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Malus includes *Docynia* (Maleae, Rosaceae): evidence from phylogenomics and morphology

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Running title: *Malus* includes *Docynia*

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Abstract: *Docynia* has been treated as a separate genus or merged into *Cydonia* or *Docyniopsis*. Our phylogenomic evidence from 797 single-copy nuclear genes and plastomes confirmed the sister relationship between *Docynia* and *Docyniopsis*. Integrating the phylogenomic and morphological evidence, we propose to accept a broad generic concept of *Malus* and merge *Docynia* into *Malus*. Three new combinations are also made here: *Malus delavayi* (Franch.) B.B.Liu, *M. indica* (Colebr.) B.B.Liu, and *M. longiunguis* (Q.Luo & J.L.Liu) B.B.Liu.

Keywords: *Docynia*, *Malus*, nomenclatural transfer, phylogenomics, taxonomy

Introduction

Docynia Decne. is a genus of apple-related plants endemic to East and Southeast Asia and comprises approximately three species: *D. delavayi* (Franch.) C.K.Schneid., *D. indica* (Colebr. ex Wall.) Decne., and *D. longiunguis* Q.Luo & J.L.Liu (Yu and Ku 1974; Gu and Spongberg 2003; Luo et al. 2011). Due to the easily distinguished multiple ovules per locule (3-10 in *Docynia* vs. 2 in *Malus* Mill.), *Docynia* has been recognized as a separate genus in a series of taxonomic treatments (i.e., Decaisne 1874; Focke 1888; Koehne 1893; Rehder 1940, 1949; Yu and Ku 1974; Robertson et al. 1991; Kalkman 2004). However, due to the shared multiple ovules per locule with *Cydonia* Mill., Roemer (1847) and Wenzig (1883) proposed an alternative taxonomic treatment, merging *Docynia* into *Cydonia*.

Recent phylogenetic and phylogenomic studies presented strong topological discordance among nuclear/plastid genes, and also showed cytonuclear conflicts (referring to Fig. 1 in Liu et al. 2022). *Docynia* has shown to be closely related to *Docyniopsis* (C.K.Schneid.) Koidz. (= *Malus* sect. *Docyniopsis* C.K.Schneid.) based on the plastomes and the nuclear sequences (Lo and Donoghue 2012; Liu et al. 2019, 2020a, 2020b, 2022; Jin et al. 2023). Several shared morphological characteristics have also supported their close relationship, i.e., cone-shaped non-adnate part of the ovaries, fully connate carpels, incurved and persistent calyx, numerous scattered sclereids throughout the flesh, juvenile leaves deeply lobed, and similar flavonoid chemistry (Williams 1982; Robertson et al. 1991; Kalkman 2004). However, Jin (2014) proposed an alternative phylogenetic inference based on the whole plastome, the sister relationship between *Docynia* and *Cydonia*. Additionally, Xiang et al. (2017) inferred an close relationship between *Docynia* and *Eriolobus* M.Roem. based on the transcriptomic data. Our phylogenomic analyses, which incorporated 797 single-copy nuclear genes (SCN genes) and whole plastome data, provided a robust backbone of the apple and its allies in the framework of the tribe Maleae (Fig. 1).We resolved the phylogenetic position of *Docynia*, placing it within *Malus* sensu lato (Liu et al. 2022).

In this study, we aim to transfer three currently recognized species of *Docynia* to *Malus*.

Materials and methods

We sampled 77 individuals in the framework of Maleae, of which 39 were apple-related species, and the other 38 were outgroup species. All these 77 samples were performed for deep genome skimming (DGS) sequencing with 5-10G data for each sample. We assembled the whole plastome using NOVOPlasty v. 4.3.1 (Dierckxsen et al., 2016) and a successive assembly approach (Liu et al., 2021). Given the rich genomic resources in various lineages of Rosaceae, we screened 797 nuclear SCN genes from six genomes, *Malus baccata* (L.) Borkh., *M. domestica* (Suckow) Borkh., *Pyrus betulifolia* Bunge, *P. bretschneideri* Rehder, *P. ussuriensis* Maxim. × *P. communis* L., and *P. pyrifolia* (Burm.f.) Nakai. We assembled these 797 nuclear SCN genes for these 77 samples using HybPiper pipeline v. 1.3.1 (Johnson et al., 2016). The assembled sequences were then cleaned with a series of procedures, such as trimAL v. 1.2 (Capella-Gutiérrez et al. 2009), AMAS v. 1.0 (Borowiec 2016), TreeShrink v. 1.3.9 (Mai & Mirarab 2018), and Spruceup (Borowiec 2019). We combined the concatenated and coalescent-based methods for accurate phylogenetic inference. As for the

