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Refining the phylogeny and taxonomy of the apple tribe Maleae (Rosaceae): insights from phylogenomic analyses of 563 plastomes and a taxonomic synopsis of Photinia and its allies in the Old World

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Refining the phylogeny and taxonomy of the apple tribe Maleae (Rosaceae):
insights from phylogenomic analyses of 563 plastomes and a taxonomic
synopsis of *Photinia* and its allies in the Old World

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Running title: refining the phylogeny and taxonomy of the apple tribe

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Abstract:

This study addresses the longstanding absence of a comprehensive phylogenetic backbone for the apple tribe Maleae, a deficiency attributed to limited taxon and marker sampling. We conducted an extensive taxon sampling, incorporating 563 plastomes from a diverse range of 370 species encompassing 26 presently recognized genera. Employing a range of phylogenetic inference methods, including RAxML and IQ-TREE2 for Maximum Likelihood (ML) analyses, we established a robust phylogenetic framework for the Maleae tribe. Our phylogenomic investigations provided compelling support for three major clades within Maleae. By integrating nuclear phylogenetic data with morphological and chromosomal evidence, we propose an updated infra-tribal taxonomic system, comprising subtribe Malinae Reveal, subtribe Lindleyinae Reveal, and subtribe Vauquelininae B.B.Liu (subtr. nov.). Plastid phylogenetic analysis also confirmed the monophyly of most genera, except for *Amelanchier*, *Malus*, *Sorbus* sensu lato, and *Stranvaesia*. In addition, we present a comprehensive taxonomic synopsis of *Photinia* and its morphological allies in the Old World, recognizing 27 species and ten varieties within *Photinia*, three species and two varieties within *Stranvaesia*, and two species and three varieties within *Weniomeles*. Furthermore, we also lectotypified for 12 names and made two new combinations. This research fills critical gaps in the evolutionary history of the tribe Maleae and provides a refined taxonomic framework for future botanical studies.

Keywords:

classification, lectotype, nomenclature, *Pourthiaea*, *Stranvaesia*, typification, *Weniomeles*

Introduction

The apple tribe Maleae, one of the sixteen tribes within the Rosaceae family, comprises approximately 27 genera and 912 species, with a widespread distribution across the Northern Hemisphere (Robertson et al. 1991; Lu et al. 2003; Phipps et al. 2014). This tribe includes diverse genera such as *Kageneckia* Ruiz & Pav., *Lindleya* Kunth, and *Vauquelinia* Corrêa ex Bonpl., noted for their follicles and capsules, alongside pome-bearing genera previously categorized under the subfamily Maloideae (Morgan et al. 1994). The monophyly of this lineage has been confirmed by a series of phylogenetic studies (Potter et al. 2007; Zhang et al. 2017; Xiang et al. 2017; Liu et al. 2020a, 2022). However, despite these endeavors, earlier phylogenetic studies, limited by the scope of plastid and nuclear markers, failed to definitively resolve the intergeneric relationships within Maleae (Phipps et al. 1991; Verbylaitė et al. 2006; Campbell et al. 2007; Li et al. 2012; Lo and Donoghue 2012; Sun et al. 2018). The advent of phylogenomic approaches has opened new avenues, offering significant potential in unraveling the phylogenetic relationships within this lineage, particularly given its history of complex reticulation events. Nonetheless, due to the substantial costs associated with sequencing, recent phylogenomic studies have only included limited taxon sampling for phylogenetic analysis, as seen in the works of Liu et al. (2022), Jin et al. (2023a), and Zhang et al. (2023).

The chloroplast genome, assembled from genome skimming data (Straub et al. 2012), has played a pivotal role in plant systematics and phylogenetics (Guo et al. 2022). Its highly conserved nature, combined with areas of variable sequences, makes it an ideal candidate for phylogenetic analysis (Gitzendanner et al. 2018). Furthermore, this genetic stability, along with the non-

recombinant of plastomes and often uniparental inheritance, offers a consistent and reliable framework for studying plant lineage and evolution, and the plastome-based phylogenetic inference has been successfully utilized in exploring the shallow (Zhang et al. 2017; Liu et al. 2019, 2020a, 2020b; Su et al. 2021) and deep phylogenies (Li et al. 2019, 2021). In our study, we have compiled 563 plastomes from genome skimming data and aim to construct a comprehensive plastome-based phylogenetic framework for the Maleae tribe.

In the scientific domain, taxonomy—the systematic classification and naming of living organisms—maintains a pivotal role in biological research (Sosef et al. 2020). Within this broad discipline, nomenclature emerges as a crucial subfield, devoted to establishing and adhering to precise rules and standards for the designation of organisms. This aspect is particularly critical in botany, where a comprehensive nomenclatural compendium is of paramount importance. Such compendia provide an exhaustive collection of plant species names, meticulously documenting their validity, historical significance, typification, hierarchical categorization, and other intricate facets of nomenclature (Turland 2019). Functioning as indispensable references, these compendia enhance accuracy and uniformity in plant taxonomy. The quest for nomenclatural clarity extends beyond academic interest, affecting areas such as ecological conservation, agricultural innovation, and pharmaceutical research. By presenting a universally recognized and rigorously validated nomenclatural framework, these synopses not only facilitate the organization of data but also streamline communication among botanical scientists. Consequently, this enhances interdisciplinary collaboration and ensures the precise application of botanical knowledge across various scientific fields.

The taxonomic delimitation and phylogenetic relationship between *Photinia* Lindl. and its morphologically related genera in the Old World have been a subject of debate for centuries. In the Old World, the *Photinia*-affiliated genera comprised four groups: the deciduous genus *Pourthiaea* Decne., and the evergreen genera *Photinia*, *Stranvaesia* Lindl., and *Weniomeles* B.B.Liu. *Photinia* was initially described with a single evergreen species, *P. arbutifolia* Lindl., and later expanded to include four evergreen species (Lindley 1821). Subsequently, de Candolle (1825) incorporated two deciduous species into *Photinia*, thereby establishing the genus *Photinia*, encompassing both evergreen and deciduous species. *Photinia* has been recognized to comprise about 60 species, both evergreen and deciduous, distributed disjointedly across East and Southeast Asia, and Mexico (Rehder 1940; Vidal 1965; Yu 1974; Phipps et al. 1990; Robertson et al. 1991; Phipps 1992; Lu et al. 2003). Decaisne (1874) observed distinctive warty peduncles and pedicels on the fruits of deciduous species, setting them apart from their evergreen counterparts, leading to the establishment of these deciduous species under the newly formed genus *Pourthiaea*. This classification, recognizing *Pourthiaea* as a separate genus, gained widespread acceptance among botanists, including Nakai (1916), Ohashi et al. (1989), Iketani and Ohashi (1991, 2001), Liu and Hong (2016a, 2016b, 2017), and Liu et al. (2023b). The separate generic status of *Pourthiaea* has also been further substantiated by recent molecular studies (Guo et al. 2011; Li et al. 2012; Zhang et al. 2017; Sun et al. 2018; Liu et al. 2019, 2022). Furthermore, Phipps (1992) revealed that the five species and three varieties of *Photinia* indigenous to Central America exhibit distinct morphological characteristics compared to the *Photinia* species from East Asia. This distinction was corroborated by phylogenomic evidence, which employed whole plastome and nuclear ribosomal DNA (nrDNA) datasets. Based on these

findings, these Central American species were reclassified into a newly proposed genus, *Phippsiomeles* B.B.Liu & J.Wen, as elaborated in Liu et al. (2019).

First described by Lindley in 1837, the red-fruit genus *Stranvaesia* is a relatively small group, encompassing five species native to China, the Himalayas, and Southeast Asia (Lu et al. 2003). Morphologically similar to *Photinia*, *Stranvaesia* is distinguishable by its unique characteristics, including a four- or five-chambered ovary and dehiscent fruits. These distinct features have led to its classification as a separate genus in numerous taxonomic studies spanning from the mid-19th to early 21st centuries (Roemer 1847; Decaisne 1874; Wenzig 1883; Focke 1888; Koehne 1893; Rehder 1940, 1949; Yu 1974; Lu et al. 2003). However, this classification was challenged by Kalkman (1973), who observed negligible differences in the number of carpels between *Stranvaesia* and *Photinia*. He noted that the supposedly dehiscent fruits of *Stranvaesia davidiana* Decne. did not exhibit dehiscence in botanical garden observations, leading to the proposal of merging *Stranvaesia* into *Photinia* due to these morphological similarities. Despite this, the relationship between these two genera has been a long-standing taxonomic puzzle, with some botanists advocating for their distinct genus status (Yu 1974; Lu et al. 2003), while others supported merging them (Lu et al. 1991; Li 1992; Zhang 1992). Recent phylogenetic and phylogenomic studies have shed light on this controversy. For instance, based on two chloroplast DNA regions and one nuclear ribosomal Internal Transcribed Spacer (nrITS) sequence, Guo et al. (2011) inferred that *Photinia davidsoniae* Rehder & E.H.Wilson (= *P. bodinieri* H.Lév.) and *P. nussia* (Buch.-Ham. ex D.Don) Kalkman (= *Stranvaesia nussia* (Buch.-Ham. ex D.Don) Decne.) formed a clade with strong support; however, the phylogenetic relationship between this clade and *Photinia* has been uncertain due to the limited informative sites. Liu et al. (2019) expanded the taxon sampling in their phylogenomic study within the Maleae framework, providing strong support for a redefined *Stranvaesia* clade, including three species, *S. bodinieri* (H.Lév.) B.B.Liu & J.Wen, *S. oblanceolate* (Rehder & E.H.Wilson) Stapf, and *S. nussia* (type species). Additionally, Liu et al. (2019) identified a novel distinguishing character for *Stranvaesia* not previously used in differentiating it from *Photinia*: the presence of a cluster of sclereids forming an ellipsoid between carpels in the flesh of pomes. This discovery, alongside the robust phylogeny, led to a redefinition of the generic limits of *Stranvaesia* and several nomenclatural changes. Further molecular analysis by Guo et al. (2020) confirmed the distinct phylogenetic placement of *Stranvaesia* and introduced another distinguishing trait: the unarmed branches of young trees. Despite this progress, ongoing uncertainties in the generic delimitation of *Photinia* and *Stranvaesia* persist due to factors like insufficient sampling (Liu et al. 2019) and limited informative sites (Guo et al. 2011, 2020). The complexity is compounded by polyploidy and hybridization-driven lineages, which challenge traditional taxonomic treatments. Jin et al. (2023a) provided further insights, suggesting that the origin of the redefined genus *Stranvaesia* may involve allopolyploidy and introgression, with the most recent common ancestor (MRCA) of *Stranvaesia bodinieri* likely acting as the maternal parent and an extinct lineage as the paternal parent. Consequently, *Stranvaesia bodinieri* was proposed as a new genus, *Weniomeles*, characterized by purple-black fruits, thorny trunks and/or branches, and a fruit core with multiloculars separated by a sclereid layer and a sclereid cluster at the top of the locules (Fig. 1A).

