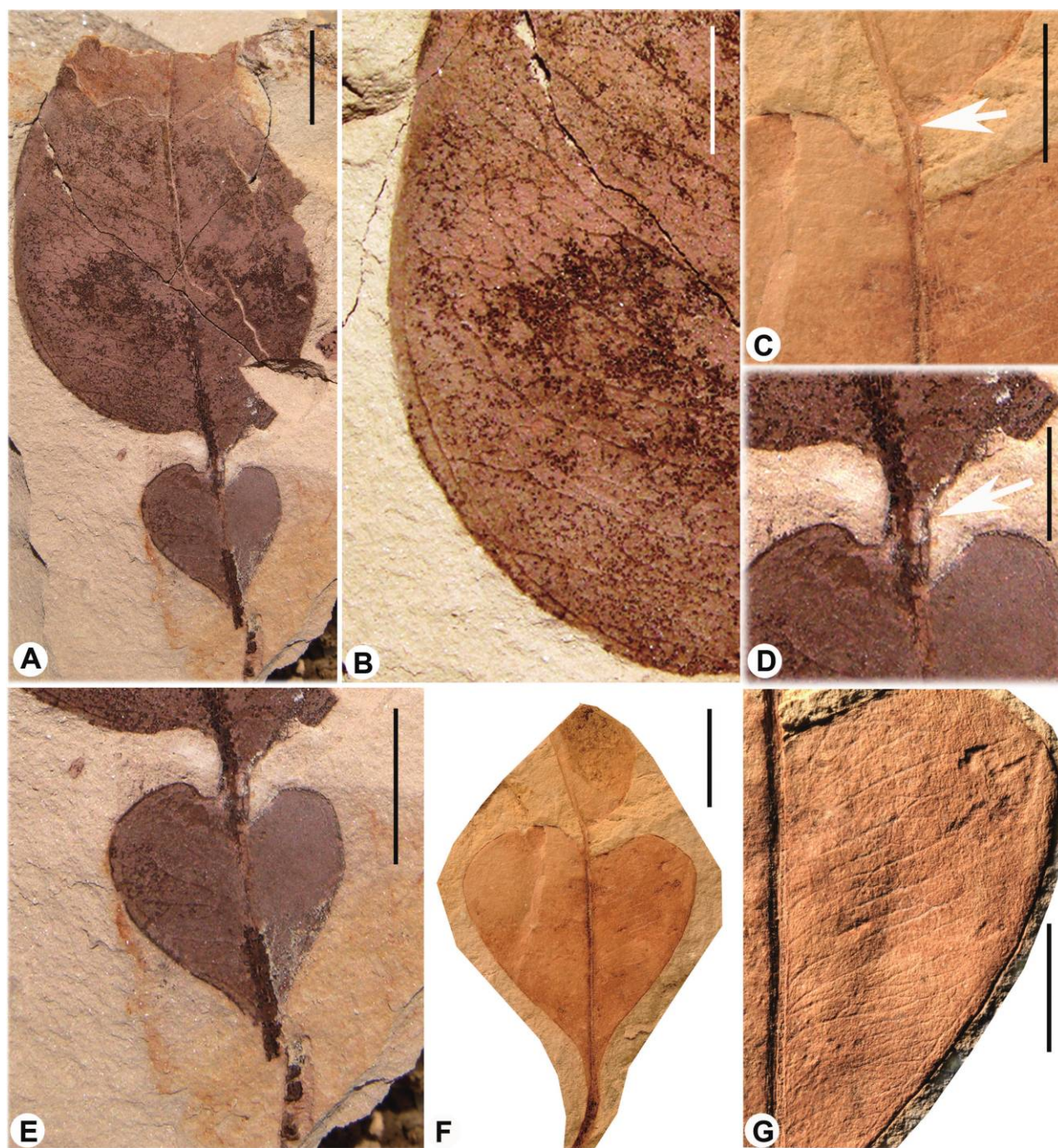


Fig. 1 *Citrus linczangensis* sp. n. **A**, Whole leaf, holotype specimen LUMCD090206-022A, showing the size and the proportion. Scale bar = 1 cm. **B**, Details of leaflet in **A** showing the intramarginal vein, entire margin, and fine venation. Scale bar = 5 mm. **C**, **D**, Articulated petiole, LUMCD090225-012A and LUMCD090206-022A; arrows point to the articulated nodes. Scale bar = 5 mm. **E**, **F**, Petiole wing, LUMCD090206-022A and LUMCD090225-012A; note the size variation. Scale bar = 1 mm. **G**, Petiole wing venation, LUMCD090225-012A, showing pinnate venation and an intramarginal vein. Scale bar = 5 mm.