concatenated-based method, we performed Maximum Likelihood (ML) tree inference using RAxML 8.2.12 (Stamatakis 2014) and IQ-TREE2 v. 2.1.3 (Minh et al. 2020). The shrunk trees from TreeShrink (Mai and Mirarab 2018) were used as input to estimate a coalescent-based species tree with ASTRAL-III (Zhang et al. 2018). The detailed parameters refer to the materials and methods in Liu et al. (2022).

Results and discussion

The phylogenetic relationship between *Docynia* and *Malus* has been controversial for several centuries. All these nine nuclear and plastid trees in our study (Liu et al., 2022) supported the paraphyly of *Malus* s.s., with *Docynia* nested within it (Fig. 1), and this was also confirmed in several recent molecular studies (Lo and Donoghue 2012; Xiang et al. 2017; Liu et al. 2020a). Although the monophyly of narrowly circumscribed small genera in *Malus* s.l., including *Chloromeles* (Decne.) Decne., *Docynia*, *Docyniopsis*, *Eriolobus* M.Roem., and *Malus* sensu stricto, we believe that such narrow generic concepts may be impractical for use by botanists, ecologists, conservation biologists, and horticulturalists. Taxonomic circumscription today should serve not only the taxonomists but also the broad biological community, more importantly, educate the general public (Wen et al. 2015, 2017; Funk, 2018). With all these considerations, we propose using the broad generic concept of *Malus* and formally transferring the three currently recognized species of *Docynia* to *Malus* in the following text.

Taxonomic treatment

***Malus delavayi* (Franch.) B.B.Liu, comb. nov.**

Fig. 2

Chinese name: 云南多依(yun nan duo yi)

Pyrus delavayi Franch., Pl. Delavay. 227, t. 47 (1890) [Pirus]. Type: CHINA. Yunnan: “in montibus calcareis ad Mao-kou-tchang, supra Tapin-tze, prope Tali, alt. 2200 m.”, 14 April 1884, *P.J.M. Delavay 466* (**lectotype, designated here**: P [barcode P01819347]!; isolectotype: L [barcode L0019412]!). ibidem, *P.J.M. Delavay 890* (syntype: K [barcode K000758091]!). in silvis ad orientem versus montis Hee-chan-tong, alt. 2500 m, 5 April 1887 (syntypes: K [barcode K000758090]!, K [barcode K000758092]!). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p01819347

Eriolobus delavayi C.K.Schneid., Ill. Handb. Laubholzk. i. 727 (1906). Type: Based on *Pyrus delavayi* Franch.

Docynia delavayi (Franch.) C.K.Schneid., Repert. Spec. Nov. Regni Veg. 3: 180 (1906). Type: Based on *Pyrus delavayi* Franch.

Cydonia delavayi (Franch.) Cardot, Bull. Mus. Natl. Hist. Nat. 1918, xxiv. 63. Type: Based on *Pyrus delavayi* Franch.

Cotoneaster bodinieri H.Lév., Bull. Géogr. Bot. 25: 44 (1915). Type: CHINA. Yunnan: “montagnes près de la frontière du Kouy-Tchéou; à Kiang-Ty”, 9 April 1897, *G. Bodinier s.n.* (holotype: E

[barcode E00010834]!; isotype: A [barcode 00026464]!). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00010834

Distribution: China (Guizhou, Sichuan, and Yunnan).

Malus indica **(Colebr.) B.B.Liu, comb. nov.**

Fig. 3,4

Chinese name: 多依 (duo yi)

Pyrus indica Colebr., Pl. Asiat. Rar. (Wallich). 2(8): 56 (t. 173) (1831). Type: INDIA. “Khasia reg. temp. alt. 6000 pds”, *J.D. Hooker & T. Thomson 510* (**lectotype, designated here**: M [barcode M0213698]!). “Sikkim reg. temp. alt. 7-1000 pds.”, *J.D. Hooker & T. Thomson 509* (syntype). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.m0213698

Cydonia indica (Colebr.) Spach, Hist. Nat. Vég. (Spach) 2: 158 (1834). Type: Based on *Pyrus indica* Colebr.