Our study focuses on three key goals: 1) To establish a robust phylogenetic backbone for the apple tribe Maleae, 2) To update and refine the infra-tribal taxonomic system within Maleae, and 3)

To compile a detailed taxonomic synopsis of *Photinia* and its closely related groups in the Old World.

Materials and Methods

Taxon sampling, DNA extraction, and sequencing

In this study, we meticulously compiled 563 plastomes to estimate an extensive plastid framework for the apple tribe Maleae. This collection encompasses 559 individuals, representing almost all genera within the tribe, except for the Madeira endemic genus, *Chamaemeles* Lindl. We employed *Gillenia* Moench, comprising two species from four individuals, as the outgroup. Our dataset included 559 ingroup samples, covering a wide spectrum of species diversity across various genera: 14 out of 24 species *Amelanchier* Medik. (14 individuals), all two species in *Aronia* Medik. (two individuals), all four species in *Chaenomeles* Lindl. (seven individuals), 63 taxa out of 261 species in *Cotoneaster* Medik. (63 individuals), 20 out of 222 species in *Crataegus* L. (33 individuals), one species in *Cydonia* Mill. (two individuals), one species in *Dichotomanthes* Kurz (two individuals), six out of 11 species in *Hesperomeles* Lindl. (six individuals), one species in *Heteromeles* M.Roem. (two individuals), all four species in *Kageneckia* Ruiz & Pav. (four individuals), one species in *Lindleya* Kunth (one individual), one out of five species in *Malacomeles* (Decne.) Decne. (two individuals), three species in *Osteomeles* Lindl. (three individuals), one species in *Peraphyllum* Nutt. (two individuals), three out of five species in *Phippsiomeles* (three individuals), 20 out of 27 species in *Photinia* (31 individuals), 14 species in *Pourthiaea* (53 individuals), one species in *Pseudocydonia* (C.K.Schneid.) C.K.Schneid. (three individuals), three species in *Pyracantha* M.Roem. (five individuals), 17 out of 83 species in *Pyrus* L. (26 individuals), 30 out of 42 species in *Raphiolepis* Lindl. (40 individuals), all three species in *Stranvaesia* (three individuals), five species in *Vauquelinia* Corrêa ex Bonpl. (five individuals), and one species in *Wenimeles* (three individuals). Notably, we sampled 50 species and cultivars in *Malus* Mill. (94 individuals) and 99 species out of 160 in *Sorbus* L. sensu lato (142 individuals), encompassing subgroups like *Aria* (Pers.) Host, *Chamaemespilus* Medik., *Cormus* Spach, *Micromeles* Decne., *Torminalis* Medik., and *Sorbus* sensu stricto. This comprehensive survey thus provides a significant insight into the plastid diversity of the Maleae tribe, covering a broad range of species and varieties across its numerous genera.

Total genomic DNAs were extracted from silica-gel dried leaves and herbarium specimens using a modified cetyltrimethylammonium bromide (CTAB) method, as described by Li et al. (2013). This extraction was performed at the State Key Laboratory of Plant Diversity and Specialty Crops, Institute of Botany, Chinese Academy of Science (IBCAS) in China. The subsequent library preparation and sequencing processes were conducted at the Novogene laboratory in Beijing, utilizing the NEBNext® Ultra™ II DNA Library Prep Kit, designed specifically for the Illumina® platform. We generated paired-end reads of 150 bp using the Illumina HiSeq 2500 Instrument (Novogene Beijing). This approach ensured high-quality DNA sequencing, which is important for our research objectives.

193 Plastome assembly and annotation

194 In our study, we innovatively adopted the Successive Approach combining Reference-based and
 195 De novo assembly (SARD approach; Liu et al. 2023b), a method offering the possibility of obtaining
 196 nearly all plastome-related reads, thus facilitating the production of high-quality chloroplast genomes
 197 even from datasets with low coverage. For initial data preparation, we used Trimmomatic v. 0.33
 198 (Bolger et al. 2014) for quality trimming and adapter removal, complemented by FastQC 0.11.8
 199 (Andrews 2018) for quality assessment. We then employed NOVOPlasty v. 4.3.3 (Dierckxsens et al.
 200 2016), a de novo assembly program known for its accuracy and efficiency. The seed sequence chosen
 201 was the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*), a 600 bp plastome-
 202 specific sequence with absence in the mitochondrial genome, to initiate the assembly process. While
 203 NOVOPlasty performs well for the deeply sequenced data, the SARD approach is notably effective
 204 even with lower-quality raw data. For the assembly process with SARD approach, all plastome-
 205 related reads were aligned to a reference genome using Bowtie 2 (Langmead and Salzberg 2012),
 206 followed by generating a consensus sequence through Geneious Prime (Kearse et al. 2012).
 207 Concurrently, a *de novo* assembly was conducted using SPAdes 3.13.1 (Bankevich et al. 2012),
 208 which included meticulous error correction and employed a range of K-mer lengths (21, 33, 55, 77).
 209 The final step involved aligning scaffolds from the de novo assembly and contigs from NOVOPlasty
 210 to the draft plastome, and this step will effectively correct errors and ambiguities introduced from the
 211 first step, yielding a high-quality complete plastome.

212 We annotated the assembled plastid genomes using the PGA tool (Qu et al. 2019) with a closely
 213 related plastome as a reference. This process was followed by a thorough manual review of the
 214 coding sequences. We then translated these sequences into proteins using Geneious Prime to confirm
 215 the accuracy of the start and stop codons. To precisely delineate the boundaries of the large-single
 216 copy (LSC), small-single copy (SSC), and inverted repeats (IRs) regions, we employed the Find
 217 Repeats function in Geneious Prime based on the characteristic presence of two reverse
 218 complementary repeats in the plastomes of Rosaceae species. After this detailed annotation process,
 219 we converted our custom annotations into the format required for NCBI submissions. This involved
 220 creating both FASTA files and five-column feature tables, a task we accomplished using the
 221 GB2sequin tool (Lehwark and Greiner 2019). This meticulous approach ensured our data was not
 222 only accurate but also compliant with NCBI submission standards.

223 Data matrix generation and sequencing cleaning

224 Our previous studies have consistently shown that phylogenetic trees derived from entire
 225 plastome datasets and the 79 concatenated plastid protein-coding sequences (plastid CDSs) yield
 226 almost identical topologies within the apple tribe framework (Liu et al. 2020a, 2020b, 2022). This
 227 similarity underscores the minimal influence of potential misalignments in the intron regions.
 228 Consequently, in this study, we opted to utilize the whole plastome for phylogenetic inference. To
 229 mitigate systematic errors stemming from alignment inaccuracies, we applied trimAL v1.2 (Capella-
 230 Gutiérrez et al. 2009) to fine-tune the alignment of the plastome. Additionally, we incorporated
 231 Spruceup (Borowiec 2019) to identify, visualize, and eliminate outlier sequences. In this process, we
 232 set a window size of 50 and an overlap of 25, ensuring a rigorous and precise approach to enhance

the quality and reliability of our phylogenetic analysis.

Phylogenomic analyses based on various inference methods

In our comprehensive study, we implemented a variety of robust inference methodologies to achieve precise and reliable phylogenetic results. Initially, we employed PartitionFinder2 (Stamatakis 2006; Lanfear et al. 2016) to identify the most appropriate partitioning schemes and molecular evolution models, utilizing its default settings. This critical step ensured that the chosen models and schemes were best suited for our dataset, enhancing the accuracy of our subsequent analyses.

For estimating Maximum Likelihood (ML) trees, we utilized the advanced capabilities of IQ-TREE2 v. 2.2.0.3 (Minh et al. 2020), conducting analyses with 1000 SH-aLRT and ultrafast bootstrap replicates. This method provided us with a robust statistical framework to evaluate the reliability of the phylogenetic tree branches. In parallel, we used RAxML v. 8.2.12 (Stamatakis 2014), adopting the GTRGAMMA model for each partition. This process included running 200 rapid bootstrap replicates to support the clade structures in our phylogenetic tree, thus ensuring a comprehensive and reliable assessment of clade support.

Synopsis of nomenclature and typification

Over 11 years, from 2013 to 2023, we conducted an in-depth taxonomic study to meticulously examine all the names published under the genus *Photinia* and its related genera. This comprehensive review was not a trivial undertaking; it involved a thorough exploration of multiple renowned online botanical databases. These included Tropicos (accessible at <https://www.tropicos.org>), the International Plant Names Index (IPNI) at <https://www.ipni.org/>, and The Plant List, available at <http://www.theplantlist.org/>. Our investigation extended beyond these databases to encompass a wide range of literature pertinent to the genus *Photinia*, ensuring no relevant information was overlooked.

In addition to collating and reviewing the names, a critical aspect of our study involved the rigorous evaluation of the validity of each name. This process was guided by the principles and standards outlined in the Shenzhen Code (Turland et al. 2018). The Shenzhen Code, a comprehensive set of guidelines for botanical nomenclature, provided a robust framework for our assessment. We carefully applied these rules to determine the legitimacy and correctness of the nomenclature used in the existing literature and databases. Through this detailed and systematic approach, our study aimed to clarify the taxonomy of *Photinia* and its related genera, contributing significantly to the field of botanical nomenclature and taxonomy.