morphology. Winged petioles or rachises occur in several angiosperm families, including Anacardiaceae, Cunoniaceae, Juglandaceae, Rutaceae, and Sapindaceae. Leaves of Rutaceae can be distinguished from those of the other families by several features, including differences in leaf architecture (unifoliolate

vs. pinnately compound leaves) and leaf margin. *Pterocarya stenoptera* C. de Candolle (Juglandaceae) leaves often possess winged rachises, but the uniformly serrate leaflet margins and pinnately compound leaves differ from *Citrus*. *Harpullia alata* F. Muell. (Sapindaceae) also possesses a winged petiole and



rachis, but its irregularly toothed margin and narrower leaflet shape is readily distinguished from our specimens. *Weinmannia* L. (Cunoniaceae) and *Rhus* L. (Anacardiaceae) display pinnately compound leaves with a different margin type than our fossil specimens. Within Rutaceae, some genera—for example, *Galipea* Aubl., *Burkillanthus* Swingle, *Citrus*, *Fortunella* Swingle, and *Paramignya* Wight—may have winged and articulated petioles, but in most cases (excluding *Citrus*), the wing is considerably smaller (Fischer and Butzmann 1998) than found in *Citrus linczangensis*. The genus *Chymenia* Swingle is a close relative of *Citrus* with similar leaf morphology. However, it can be separated from most *Citrus* species by the lack of articulation between leaflet and petiole wing and by its short petiole, ~1/10–1/20 the length of the leaf blade, which is readily distinguished from that of *Citrus linczangensis* (~1/8).

The fossil leaves resemble *Citrus* in the combination of characteristics including the possession of an articulated and broadly winged petiole, an intramarginal venation that is well developed in the lower part of the lamina, and an entire margin (the latter feature known only in *Citrus maxima*; fig. 2E). The presence of an intramarginal vein in the lower part of the lamina, giving way to standard secondary looping in the upper part of the lamina, is a distinctive feature sometimes seen in *Citrus reticulata* (fig. 2A) and *Citrus aurantifolia* (fig. 2B). Although some species of *Citrus* lack an intramarginal vein (fig. 2C–2F) and in some species its occurrence is variable, the presence of this feature in the fossil helps to support our assignment to this genus. The entire margin observed in the fossils also occurs in *C. maxima* (fig. 2E); however, other extant species have crenulate margins (fig. 2A–2D, 2F). Hence, leaf margin types in *Citrus* are species specific, and the entire margin does not preclude our assignment of the fossils to this genus. Shapes and sizes of petiole wing within *Citrus* are also variable, from inconspicuous (fig. 2A, 2F) through medium (fig. 2E) to much larger (fig. 2D). Among extant *Citrus* species, our fossils show affinity with *C. maxima* (fig. 2E) on the basis of their overall shape and proportions, especially their cordate shape of petiole wing and entire margin. However, because no extant species resembles this fossil in all characters, the designation of *Citrus linczangensis* as a new species seems to be well justified.

The oldest *Citrus*-like leaf remains were assigned to the morphogenus *Citrophyllum* from the Cretaceous (Cenomanian) of North America (Berry 1914; as *Ficus aligera* in Lesquereux 1892), but their phylogenetic relationship with extant *Citrus* has been regarded as doubtful (Gregor 1989). So far, only one previous study definitely assigned a fossil leaf to *Citrus*, that is, *Citrus meletensis* from the Pliocene of Italy (Fischer and Butzmann 1998). *Citrus linczangensis* and *C. meletensis* share some important characters—such as an intramarginal vein, an entire margin, and an articulated and distinctly winged petiole—but they are distinguished by leaf size (much smaller in

C. meletensis), the ratio of length : width (much larger in *C. meletensis*), and the wider and bigger petiole wing in *C. linczangensis*. Additional fossil material previously named *Hesperidophyllum senogalliense*, also from the Neogene of Italy, was considered synonymous with *C. meletensis* by Fischer and Butzmann (1998), although it shows an even narrower petiole wing.

Citrus was also reported on the basis of a leaf fossil from the Paleocene-Eocene boundary of Guangdong, China, by Guo (1979). However, the entire-margined lamina would be difficult to distinguish from that of numerous other angiosperm families and genera. It does not possess diagnostic characteristics, such as a winged rachis. The Lincang specimens, however, allow for a confident determination of fossil *Citrus* and provide definite evidence of the existence of *Citrus* within its native habitats since at least late Miocene.