Docynia indica (Colebr.) Decne., Nouv. Arch. Mus. Hist. Nat. 10: 131 (t. 14) (1874). Type: Based on *Pyrus indica* Colebr.

Eriolobus indica (Colebr.) C.K.Schneid., Ill. Handb. Laubholzk. i. 728 (1906). Type: Based on *Pyrus indica* Colebr.

Docynia griffithiana Decne., Nouv. Arch. Mus. Par. x. 131 (1874). Type: INDIA. “Himalaya oriental”, *Griffith 2082* (holotype: P [barcode P01819345]!; isotypes: E [barcode E00010836]!, K, CAL [accession no. 153563]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p01819345

Docynia indica var. *griffithiana* (Decne.) Ghora, Bull. Bot. Surv. India 47(1-4): 150 (2005). Type: Based on *Docynia griffithiana* Decne.

Docynia hookeriana Decne., Nouv. Arch. Mus. Par. x. (1874) t. 15. Type: INDIA. “Khasia, regio temp. alt. 5000 pds.”, *J.D. Hooker & T. Thomson 511* (holotype: P [barcode P01819346]!). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p01819346

Pyrus rufifolia H.Lév., Bull. Géogr. Bot. 25: 46 (1915), [*Pirus*]. Type: CHINA. Yunnan: “flane des coteaux arides à Lou-Pou, 3050 m, Juin 1912”, *E.E. Maire s.n.* (holotype: E [barcode E00010835]!). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00010835

Docynia rufifolia (H.Lév.) Rehder, J. Arnold Arbor. 13: 310 (1932). Type: Based on *Pyrus rufifolia* H.Lév.

Malus docynioides C.K.Schneid., Bot. Gaz. 63: 400 (1917). Type: CHINA. Sichuan: “Szechuan australis: inter Kua-pie et Ta-tiao-ko, alt. circ. 2700 m, 23 Maji 1914”, *C.K. Schneider 1349* (holotype: K [barcode K000758093]!; isotype: A [barcode 00026465]!). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758093

Docynia docynioides (C.K.Schneid.) Rehder, J. Arnold Arbor. 2(1): 58 (1920). Type: Based on *Malus docynioides* C.K.Schneid.

Distribution: Bhutan, China (Sichuan and Yunnan), India, Myanmar, Nepal, Pakistan, Sikkim, Thailand, and Vietnam.

Note: Colebrooke (1831) did not designate type for *Pyrus indica* in the protologue, and Decaisne (1874) transferred this species to *Docynia* as *Docynia indica* and cited two specimens. According to the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018), these two specimens are syntypes; we should select one as the lectotype.

Malus longiunguis **(Q.Luo & J.L.Liu) B.B.Liu, comb. nov.**

Fig. 5

Chinese name: 长爪多依 (chang zhua duo yi)

Docynia longiunguis Q.Luo & J.L.Liu, Bull. Bot. Res., Harbin 31(4): 389 (-391; fig. 1) (2011). Type: CHINA. Sichuan: Xichang, Lushan, alt. 1860 m, 18 March 2010, *Q. Luo 010304* (holotype: HXCH = Herbarium of Xichang College); ibidem, *Q. Luo 010303* (paratype, HXCH); ibidem, alt. 2368 m, on sunny slope, 16 March 2010, *Q. Luo & Y.F. Tian 010301* (paratype); ibidem, *Q. Luo & Y.F. Tian 010302* (paratype).

Distribution: China (Sichuan).

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Figure legends

Fig. 1 Maximum Likelihood (ML) tree of *Malus* within Maleae inferred from RAxML analysis using the concatenated 797 single-copy nuclear genes (SCNs) supermatrix (A), the upper left inset is a portion of the RAxML tree of *Malus* based on the 78 concatenated plastid coding sequences (CDSs) supermatrix. (Adapted from Figs 2 & 5 in Liu et al., 2022)

Fig. 2 *Malus delavayi* (Franch.) B.B.Liu. **A** overview of tree **B** leaf branch **C** inflorescence branch **D** flower buds **E** flower **F** young fruits. Photo credits to Jian Huang.