Results

A plastid phylogenetic backbone of *Photinia* and allies

We newly generated 147 complete plastomes for this study, and we collected 563 plastomes representing 370 species to create a detailed phylogenetic framework for the apple tribe. Our efforts resulted in a comprehensive aligned plastome matrix that was used for ML analyses. This matrix, spanning a significant length of 158,752 base pairs, was meticulously curated with poorly aligned

regions being carefully trimmed to ensure the accuracy of our phylogenetic inferences.

We successfully generated two phylogenetic trees using the ML method, i.e., RAxML and IQ-TREE trees. Remarkably, all these phylogenetic trees consistently corroborated the monophyly of three major clades within the apple tribe (Fig. 2; Suppl. material 2, 3). Clade I, identified as the most basal of the three, comprises two genera: *Lindleya* and *Kageneckia*. This clade lays the foundation of our phylogenetic understanding of the tribe. Clades II and III, on the other hand, demonstrate a sister relationship to each other and, collectively, they are sister to Clade I. Clade II is uniquely composed of a single genus, *Vauquelinia*, highlighting its distinct evolutionary path within the tribe. Clade III is particularly noteworthy as it corresponds to what was previously known as the subfamily Maloideae, encompassing approximately 24 genera. One of the significant achievements of this study is the confirmation of the monophyly of most genera represented in the plastid tree. This finding solidifies the genetic distinctiveness of these genera within the apple tribe. However, there were notable exceptions, including *Amelanchier*, *Malus*, *Sorbus* s.l., and *Stranvaesia*.

Discussion

A well-supported phylogenetic backbone of Maleae with comprehensive taxon sampling

As a prominent member of the nine tribes within the subfamily Amygdaloideae, the apple tribe Maleae has been consistently supported as a monophyletic group. However, accurately resolving its phylogenetic relationships has remained a significant challenge. This difficulty is primarily attributed to limitations in informative genetic sites and taxon sampling, as highlighted in studies by Lo and Donoghue (2012) and Liu et al. (2022). These limitations have historically hindered our understanding of the complex evolutionary history of Maleae.

In the era of Sanger sequencing, Lo and Donoghue (2012) made a substantial contribution by assembling a dataset comprising 486 individuals, representing 331 species across 27 previously recognized genera. This dataset, one of the largest of its kind, utilized 11 plastid regions and one nrITS sequence. However, with the benefit of hindsight and advancements in genetic research, it is now clear that such a limited number of plastid and nuclear regions is insufficient for estimating a robust phylogenetic backbone.

Next-generation sequencing (NGS) technologies, along with decreasing sequencing costs and user-friendly bioinformatics tools, have revolutionized phylogenetic inference. The transition from Sanger sequencing to NGS has allowed for more comprehensive and detailed genetic analysis. A notable example of this progress is the work of Zhang et al. (2017), who estimated a plastid framework for the Rosaceae family using 122 plastomes, including 41 species from the Maleae tribe. This study marked a significant step in our evolutionary understanding of Maleae. Following this, there has been a surge of global research efforts to elucidate the phylogenetic relationships within Maleae using plastome-level datasets. Pioneering studies by B.B. Liu et al. (2019, 2020a, 2020b, 2022), Meng et al. (2021), Ulaszewski et al. (2021), G.N. Liu et al. (2023a, 2023b), Jin et al. (2023a), and Ma et al. (2023) have significantly contributed to this field. These studies have employed extensive plastome datasets, vastly improving upon previous efforts in terms of both scale and depth. However, a common limitation of these studies has been the relatively narrow focus on a few species within Maleae or specific lineages. This has resulted in an incomplete phylogenetic picture of

Maleae. More comprehensive and inclusive research is needed, as it would provide a more comprehensive understanding of Maleae. Such an approach would involve extensive sampling across the tribe's entire spectrum, incorporating a wide range of species to cover the full breadth of its genetic diversity.

Since the groundbreaking plastome-level study by Zhang et al. (2017), the field of plant systematics has witnessed a remarkable accumulation of well-assembled plastomes in public data repositories, notably the National Center for Biotechnology Information (NCBI). In our current study, we have taken an in-depth approach to explore these published plastomes, downloading 416 well-assembled ones. Moreover, to construct a robust phylogenetic backbone for the apple tribe Maleae, we have collected an extensive dataset of 563 plastomes (Fig. 2; Suppl. material 2, 3). This dataset includes 258 plastomes newly assembled by our team (Suppl. material 1), showcasing our commitment to advancing the phylogeny of Maleae. The resulting plastome-based phylogenetic framework represents the most comprehensive analysis of the Maleae tribe to date, surpassing all previous efforts in its depth and breadth. Looking ahead, the phylogenomic era, characterized by the analysis of hundreds or even thousands of single-copy nuclear genes (SCNs), is rapidly gaining momentum across the plant systematic community (Liu et al. 2021). This innovative approach is not limited to angiosperm lineages but extends to other groups, such as ferns and bryophytes. The nuclear SCNs-based research promises to revolutionize our understanding of plant evolution, offering unprecedented insights into the genetic underpinnings of diverse plant groups and various fields (Jin et al. 2023a; Xu et al. 2023). As we delve deeper into this new era, our study serves as a critical stepping stone, providing a robust and comprehensive framework that will undoubtedly facilitate future research. By leveraging the power of plastome data and the emerging techniques in phylogenomic analysis, we are poised to uncover new layers of complexity and diversity within the plant kingdom, enriching our understanding of its evolutionary history.

An updated infra-tribal classification of Maleae

Numerous prior studies have consistently confirmed the close phylogenetic relationship between the dry-fruited genera (*Kageneckia*, *Lindleya*, and *Vauquelinia*) and the pome-bearing genera. These studies have employed a range of methodologies, from the utilization of singular or multiple plastid and nuclear markers (Morgan et al. 1994; Evans et al. 2000; Evans and Campbell, 2002; Evans and Dickinson, 2005; Verbylaité et al. 2006; Campbell et al. 2007; Poter et al. 2007; Li et al. 2012; Lo and Donoghue, 2012; Sun et al. 2018) to more recent phylogenomic approaches (Xiang et al. 2017; Zhang et al. 2017; Liu et al. 2019, 2020a, 2022; Jin et al. 2023a; Zhang et al. 2023). Initial studies by Campbell et al. (2007) and Poter et al. (2007) collectively classified these dry-fruited genera and the pome-bearing genera under tribe Pyreae (equivalent to tribe Maleae), subsequently redefining the pome-bearing genera, formerly known as subfamily Maloideae, as subtribe Pyrinae (or Malinae). Despite these developments, the precise phylogenetic relationships and taxonomic status of *Kageneckia*, *Lindleya*, and *Vauquelinia* remained unresolved.

In our research, we incorporated representative species from *Kageneckia*, *Lindleya*, and *Vauquelinia*, the three dry-fruited genera, to more precisely determine their phylogenetic relationships with the pome-bearing genera. The plastid phylogeny (Fig. 2; Suppl. material 2, 3) indicates a clear successive sister relationship between a combined clade (*Kageneckia* + *Lindleya*)

and *Vauquelinia*, relative to the pome-bearing genera. Morphologically, these three clades can be easily distinguished, a distinction further elaborated in the identification key provided later. Consequently, this study not only elucidates the phylogenetic placement of these dry-fruited genera within the tribe but also significantly contributes to refining their taxonomy.

While the maternally inherited characteristics of plastomes in the Maleae tribe obviate the need for orthology inference, their utility is somewhat limited in identifying hybridization and polyploidization events (McKain et al. 2018; Guo et al. 2022). The complex evolutionary processes within Maleae, such as hybridization, polyploidization, and incomplete lineage sorting, have profoundly influenced its origin and diversification. This is evident from a series of phylogenomic studies that highlight cytonuclear discordance within the tribe (refer to Fig. 1A,B and studies by Hodel et al. 2022; Liu et al. 2022; Jin et al. 2023a; Zhang et al. 2023). Consequently, inferences drawn from plastome-based phylogenetics primarily reflect maternal lineage and do not fully capture the intricate evolutionary history of Maleae. However, the phylogenetic topologies inferred from hundreds of SCN genes, as illustrated in our previous studies (Liu et al. 2022; Jin et al. 2023a), lend strong support to the three major clades identified in our plastid tree (Fig. 2; Suppl. material 2, 3). These findings have led us to formally propose a taxonomic system for the tribe Maleae, delineating it into three subtribes. The newly proposed classification follows our plastome-based discoveries, and is further enriched by insights from extensive nuclear genomic data, thus providing a more holistic and detailed understanding of the evolutionary dynamics of Maleae.

The refinement of the infra-tribal taxonomy within the tribe Maleae presents pivotal implications across various biological and applied research domains (Liu et al. 2023b). Enhanced resolution of phylogenetic relationships within the tribe facilitates a more nuanced understanding of both genetic and ecological diversity, pivotal for biodiversity conservation strategies. Accurate phylogenetic delineations are instrumental in preserving intra-tribal genetic variation, a crucial aspect of maintaining ecological resilience. In agro-biological and horticultural spheres, this revised classification provides a foundational framework for advancing selective breeding programs, particularly in developing cultivars with enhanced disease resistance and adaptability to climatic variations (Jin et al. 2023b). Additionally, the reclassification contributes significantly to the broader scientific discourse on plant evolutionary biology and phylogenetics, offering insights into speciation and diversification processes. This paradigm shift in Maleae taxonomy underscores the necessity for ongoing taxonomic reassessment in botanical science, reflecting the dynamic nature of phylogenetic knowledge.

Tribe **Maleae** Small, Man. S.E. Fl. 632. 1933. Type: *Malus* Mill.
= Pyraeae Baill., Hist. Pl. 1: 442, 475. 1869. Type: *Pyrus* L.