Fossil History of the Rutaceae

The fossil history of Rutaceae (subfamilies Rutoideae and Toddalioidae) has been summarized in detail (Gregor 1989), but additional records have accumulated since then. Pollen records that have been attributed to Rutaceae (i.e., *Rutaceoipollis* Sung et Tsao 1978 ex 1980) have been traced back to the Late Cretaceous in China but are mainly confined to the Cenozoic (Song et al. 2004). The earliest reliable record of Rutaceae is considered to be *Rutaspermum biornatum* from the Late Cretaceous of Germany (Knobloch and Mai 1986), although some biogeographic investigations (Appelhans et al. 2012) have inferred a possible African origin. Among Rutaceae, the subfamilies Rutoideae (e.g., *Zanthoxylum*, *Fagara*, *Evodia*, and *Rutaspermum*) and Toddalioidae (e.g., *Phellodendron*, *Fagaropsis*, and *Toddalia*) are widely distributed in the Cenozoic sediments of the Northern Hemisphere, with abundant seed records beginning in the Eocene (Collinson et al. 2012). *Ptelea* fruits have been recognized from the Miocene (Call and Dilcher 1995) and Eocene (Manchester and O'Leary 2010) of western North America.

Besides the subfamilies mentioned above, the only other subfamily for which fossils are known is the Aurantioideae. Recent reports on Aurantioideae fossils give us the opportunity to trace its fossil history. Pan (2010) reported a *Clausena* leaf fossil from the Oligocene of Ethiopia, representing the oldest record of the subfamily, and suggested an African origin for this group. The leaf fossils *C. meletensis* from the Pliocene of Italy (Fischer and Butzmann 1998) and *C. linczangensis* treated herein provide additional fossil evidence of Aurantioideae.

Because of the many cultivars of great economic value of *Citrus*, the origin and phylogenetic history of this genus and its subfamily have attracted the interest of many botanists (Gmitter and Hu 1990; Pfeil and Crisp 2008). Some studies (Spiegel-Roy and Goldschmidt 1996; Mabberley 2004) have recognized three to eight original species of *Citrus* apart from

Fig. 2 Extant *Citrus* leaves for comparison. Photograph from Kunming Institute of Botany, Chinese Academy of Science, China. Scale bar = 1 cm. A, *Citrus reticulata* Blanco (KUN0595327). B, *Citrus aurantifolia* (Christ) Swing. (KUN0595172). C, *Citrus limonia* Osbeck. (KUN0595268). D, *Citrus cavaleriei* H. Léveillé ex Cavalerie (KUN0595223). E, *Citrus maxima* (Burman) Merrill. (KUN0515919). F, *Citrus medica* L. (KUN0812727).

many derived wild hybrids and cultivated species, but its fossil history before archeological records are less known. *Citrus meletensis* (Fischer and Butzmann 1998) confirms that *Citrus* occurred in the Pliocene of Europe and outside of its modern native geographic distribution. In addition, recognition of *C. linczangensis* in the late Miocene of Yunnan, China, expands the fossil history of this genus and implies that southwestern and southern China (Gmitter and Hu 1990) may be one of potential areas of early diversification and supports the hypothesis of southeastern Asia origin of *Citrus* (Nicolosi et al. 2000).

Evolutionary Implications

Citrus consists of two subgenera, *Papeda* and *Citrus*, recognized by Swingle and Reece (1967) on the basis of the presence of acridic oil in the fruit and the width of the petiole wing compared with leaflets. This division has been supported by some studies of molecular phylogeny (Nicolosi et al. 2000). Subgenus *Papeda* has a wing with a width more than 3/4 that of the leaflet (e.g., *C. cavaleriei*; fig. 2D), whereas in subgenus *Citrus*, the wing is subcordate and the petiole wing is less than 3/4 width that of the leaflet (e.g., *C. maxima*; fig. 2E). According to this criterion, our fossil species would be assigned easily to the subgenus *Citrus*, but its petiole wing is much longer and wider than exists in extant species of subgenus *Citrus* (fig. 2A, 2E). A previous study (Scora 1975) concluded

that a relatively larger petiole wing may be a primitive condition within *Citrus*. This concept seems to be supported by the especially large petiole wing in our fossil *C. linczangensis*, which is nearly half the width of the leaflet, but we do not have enough specimens to judge the variability that might have been present. So far, *C. linczangensis* represents the oldest reliable record of *Citrus* and provides an important node for inferring the evolutionary history of extant species in subgenus *Citrus*.

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