Fig. 3 *Malus indica* (Colebr.) B.B.Liu. **A** young fruits **B** fruit (cross section) **C** fruit (longitudinal section) **D** flower **E** leaf branch **F** overview of tree. Photo credits: A, B, D, E, and F to Jian Huang; C to Bin-Jie Ge.

Fig. 4 Illustration of *Malus indica* (redrawn from Pl. Asiat. Rar. (Wallich). 2: t. 173, 1831) **A** lobed-leaf **B** inflorescence branch **C** fruit **D** cross section of fruit **E** longitudinal section of fruit.

Fig. 5 *Malus longiunguis* (Q.Luo & J.L.Liu) B.B.Liu **A** fruit branch **B** flower **C** young fruit. Photo credits: A, B, and C to Qiang Luo.

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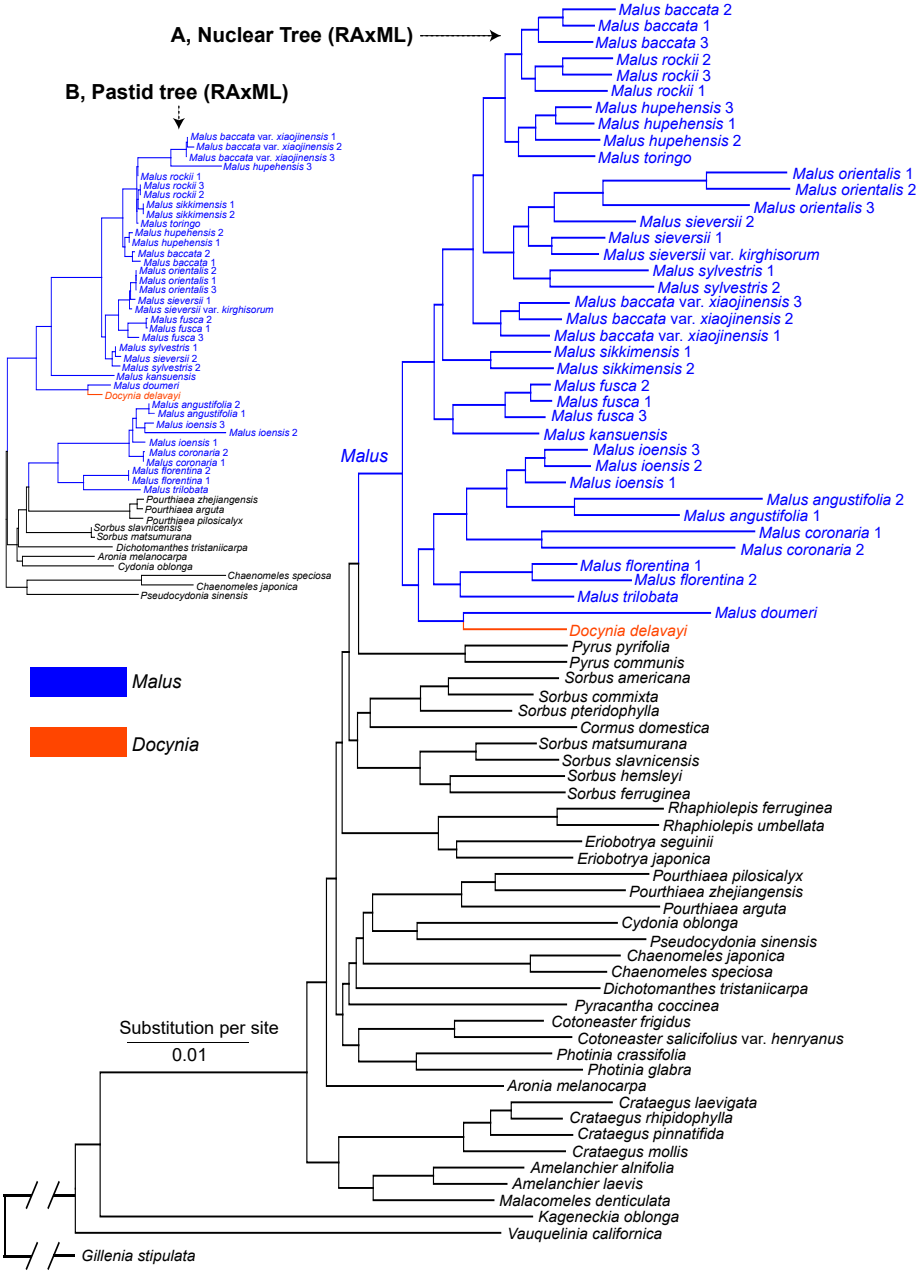