Key to subtribes of Maleae:

- 1a. Fruit capsule; Central & South America; $2n = 34$ subtribe Lindleyinae
- 1b. Fruit follicle or pome; Northern Hemisphere; $2n = 30$ or 34
- 2a. Leaf margins usually horny; carpels free; flowers: perianth and androecium perigynous; fruits woody capsules surrounded by a hypanthium, splitting into 5 follicles; seed winged; $2n = 30$ subtribe Vauquelininae

2b. Leaf margins not horny; carpels $\pm$ adnate to hypanthium; flowers: perianth and androecium epigynous; fruits pomes; seeds not winged or pyrenes; $2n = 34$ subtribe Malinae

1. Subtribe **Malinae** Reveal, Phytoneuron 2012-33: 2. 2012.

$\equiv$ Malaceae Small, Fl. S.E. U.S. [Small]. 529. 1903, nom. cons. Type: *Malus* Mill.

This tribe contains ca. 24 genera (ca. 905 species), *Amelanchier* (24 species), *Aronia* (two species), *Chaenomeles* (four species), *Chamaemeles* (one species), *Cotoneaster* (261 species), *Crataegus* (222 species), *Cydonia* (one species), *Dichotomanthes* (one species), *Hesperomeles* (11 species), *Heteromeles* (one species), *Malacomeles* (five species), *Malus* (33 species), *Osteomeles* (two species), *Peraphyllum* (one species), *Phippsiomeles* (five species), *Photinia* (27 species), *Pourthiaea* (seven species), *Pseudocydonia* (one species), *Pyracantha* (six species), *Pyrus* (83 species), *Rhaphiolepis* (42 species), *Sorbus* sensu lato (*Chamaemespilus*, *Aria*, *Torminalis*, *Cormus*, *Micromeles*, and *Sorbus* sensu stricto; ca. 160 species), *Stranvaesia* (three species), and *Weniomeles* (two species). $2n = 34$.

2. Subtribe **Lindleyinae** Reveal, Phytoneuron 2012-37: 217. 2012.

$\equiv$ Lindleyaceae J. Agardh, Theoria Syst. Pl. 166. 1858. Type: *Lindleya* Kunth., nom. cons.

This subtribe contains two genera, *Lindleya* (one species) and *Kageneckia* (ca. three species), distributed in Central and South America. $2n = 34$.

3. Subtribe **Vauquelininae** B.B. Liu, **subtr. nov.** Type: *Vauquelinia* Corrêa ex Bonpl.

Large shrubs or small trees, evergreen. Leaves simple, coriaceous, with serrate margins. Inflorescences terminal, 15–25+-flowered, compound corymbs. Flowers bisexual, 5-merous. Hypanthium hemispherical. Sepals 5, erect, broadly ovate, valvate. Petals 5, white, oblong-ovate to oblong-obovate. Stamens 18–20. Carpels 5, free from hypanthium, ventrally connate; ovules 2 per cell, ascending, apotropous. Fruits capsules, broadly ovoid, sericeous, ventrally (fully) and dorsally (in distal 1/2) dehiscent, splitting into 5 follicles; hypanthium persistent; sepals persistent, erect; styles persistent. Seeds 2 per follicle. $2n = 30$.

This subtribe comprises only one genus, *Vauquelinia*, with about three species distributed in Mexico and the Southwestern United States.

A taxonomic synopsis of *Photinia* and its morphological allies in the Old World

Within the Old World, the genus *Photinia* and its morphologically allied genera comprise four distinct groups. These include the deciduous genus *Pourthiaea* and three evergreen genera: *Photinia*, *Stranvaesia*, and *Weniomeles* (Liu et al. 2019; Jin et al. 2023a). The genus *Pourthiaea* has been thoroughly evaluated and generated a comprehensive checklist of 213 names (Lou et al. 2022). In our current study, we shift our focus to the remaining three evergreen genera: *Photinia*, *Stranvaesia*, and *Weniomeles*. Our objective is to conduct an in-depth nomenclature assessment and typification for these genera. This entails a critical review of the existing names, verification of their validity according to botanical nomenclature rules, and clarification of type specimens for each taxon. Our analysis aims to provide clarity and precision in the taxonomic classification of these genera, contributing to a better understanding of their evolutionary relationships and aiding in their accurate identification and study in botanical and ecological research.

433 ***Photinia* Lindl., Bot. Reg. 6: t. 491. 1820. nom. cons.**

434 石楠属 (Chinese name); pinyin (spelled as sounds in Chinese): shi nan shu

435 Type: *Photinia serrulata* Lindl., nom. illeg. ≡ *Crataegus glabra* Thunb. ≡ *Photinia glabra* (Thunb.)
436 Franch. & Sav., type conserved by Nesom & Gandhi (2009).

437 Approximately 27 species and ten varieties are found across East, South, and Southeast Asia.

438 **1. *Photinia anlungensis* T.T.Yu, Acta Phytotax. Sin. 8: 228. 1963.**

439 安龙石楠 (Chinese name); pinyin (spelled as sounds in Chinese): an long shi nan

440 Type: CHINA. Guizhou: Anlong, 15 June 1960, C.S. Chang & Y.T. Chang 5359 (holotype: PE
441 [barcode 00061327!]; isotype: HGAS [barcode 021155!]).

442 ≡ *Pyrus anlungensis* (T.T.Yu) M.F.Fay & Christenh., Global Fl. 4: 95. 2018.

443 Distribution: China (Guizhou).

444

445 **2. *Photinia beckii* C.K.Schneid., Ill. Handb. Laubholz. [C.K.Schneider] 1: 707. 1906.**

446 椭圆叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): tuo yuan ye shi nan

447 Type: CHINA. Yunnan: Mengtze, woods, 5500 feet, A. Henry 9795A (lectotype, designated by
448 Pathak et al. (2021: 39): E [barcode E00010996!]; isolectotypes: A [barcode 00045594!], US
449 [barcode 00097493!]). Image of lectotype available from
450 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00010996>

451 ≡ *Pyrus beckii* (C.K.Schneid.) M.F.Fay & Christenh., Global Fl. 4: 98. 2018.

452 Distribution: China (Yunnan).

453

454 **3. *Photinia berberidifolia* Rehder & E.H.Wilson, Pl. Wilson. (Sargent) 1(2): 191. 1912.**

455 小檗叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): xiao bo ye shi nan

456 Type: CHINA. Sichuan, Tung Valley, CHINA. Tung valley, May 1904, E.H. Wilson 3508 (holotype:
457 A [barcode 00038561!]; isotypes: A [barcode 000385610!], K [barcode K000758250!]). Image
458 of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00038561>

459 ≡ *Pyrus berberidifolia* (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4: 98. 2018.

460 Distribution: China (Sichuan).

461

462 **4. *Photinia chihsiniana* K.C.Kuan, Acta Phytotax. Sin. 8(3): 227. 1963.**

463 临桂石楠 (Chinese name); pinyin (spelled as sounds in Chinese): lin gui shi nan

464 Type: CHINA. Guangxi: Lingui, 8 May 1950, C.S. Chung 808097 (holotype: IBK [barcode
465 IBK00062054!]; isotypes: GAC [barcode GAC0010558], IBSC [barcode 0004364!], PE
466 [barcode 00299791!]). ibidem, 22 November 1953, C.F. Liang 31096 (paratypes: GAC
467 [barcode GAC0010567!], IBSC [barcode 0004332!], KUN [barcode 607115!], PE [barcode
468 00299793!], SYS [barcode sys00075317!]). Lingui, Yanshan, 20 April 1951, C.S. Chung
469 808829 (paratypes: GAC [barcode GAC0010559!], IBSC [barcode 0318308!], PE [barcode
470 00299794!]). ibidem, C.S. Chung 808871 (paratypes: GAC [barcode GAC0010557!], IBK
471 [barcode IBK00062057!], IBK00062205!], IBSC [barcode 0318305!, 0318306!]). ibidem, 23
472 July 1950, C.S. Chung 808679 (paratypes: GAC [barcode GAC0010573!], IBK [barcode
473 IBK00062224!], IBSC [barcode 0318307!]). Pinglou, 23 April 1958, Z.Z. Chen 52327
474 (paratypes: IBK [barcode IBK00062052!], IBK00190808!], IBSC [barcode 0335042!], KUN
475 [barcode 607345!]). Guilin, 8 July 1937, W.T. Tsang 27773 (paratypes: IBSC [barcode
476 0318304!], SYS [barcode SYS00074928!]). ibidem, August 1937, W.T. Tsang 27992
477 (paratypes: IBSC [barcode 0318303!], SYS [barcode sys00095740!]). ibidem, 29 March 1948,
478 C.N. Tang 13423 (paratype: IBK [barcode IBK00062056!]).

479 ≡ *Pyrus chihsiniana* (K.C.Kuan) M.F.Fay & Christenh., Global Fl. 4: 100. 2018.

480 Distribution: China (Guangxi and Hunan).

481
482 **5. *Photinia chingiana* Hand.-Mazz., *Sinensia* 2: 125. 1932.**

483 宜山石楠 (Chinese name); pinyin (spelled as sounds in Chinese): yi shan shi nan

484 Type: CHINA. Kwangsi (Guangxi, Yishan): Bui-tung, Nibai ad conf. prov. Kweichow, 1000 m, in
485 silvis apertis vel ripis rivorum, raro, 27 June 1928, *R.C. Ching* 6244 (lectotype, designated by
486 Pathak et al. (2021: 39): NY [barcode NY00436112!; isolectotypes: IBSC [barcode 0004365!],
487 NAS [barcode NAS00071252!, NAS00071253!], PE [barcode 00026318!]). Image of lectotype
488 available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00436112>

489 ≡ *Pyrus chingiana* (Hand.-Mazz.) M.F.Fay & Christenh., *Global Fl.* 4: 100. 2018.

490 Distribution: China (Guangxi and Guizhou).

491
492 **5a. *Photinia chingiana* var. *chingiana***

493 宜山石楠 (原变种) (Chinese name)

494 = *Photinia austroguizhouensis* Y.K.Li, *Bull. Bot. Res.*, Harbin 6(4): 107. 1986. Type: CHINA.

495 Guizhou: Libo, *M.Z. Yang et al.* 810333 (holotype: HGAS; isotype: PE [barcode 01432751!]).

496 = *Photinia simplex* Y.K.Li & X.M.Wang, *Bull. Bot. Res.*, Harbin 8(3): 133. 1988. Type: CHINA.

497 Guizhou: Sandu County, Yaorensan, *Y.K. Li* 10173 (holotype: HGAS; isotype: PE [barcode
498 01432750!]).

499 = *Photinia kwangsiensis* H.L.Li, *J. Arnold Arbor.* 26: 62. 1945. ≡ *Pyrus kwangsiensis* (H.L.Li)
500 M.F.Fay & Christenh., *Global Fl.* 4: 109. 2018. Type: CHINA. Guangxi: Xiangzhou, Yaoshan,
501 22 October 1936, *C. Wang* 40293 (holotype: A [barcode 00045591!]; isotypes: IBK [barcode
502 IBK00190811!], IBSC [barcode 0004367!], PE [barcode 00039504!]). Image of holotype
503 available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00045591>

504 Distribution: China (Guangxi and Guizhou).

505
506 **5b. *Photinia chingiana* var. *lipingensis* (Y.K.Li & M.Z.Yang) L.T.Lu & C.L.Li, *Acta Phytotax.*
507 ***Sin.* 38(3): 277. 2000.****

508 黎平石楠 (Chinese name); pinyin (spelled as sounds in Chinese): li ping shi nan

509 Type: CHINA. Guizhou: Liping, Zhongchao, October 1987, *D.F. Huang* 714 (holotype: HGAS;
510 isotype: PE [barcode 01432752!]).

511 ≡ *Photinia lipingensis* Y.K.Li & M.Z.Yang, *Bull. Bot. Res.*, Harbin 8(3): 134. 1988.

512 Distribution: China (Guizhou).

513
514 **6. *Photinia chiuana* Z.H.Chen, Feng Chen & X.F.Jin, *J. Hangzhou Univ.*, *Nat. Sci. Ed.*
515 **20(1): 32. 2021.****

516 裘氏石楠 (Chinese name); pinyin (spelled as sounds in Chinese): qiu shi shi nan

517 Type: CHINA. Zhejiang: Qujiang, Hunan Town, Poshi Village, Bijiashanzhuang, alt. 140 m, 20 May
518 2019, Z.H. Chen, L. Chen, & Q.S. Lin QJ19052001 (holotype: ZM; isotype: ZM).

519 Distribution: China (Zhejiang).

520
521 **7. *Photinia crassifolia* H.Lév., *Flore du Kouy-Tchéou* 349. 1915.**

522 厚叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): hou ye shi nan

523 Type: CHINA. Guizhou: Gan-chouen (=Anshun), April 1912, *J. Cavalerie* 3571 (lectotype,
524 designated by Pathak et al. (2021: 39): E [barcode E00284677!]; isolectotype: P [barcode
525 P02143158!]). Image of lectotype available from

526 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143158>

527 ≡ *Pyrus crassifolia* (H.Lév.) M.F.Fay & Christenh., *Global Fl.* 4: 101. 2018.

= *Photinia cavaleriei* H.Lév., Repert. Spec. Nov. Regni Veg. 11: 66. 1912. later homonym. non H.Lév., Repert. Spec. Nov. Regni Veg. 4: 334. 1907. Type: CHINA. Guizhou: Tin-fan (= Huishui), June 1909, *J. Cavalerie* 3571 (holotype: E [barcode E00011309!]). Image of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011309>
 = *Photinia crassifolia* var. *denticulata* Cardot, Notul. Syst. (Paris) 3: 372. 1918. Type: CHINA. Guizhou, San-chouen (= Anshun), 1910, *J. Cavalerie* 3571-pp (lectotype, designated by Pathak et al. (2021: 39): P [barcode P02143157!]; isotype: P [barcode P02143156!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143157>
 Distribution: China (Guangxi, Guizhou, and Yunnan).

8. *Photinia cucphuongensis* T.H.Nguyên & Yakovlev, Bot. Zhurn. (Moscow & Leningrad) 65(9): 1351 (in error as 1251). 1980.

菊芳石楠 (Chinese name); pinyin (spelled as sounds in Chinese): ju fang shi nan
 Type: VIETNAM. Ninh Binh: Cuc Phuong, 29 January 1975, A.L. Takhtadjan & N.T. Hiep 8565 (holotype: LE; isotype: HN).
 ≡ *Pyrus cucphuongensis* (T.H.Nguyên & Yakovlev) M.F.Fay & Christenh.; Global Fl. 4: 101. 2018.
 Distribution: Vietnam.

9. *Photinia davidiana* (Decne.) Cardot, Bull. Mus. Natl. Hist. Nat. 25(5): 399. 1919.

红豆果树 (Chinese name); pinyin (spelled as sounds in Chinese): hong dou guo shu
 Type: CHINA. Tibet: Baoxing, Mou-Pin “now belongs to Sichuan”, 1870, A. David s.n. (holotype: P [barcode P02143103!]). Image of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143103>
 ≡ *Stranvaesia davidiana* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 179. 1874.

9a. *Photinia davidiana* var. *davidiana*

红豆果树 (原变种) (Chinese name)
 = *Stranvaesia integrifolia* Stapf, Hooker’s Icon. Pl. 23: t. 2295. 1894. ≡ *Photinia havilandii* Stapf, Bot. Mag. 149: sub t. 9008. 1924, replacement name. Type: MALESIA. Borneo: Kinabalu, G.D. Haviland 1071 (holotype: K [barcode K000758362!]; isotypes: K [barcode K000758363!], BM [barcode BM000602185!]). Image of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758362>
 = *Stranvaesia henryi* Diels, Bot. Jahrb. Syst. 36(5, Beibl. 82): 52. 1905. Type: CHINA. Sichuan, February 1890, A. Henry 8953 (lectotype, designated by Vidal (1965: 232): K [barcode K000758304!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758304>
 = *Photinia niitakayamensis* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 103. 1911. ≡ *Stranvaesia niitakayamensis* (Hayata) Hayata, Icon. Pl. Formosan. 8: 33. 1919. Type: CHINA. Taiwan: Chiayi, Yushan, Mt. Niitaka, S. Nagasawa 551 (lectotype, designated here: KYO [barcode KYO00022357!]; isolectotype: KYO [barcode KYO00022358!]).
 = *Pyrus cavaleriei* H.Lév., Repert. Spec. Nov. Regni Veg. 11: 67. 1912. Type: CHINA. Guizhou: Pin-Fa, *J. Cavalerie* 3569 (holotype: P [barcode P02143101!]; isotypes: A [barcode 00045576!], E [barcode E00011338!, E00284670!], P [barcode P02143100!, P02143102!]). Image of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143101>
 = *Photinia undulata* var. *formosana* Cardot, Notul. Syst. (Paris) 3: 372. 1914. ≡ *Photinia davidiana* var. *formosana* (Cardot) H.Ohashi & Iketani, J. Jap. Bot. 69(1): 22. 1994. Type: CHINA. Formose (Taiwan): Arisan (Alishan), L.U. Faurie 77 (lectotype, designated by Wang et al. (2018: 90): P [barcode P02143109!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143109>

578 = *Photinia davidiana* f. *latifolia* Cardot, Bull. Mus. Natl. Hist. Nat. 25(5): 399. 1919. Type: CHINA.
 579 Yunnan: bois de Kou-toui, au-dessus de Mo-so-yn, *J.M. Delavay* 3978 (holotype: L [barcode
 580 1901178!]).
 581 = *Stranvaesia salicifolia* Hutch., Bot. Mag. 146: t. 8862. 1920. ≡ *Stranvaesia davidiana* var.
 582 *salicifolia* (Hutch.) Rehder, J. Arnold Arbor. 7(1): 29. 1926. Type: Based on *Stranvaesia*
 583 *salicifolia* Hutch. Type: CHINA. Hupeh (Hubei): north and south of Ichang, alt. 1300-2000 m,
 584 October 1907, *E.H. Wilson* 382a (**lectotype, designated here**: A [barcode 00045607!]). Image
 585 of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00045607>
 586 Distribution: China (Gansu, Guangxi, Guizhou, Hubei, Jiangxi, Shaanxi, Sichuan, Taiwan, Yunnan)
 587 and Malaysia (Kinabalu).
 588

589 **9b. *Photinia davidiana* var. *undulata* (Decne.) Long Y. Wang, W. Guo & W. B. Liao, Phytotaxa**
 590 **361(1): 91. 2018.**

591 波叶红豆果树 (Chinese name); pinyin (spelled as sounds in Chinese): bo ye hong dou guo shu
 592 Type: CHINA. Kouy-Tcheou (= Guizhou): *Perny s.n.* (holotype: P [barcode P02143104!]; isotype: P
 593 [barcode P02143105!]). Image of holotype available from
 594 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143104>
 595 ≡ *Stranvaesia undulata* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 179. 1874. ≡ *Eriobotrya undulata*
 596 (Decne.) Franch., Pl. Delavay. 226. 1890. ≡ *Photinia undulata* Cardot, Bull. Mus. Natl. Hist.
 597 Nat. 25: 399. 1919. ≡ *Stranvaesia davidiana* var. *undulata* (Decne.) Rehder & E.H. Wilson, Pl.
 598 Wilson. 1(2): 192. 1912.
 599 = *Stranvaesia davidiana* var. *suoxiyuensis* C.J. Qi & C.L. Peng, J. Wuhan Bot. Res. 7(3): 239. 1989
 600 Type: CHINA. Hunan: Cili, *C.L. Peng & C.L. Long* 120358 (holotype: CSFC).
 601 Distribution: China (Fujian, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Shaanxi, Sichuan, Yunnan,
 602 and Zhejiang) and Vietnam (Tonkin).
 603

604 **10. *Photinia glabra* (Thunb.) Franch. & Sav., Enum. Pl. Jap. 1(1): 141. 1873.**