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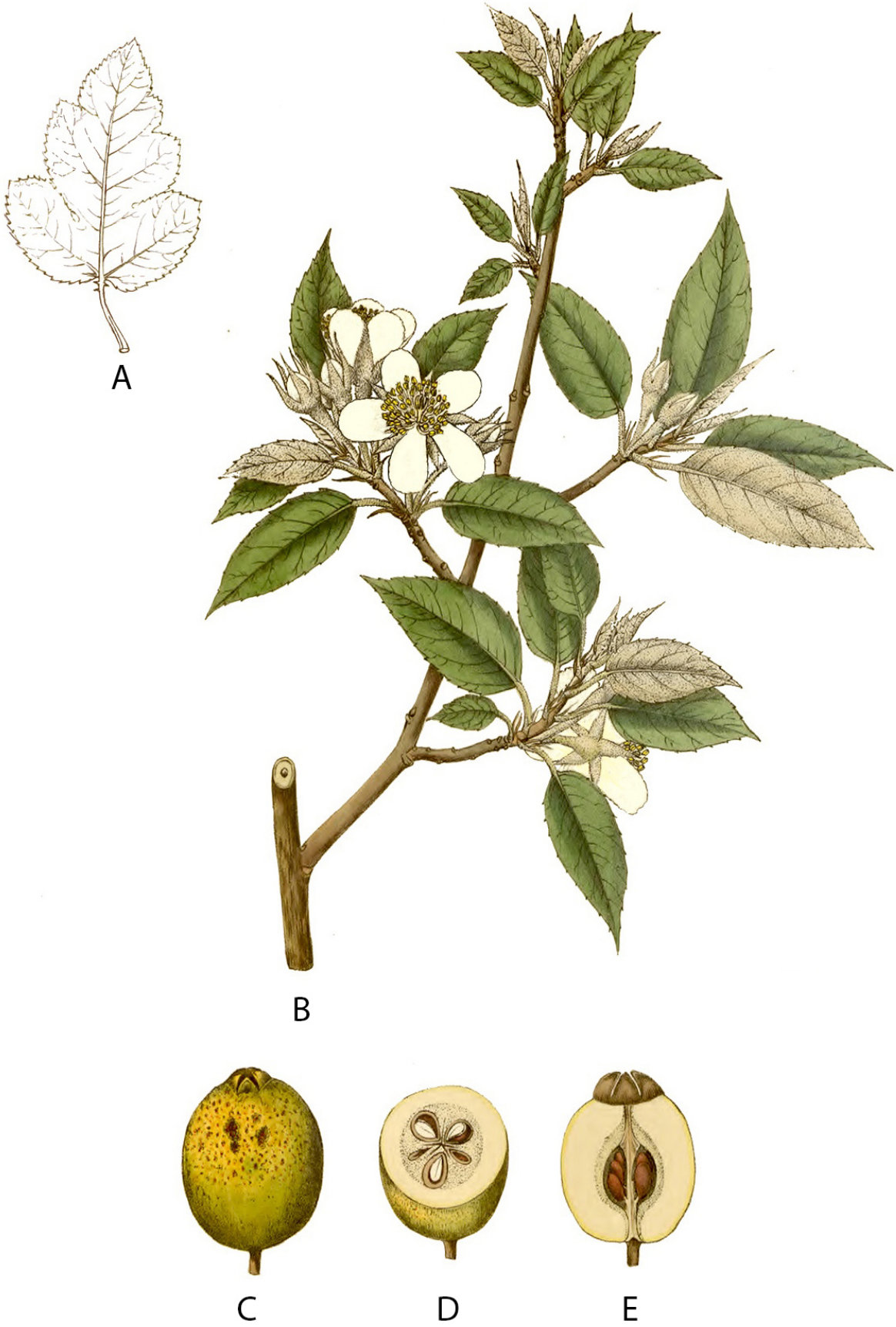

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