605 光叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): guang ye shi nan
 606 Type: JAPAN. Kanname, *Thunberg* 11860 (syntype). *ibidem*, *Thunberg* 11861 (syntype).
 607 ≡ *Crataegus glabra* Thunb., Syst. Veg., ed. 14 (J. A. Murray). 465. 1784. ≡ *Mespilus glabra* Poir.,
 608 Encycl. [J. Lamarck & al.] 4(2): 446. 1798. ≡ *Photinia serrulata* Lindl., Trans. Linn. Soc.
 609 London 13: 103, t. 10 (1821), nom. illeg. ≡ *Photinia glabra* (Thunb.) Poit., Rev. Hort. (Paris)
 610 11: 228. 1849. ≡ *Photinia glabra* (Thunb.) Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg
 611 19(2): 178. 1873, isonym. ≡ *Photinia glabra* (Thunb.) Decne., Nouv. Arch. Mus. Hist. Nat. 10:
 612 140. 1874, isonym. ≡ *Pyrus thunbergii* M.F. Fay & Christenh., Global Fl. 4: 123. 2018.
 613 = *Photinia glabra* var. *typica* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 19(2): 179. 1873.
 614 Distribution: China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi,
 615 Sichuan, Yunnan, and Zhejiang), Japan, Myanmar, Thailand, and Vietnam.
 616

617 **11. *Photinia griffithii* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 142. 1874.**

618 Fig. 3

619 球花石楠 (Chinese name); pinyin (spelled as sounds in Chinese): qiu hua shi nan
 620 Type: BHUTAN. Himalaya orientalis, 1837-1838, *Griffith* 2087 (lectotype, designated by Wang et
 621 al. (2019: 599): P [barcode P02143170!]; isotypes: K [barcode K000758185!], L [barcode
 622 L0019505!], M [barcode M-0213887!]). Image of lectotype available from
 623 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143170>
 624 ≡ *Eriobotrya griffithii* (Decne.) Franch., Pl. Delavay. 1: 224. 1890. ≡ *Photinia serrulata* var.
 625 *congestiflora* Cardot, Notul. Syst. (Paris) 3: 373. 1918. nom. superfl. ≡ *Pyrus griffithiana*
 626 M.F. Fay & Christenh.; Global Fl. 4: 105. 2018.

- 627 = *Photinia glomerata* Rehder & E.H.Wilson, Pl. Wilson. (Sargent) 1(2): 190. 1912. ≡ *Pyrus*
628 *glomerata* (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4: 105. 2018. Type:
629 CHINA. Yunnan, Szemao, A. Henry 11716 (lectotype, selected by Vidal (1965: 226), first step;
630 second step, designated by Wang et al. (2019: 599): E [barcode E00011310!]; isolectotypes: A
631 [barcode 00038560!], K [barcode K000758251!], MO [barcode MO-255089!], US [barcode
632 00097496!]). A. Henry 11716A (syntypes: US [barcode 00097497!], A [barcode 00045567!], A
633 [barcode 00045568!], E [barcode E00284676!], K [barcode K000758252!], MO [barcode MO-
634 255088!]). Image of lectotype available from
635 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011310>
636 = *Photinia franchetiana* Diels, Notes Roy. Bot. Gard. Edinburgh 5: 272. 1912. Type: CHINA.
637 Yunnan, G. Forrest 487 (holotype: E [barcode E00011311!]). Image of holotype available from
638 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011311>
639 = *Photinia glomerata* Rehder & E.H.Wilson var. *cuneata* T.T.Yu, Acta Phytotax. Sin. 8(3): 227.
640 1963. Type: CHINA. Yunnan, Yung-jen, H.T. Tsai 52879 (holotype: PE [barcode 00336359!];
641 isotypes: IBSC [barcode 0318765!], PE [barcode 00336360!], A [barcode 00137699!], NAS
642 [barcode NAS00071255!], KUN [barcode 608247].
643 = *Photinia glomerata* Rehder & E.H.Wilson var. *microphylla* T.T.Yu, Acta Phytotax. Sin. 8(3): 227.
644 1963. Type: CHINA. Yunnan, Teng-chuan, Mt. Chih-shan, R.C. Ching 24894 (holotype: PE
645 [barcode 00336361!]; isotypes: PE [barcode 00336291!], KUN [barcode 607608].
646 = *Photinia semiserrata* H.Li, Fl. Dulongjian Reg. 131. 1993, nom. nud.
647 Distribution: Bhutan and China (Hubei, Sichuan, and Yunnan).

649 **12. *Photinia integrifolia* Lindl., Trans. Linn. Soc. London 13(1): 103, t. 10. 1821.**

- 650 全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): quan yuan shi nan
651 Type: NEPAL. 7 November 1821, Wallich 669 (lectotype, selected by Kalkman (1973: 419)
652 ‘holotype’, first step; second step, designated by Pathak et al. (2019: 184): K [barcode
653 K001111555!]; isolectotypes: E [barcode E00011312!], GH [barcode 00045579!], GZU
654 [barcode 000283019!], K [barcode K000758314!, K001111556!], L [barcode L0019506!,
655 L0019507!], P [barcode P02143206!], NY [barcode 00436120!]). Image of lectotype available
656 from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k001111555>
657 ≡ *Eriobotrya integrifolia* (Lindl.) Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 45(4): 304. 1877. ≡
658 *Pyrus integrifolia* (Lindl.) M.F.Fay & Christenh., Global Fl. 4: 108. 2018.
659 Distribution: Bangladesh, Bhutan, China (Guangxi, Guizhou, Tibet, Yunnan), India (Arunachal
660 Pradesh, Assam, Manipur, Meghalaya, Sikkim, Tamil Nadu, Uttar Pradesh, West Bengal),
661 Indonesia (Gunung Ulu Kali, Pahan, Java, Lesser Sunda Isl.), Laos, Myanmar (Chin, Kachin,
662 Mandalay, Sagaing), Nepal, Thailand, and Vietnam.

664 **12a. *Photinia integrifolia* var. *integrifolia***

665 Fig. 4

666 全缘石楠 (原变种) (Chinese name)

- 667 = *Pyrus integerrima* Wall. ex D.Don, Prodr. Fl. Nepal. 237. 1825, nom. illeg. superfl. ≡ *Photinia*
668 *integerrima* (Wall. ex D.Don) N.P.Balakr., Fl. Jowai 1: 191. 1981.
669 = *Photinia scandens* Stapf, Bot. Mag. 149: sub t. 9008. 1924. ≡ *Stranvaesia scandens* (Stapf) Hand.-
670 Mazz., Symb. Sin. 7(3): 483. 1933. Type: CHINA. Yunnan: Shweli-Salwin divide, G. Forrest
671 9329 (holotype: E [barcode E00011339!]; isotypes: K [barcode K000758309!], IBSC [barcode
672 0318894!]). Image of holotype available from
673 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011339>
674 = *Photinia myriantha* Merr., Brittonia 4: 82. 1941. Type: MYANMAR. Adung Valley, F.K.Ward
675 9276 (holotype: A [barcode 00026802!]); Ngawchang Valley, near Black Rock, F.K. Ward 359

- (paratype: NY [barcode 00436121!]). Image of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00026802>
- = *Photinia integrifolia* var. *yunnanensis* T.T.Yu, Acta Phytotax. Sin. 8(3): 229. 1963. Type: CHINA. Yunnan: Wei-si, alt. 2500 m, K.M. Feng 4167 (holotype: PE [barcode 00004602!]; isotypes: PE [barcode 00336524!, 00336554!], KUN [barcode 607497!],). Kung-shan (Champutung) alt. 1600-1800 m, K.M. Feng 8153 (paratypes: PE [barcode 00336477!, 00336552!]).
- Distribution: Bangladesh, Bhutan, China (Guangxi, Guizhou, Tibet, Yunnan), India, Indonesia, Myanmar, Nepal, Thailand, and Vietnam.
- 12b. *Photinia integrifolia* var. *flavidiflora* (W.W.Sm.) J.E.Vidal, Adansonia, n.s. 5: 227. 1965.**
 黄花全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): huang hua quan yuan shi nan
 Type: CHINA. Yunnan: Mingkwong Vally, November 1912, G. Forrest 9221 (lectotype, designated by Vidal (1965: 227): E [barcode E00011313!]; isolectotype: A [barcode 00026742!]). Hills to the N. W. Tengyueh, G. Forrest 9294 (syntypes: BM [barcode BM000602131!], E [barcode E00072939!], K [barcode K000758267!], A [barcode 00026743!]). Divide between the Tengyueh and Shweli Valleys, G. Forrest 7901 (syntype). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011313>
 = *Photinia flavidiflora* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 10: 59. 1917.
 Distribution: China (Yunnan) and Myanmar (Kachin).
- 12c. *Photinia integrifolia* var. *notoniana* (Wight & Arn.) J.E.Vidal, Addisonia 5: 227. 1965.**
 长柄全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): chang bing quan yuan shi nan
 Type: INDIA. Nilghiris, Wight 1014 (lectotype, selected by Vidal (1965: 226) 'holotype': K [barcode K000758317!]; isolectotypes: E [barcode E00011315!], P [barcode P02143139!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758317>
 = *Photinia notoniana* Wall. ex Wight & Arn., Prodr. Fl. Ind. Orient. 1: 302. 1834. = *Eriobotrya notoniana* (Wall. ex Wight & Arn.) Kurz, Prelim. Rep. Forest Pegu App. B. 48. 1875.
 = *Photinia eugenifolia* Lindl., Edwards's Bot. Reg. 23: t. 1956. 1837. = *Photinia notoniana* var. *eugenifolia* Hooker, Fl. Brit. India 2: 381. 1878. Type: INDIA. Pundua, 1832, Wallich 670B (lectotype, designated by Vidal (1965: 226): K [barcode K001111558!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k001111558>
 = *Photinia micrantha* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 143. 1874. = *Photinia notoniana* f. *micrantha* (Decne.) Koord. & Valetton, Bijdr. Boomsoort. Java 5: 364. 1900. Type: INDIA / BABGLADESH. Bengalia orientalis, Griffith 2098 (lectotype, selected by Vidal (1965: 227), first step; second step, designated by Kalkman (1973: 420): K [barcode K000758325!]; isotype: P [barcode P02143138!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758325>
 = *Photinia notoniana* var. *ceylanica* Hook.f., Fl. Brit. India 2: 381. 1878. Type: INDIA. G. Walker s.n. (lectotype, designated by Pathak et al. (2019: 185): K [barcode K000758326!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758326>
 = *Photinia notoniana* var. *macrophylla* Hook.f., Fl. Brit. India 2: 381. 1878. Type: INDIA. Khasia Hills, J.D. Hooker & T. Thomsoson s.n. (lectotype, designated by Pathak et al. (2019: 185): K [barcode K000758321!]; isolectotypes: K [barcode K000758319!, K000758322!, K000758323!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758321>
 = *Photinia sambuciflora* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 10: 60. 1917. Type: CHINA. Yunnan: Hills to the north of Tengyueh, G. Forrest 9722 (lectotype, selected by Vidal (1965: 227), first step; second step, designated here: E [barcode E00011314!]; isolectotypes: HBG [barcode HBG-511070!], BM [barcode BM000602132!]; Shweli-Salween divide, G. Forrest 12293 (syntypes: BM [barcode BM000602133!], E [barcode E00072952!], K [barcode

K000758268!]). Image of lectotype available from
<https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011314>
 Distribution: China (Yunnan), India, and Laos.

12d. *Photinia integrifolia* var. *sublanceolata* Miq., Fl. Ned. Ind.1(1): 387. 1855.

狭叶全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): xia ye quan yuan shi nan

Type: INDONESIA. Java: Surakarta, *T. Horsfield* 432 (lectotype, designated by Kalkman (1973: 420) ‘holotype’: K [barcode K000758357!]; isolectotype: BM [barcode BM000602183!]).

Image of lectotype available from
<https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758357>

= *Photinia integrifolia* var. *subdenticulata* Miq., Fl. Ned. Ind.1(1): 387. 1855. Type: INDONESIA. Java: Mount Prah, *T. Horsfield* 1135 (lectotype, designated by Kalkman (1973: 420)

‘holotype’: K [barcode K000758360!]; isolectotype: BM [barcode BM000602182!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758360>

= *Photinia dasythrysa* Miq., Fl. Ned. Ind. 1(1): 387. 1855. = *Photinia integrifolia* var. *dasythrysa*

(Miq.) J.E.Vidal, *Adansonia* 5: 227. 1965. Type: INDONESIA. Sumatra: Sunda-eilanden, *Miquel s.n.* (holotype: U [barcode U0123984!]). Image of holotype available from

<https://plants.jstor.org/stable/10.5555/al.ap.specimen.u0123984>

= *Photinia notoniana* var. *angustata* Blume ex K.Koch, *Ann. Mus. Bot. Lugduno-Batavi* 1: 250. 1864, nom. nud.

= *Photinia blumei* Decne., *Nouv. Arch. Mus. Hist. Nat.* 11: 142. 1874. Type: INDONESIA. Java, mons Malabar, 19 October 1861, *Anderson* 83 (lectotype, designated by Vidal (1965: 227): P

[barcode P02143205!]; isolectotype: K [barcode K000758361!]; *Wight* 923 (syntype: P

[barcode P02143136!]; *Wight* 924 (syntype: P [barcode P02143137!]). Image of lectotype

available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143205>

= *Photinia notoniana* f. *grandiflora* Koord. & Valetton, *Bijdr. Boomsoort. Java* 5: 364. 1900. Type: not designated.

= *Photinia notoniana* f. *vulgaris* Koord. & Valetton, *Bijdr. Boomsoort. Java* 5: 364. 1900. Type: not designated.

Distribution: Indonesia (Java and Sumatra).

13. *Photinia lanuginosa* T.T.Yu, Acta Phytotax. Sin. 8(3): 227. 1963.

Fig. 5

绵毛石楠 (Chinese name); pinyin (spelled as sounds in Chinese): mian mao shi nan

Type: CHINA. Hunan, Mt. Xuefengshan, *C.T. Li* 1882 (holotype: PE [barcode 00026329!]; isotype: IBSC [barcode 0344338!], PE [barcode 00004601!]).

= *Pyrus atalantae* M.F.Fay & Christenh., *Global Fl.* 4: 96. 2018.

Distribution: China (Hunan).

14. *Photinia lindleyana* Wight & Arn., Prodr. Fl. Ind. Orient. 1: 302. 1834.

川滇石楠 (Chinese name); pinyin (spelled as sounds in Chinese): chuan dian shi nan

Type: INDIA. Peninsula Ind. orientalis, *Wight* 1012 (lectotype, selected by Kalkman (1973: 424), first step; second step, designated by Kumar & Arumugam (2022: 117): K [barcode

K000758313!]; isolectotypes: BM [barcode BM000602140!], E [barcode E00011327!]). *Wight*

1013 (syntypes: BM [barcode BM000602139!], E [barcode E00174590!, E00174591!], GZU

[barcode GZU000283017!], K [barcode K000758312!], P [barcode P02143117!]). Image of

lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758313>

= *Photinia serrulata* var. *lindleyana* (Wight & Arn.) Wenz., *Linnaea* 38: 94. 1873. = *Pyrus*

lindleyana (Wight & Arn.) M.F.Fay & Christenh., *Global Fl.* 4: 110. 2018.

775 = *Photinia lindleyana* var. *tomentosa* Gamble, Fl. Madras 1(3): 445. 1919. ≡ *Photinia serratifolia*
 776 var. *tomentosa* (Gamble) Vivek. & B.V.Shetty, Bull. Bot. Surv. India 23(3-4): 256. 1983. ≡
 777 *Pyrus lindleyana* var. *tomentosa* (Gamble) K.S.Kumar & Arum., Indian Forester 148(1): 115.
 778 2022. Type: INDIA. Tamil Nadu, Nilgiris District, between Bangi Tappal and Sispara, alt. 7500
 779 ft. ASL, May 1889, J.S. Gamble 20638 (lectotype, designated by Kumar & Arumugam (2022:
 780 115): MH [barcode MH00234090!]).

781 Distribution: China (Sichuan and Yunnan) and India (Kerala and Tamil Nadu).

782

783 **14a. *Photinia lindleyana* var. *lindleyana***

784 滇石楠 (原变种) (Chinese name)

785 Distribution: China (Sichuan and Yunnan) and India (Kerala and Tamil Nadu).

786

787 **14b. *Photinia lindleyana* var. *yunnanensis* Cardot, Notul. Syst. (Paris) 3: 374. 1918.**

788 滇石楠 (Chinese name); pinyin (spelled as sounds in Chinese): dian shi nan

789 Type: CHINA. Yunnan: ao Kouy Chan près My Li, 1906, F. Ducloux & P. Ngeou 4242-pp
 790 (lectotype, designated here: P [barcode 02143143!]; isolectotype: P [barcode 02143144!]).

791 Yunnan: Lan argy tsin, près Lou lan, 17 April 1908, F. Ducloux & J.B. Lo 5936 (syntype: P
 792 [barcode P02143144!]).

793 Distribution: China (Yunnan).

794

795 **15. *Photinia lochengensis* T.T.Yu, Acta Phytotax. Sin. 8(3): 226. 1963.**

796 罗城石楠 (Chinese name); pinyin (spelled as sounds in Chinese): luo cheng shi nan

797 Type: CHINA. Guangxi: Lo-cheng (=Luocheng), W. Chen 84410 (holotype: IBSC; isotypes: PE
 798 [barcode 00004611!, 01790013!]). Note A.

799 ≡ *Pyrus lochengensis* (T.T.Yu) M.F.Fay & Christenh., Global Fl. 4: 110. 2018.

800 Distribution: China (Guangxi).

801 Note A: In the protologue, Yu & Guan (1963) designated the type specimen as being deposited in the
 802 herbarium “HC”, which they referenced as “Herb. Inst. Austro-Sin. Acad. Sin. Canton”. The
 803 correct standard name for this institute is the South China Botanical Garden (IBSC). However,
 804 we could not locate any specimens from this collection in IBSC. Instead, we found two isotype
 805 sheets at the PE herbarium.

806

807 **16. *Photinia loriformis* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 10: 60. 1917.**

808 带叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): dai ye shi nan

809 Type: CHINA. Yunnan, Yunnanfu (=Kunming), E.E. Maire 1118 (lectotype, designated here: E
 810 [barcode E00011317!]; isolectotypes: A [barcode A00045580!], K [barcode K000758253!]).

811 E.E. Maire 1117 (syntype: E [barcode E00285982!]), E.E. Maire 1755 (syntype: E [barcode
 812 E00285984!]), E.E. Maire 2099 (syntype: E [barcode E00285985!]). Note B. Image of lectotype
 813 available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011317>

814 ≡ *Pyrus loriformis* (W.W.Sm.) M.F.Fay & Christenh., Global Fl. 4: 111. 2018.

815 Distribution: China (Sichuan and Yunnan).

816 Note B: In the protologue, the author referenced four collections collected by E.E. Maire: 1118,
 817 1117, 1755, and 2099, all housed in the herbarium E. However, Smith did not designate a
 818 specific type, meaning all four collections are syntypes. A lectotypification is required (Turland
 819 et al. 2018). Upon examination of each specimen from the herbarium E, it was observed that
 820 E.E. Maire 1117 (barcode E00285982) and 1755 (barcode E00285984) lack flowers and fruits.
 821 E.E. Maire 2099 (barcode E00285985) has fruits, but they are damaged by worms. As a result,
 822 E.E. Maire 1118 (barcode E00011317), which is in good condition and has flowers, has been
 823 selected as the lectotype.

824

825 **17. *Photinia maximowiczii* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 143. 1874.**

826 琉球石楠 (Chinese name); pinyin (spelled as sounds in Chinese): liu qiu shi nan

827 Type: JAPAN. Bonin Islands, *Wright 80* (holotype: P [barcode P02143127!]; isotype: K [barcode
828 K000758301!]). Image of holotype available from

829 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143127>

830 = *Photinia wrightiana* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 32: 486. 1888. Type:

831 JAPAN. Bonin-sima, *Wright s.n.* (syntype). Liukiu, *A. Tashiro s.n.* (syntype).

832 Distribution: Japan (Bonin Islands and Liukiu).

833

834 **18. *Photinia megaphylla* T.T.Yu & L.T.Lu, Acta Phytotax. Sin. 18(4): 493. 1980.**

835 大叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): da ye shi nan

836 Type: CHINA. Tibet: Motuo, *Qingzang Exped. 74-4158* (holotype: PE [barcode 00026327!]).

837 = *Pyrus megaphylla* (T.T.Yu & L.T.Lu) M.F.Fay & Christenh., Global Fl. 4: 111. 2018.

838 Distribution: China (Tibet).

839

840 **19. *Photinia microphylla* (J.E.Vidal) B.B.Liu, comb. nov.**

841 少花石楠 (Chinese name); pinyin (spelled as sounds in Chinese): shao hua shi nan

842 Type: VIETNAM. Tonkin: massif du Lo Sui Tong, Près Chapa (Cha-pa and Cho-bo), 2200 m, 29

843 July 1926, *E. Poilane 12674* (holotype: P [barcode P02143106!]; isotypes: P [barcode

844 P02143107!, P02143108!]). Image of holotype available from

845 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143106>

846 = *Stranvaesia microphylla* J.E.Vidal, Notul. Syst. (Paris) 13: 300. 1949. ≡ *Pyrus pluto* M.F.Fay &
847 Christenh., Global Fl. 4: 116. 2018.

848 Distribution: Vietnam.

849

850 **20. *Photinia prionophylla* (Franch.) C.K.Schneid., Repert. Spec. Nov. Regni Veg. 3: 153.**
851 **1906.**

852 刺叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): ci ye shi nan

853 Type: CHINA. Yunnan: les taillis à Kiao che tong au dessus de Kiang yn, 30 May 1888, *J.M.*

854 *Delavay 3545* (lectotype, designated by Idrees et al. (2021: 167): P [barcode P03342590!];

855 isolectotypes: K [barcode K000758254!], LE [barcode LE01015176!]). ibidem, 28 October

856 1888, *J.M. Delavay 3545* (syntypes: K [barcode K000758255!]). Mo-so-yn, Lau Kong, 1 June

857 1884, *J.M. Delavay 1077* (syntypes: A [barcode 00026479!, 00026749!, 00026750!], P [barcode

858 P02143153!, P02143154!, P02143155!]). Image of lectotype available from

859 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758254>

860 = *Eriobotrya prionophylla* Franch. Pl. Delavay. 225, pl. 46. 1890. ≡ *Pyrus prionophylla* (Franch.)

861 M.F.Fay & Christenh., Global Fl. 4: 116. 2018.

862 Distribution: China (Sichuan and Yunnan).

863

864 **20a. *Photinia prionophylla* var. *prionophylla***

865 刺叶石楠 (原变种) (Chinese name)

866 Distribution: China (Sichuan and Yunnan).

867

868 **20b. *Photinia prionophylla* var. *nudifolia* Hand.-Mazz., Symb. Sin. 7(3): 480. 1933.**

869 无毛刺叶石楠 (变种) (Chinese name); pinyin (spelled as sounds in Chinese): wu mao ci ye shi nan

870 Type: CHINA. Yunnan: Yunnanfu (= Kunming), Prope vicum Hsiao-Magai ad septentr. urbis

871 Yünnanfu, 25°26' lat., in regionis calide temperatae inte Döge et Hsiaodjiadsum. 1800 m. 8

872 March 1914, *H. Handel-Mazzetti 404* (holotype: WU [barcode 0059448!]).

Distribution: China (Yunnan).

21. *Photinia prunifolia* (Hook. & Arn.) Lindl., Edwards's Bot. Reg. 23: sub t. 1956. 1837.

Fig. 6

桃叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): tao ye shi nan

Type: CHINA. Macao and adjacent islands, *Beechey s.n.* (lectotype, designated by Wang et al.

(2019: 68): K [barcode K000758258!]; isolectotypes: E [barcode E00369054!]. Image of

lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758258>

≡ *Photinia serrulata* var. *prunifolia* Hook. & Arn., Bot. Beechey Voy. 4: 185. 1833. ≡ *Pyrus uranus* M.F.Fay & Christenh., Global Fl. 4: 124. 2018.

= *Photinia melanostigma* Hance, J. Bot. 20: 5. 1882. Type: CHINA. Guangdong, North River,

March 1881, *B.C. Henry 21691* (holotype: BM [barcode BM000602202!]). Image of holotype

available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.bm000602202>

= *Photinia consimilis* Hand.-Mazz., Anz. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 59: 103. 1922.

Type: CHINA. Hunan: Dschaoschan (=Shaoshan), 27 October 1917, *Handel-Mazzetti 11382*

(lectotype, designated here: WU [barcode 0059452!]). Hunan: Shaoshan, 27 October 1917,

Handel-Mazzetti 11382 (syntype: WU [barcode 0059467!]). ibidem, 16 February 1918, *Handel-*

Mazzetti 11472 (syntype: WU [barcode 0059453!]). Image of lectotype available from

<https://plants.jstor.org/stable/10.5555/al.ap.specimen.wu0059467>

= *Photinia prunifolia* var. *denticulata* T.T.Yu, Acta Phytotax. Sin. 8(3): 228. 1963. Type: CHINA.

Zhejiang, Pingyang, 28 June 1959, *S.R. Zhang 5867* (holotype: PE [barcode 00026328!];

isotypes: KUN [barcode 607582!], HTC [barcode 0003151!]).

= *Photinia stapfii* Chun, nom. nud.

Distribution: Cambodia, China (Fujian, Guangdong, Guangxi, Hainan, Hongkong, Hunan, Jiangxi,

Zhejiang), and Vietnam.

22. *Photinia raupingensis* K.C.Kuan, Acta Phytotax. Sin. 8(3): 228. 1963.

饶平石楠 (Chinese name); pinyin (spelled as sounds in Chinese): rao ping shi nan

Type: CHINA. Guangdong, Raoping, Fenghuangshan, in silvis, 16 April 1931, *N.K. Chun 42691*

(holotype: IBSC [barcode 0318920!]; isotypes: AU [barcode 039768!], IBK [barcode

IBK00062558!, IBK00062559!], NAS [barcode NAS00374075!], PE [barcode 00020609!,

00004599!]).

≡ *Pyrus raupingensis* (K.C.Kuan) M.F.Fay & Christenh., Global Fl. 4: 118. 2018.

Distribution: China (Guangdong and Guangxi).

23. *Photinia serratifolia* (Desf.) Kalkman, Blumea 21(2): 424. 1973.

石楠 (Chinese name); pinyin (spelled as sounds in Chinese): shi nan

Type: not designated.

≡ *Crataegus serratifolia* Desf., Tabl. École Bot., ed. 3 (Cat. Pl. Horti Paris.) 408. 1829. ≡ *Pyrus*

serratifolia (Desf.) M.F.Fay & Christenh., Global Fl. 4: 121. 2018.

23a. *Photinia serratifolia* var. *serratifolia*

Fig. 1C

石楠 (原变种) (Chinese name)

= *Photinia glabra* var. *chinensis* Maxim., Bull. Acad. Imp. Sci. Saint-Petersbourg, sér. 3 19(2): 179.

1873. Type: CHINA. *R. Fortune A-30* (lectotype, designated here: P [barcode P00781062!];

isolectotypes: P [barcode P00781061!, P00781063!, P00781064!]). Note C. Image of lectotype

available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p00781062>

921 = *Stranvaesia argyi* H.Lév., Mem. Acad. Sci. Art. Barcelona ser. 3 12: 560. 1916. Type: CHINA.
 922 *Argy s.n.* (holotype: E [barcode E00011323!]). Image of holotype available from
 923 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011323>
 924 = *Photinia serrulata* var. *aculeata* G.H.M.Lawr., Gentes Herbarum 8: 80. 1949. Type: CHINA.
 925 Taiwan: Seisui, E.H. Wilson 11061 (**lectotype, designated here**: US [barcode 00097504!];
 926 isolectotype: A [barcode 00045608!]). Image of lectotype available from
 927 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.us00097504>
 928 Distribution: China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hebei, Hubei, Hunan,
 929 Jiangsu, Jiangxi, Shaanxi, Sichuan, Taiwan, Yunnan, and Zhejiang), Indonesia, India, Japan,
 930 and Philippines.
 931 Note C: In the protologue, the author cited only one collection of specimen, *R. Fortune A-30*, four
 932 sheets of this collection have been observed in P, one preserved well ([barcode P [barcode
 933 P00781062) was designated as lectotype here.
 934

935 **23b. *Photinia serratifolia* var. *ardisiifolia* (Hayata) H.Ohashi, J. Jap. Bot. 63(7): 234. 1988.**
 936 紫金牛叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): zi jin niu ye shi nan
 937 Type: CHINA. Taiwan: Taidong, Taito, Manchosa, 1 October 1906, G. Nakahara s.n. (**lectotype,**
 938 **designated here**: TAIF [accession no. 22366!]; isolectotype: IBSC [barcode 0285883!]).
 939 = *Photinia ardisiifolia* Hayata, Icon. Pl. Formosan. 5: 65. 1915. = *Photinia serrulata* f. *ardisiifolia*
 940 (Hayata) H.L.Li, Lloydia 14(4): 234. 1951. = *Photinia serrulata* var. *ardisiifolia* (Hayata)
 941 K.C.Kuan, Fl. Reipubl. Popularis Sin. 36: 224. 1974.
 942 Distribution: China (Taiwan).
 943

944 **23c. *Photinia serratifolia* var. *daphniphylloides* (Hayata) L.T.Lu, Acta Phytotax. Sin. 38(3): 277.**
 945 **2000.**
 946 宽叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): kuan ye shi nan
 947 Type: CHINA. Taiwan: Hualian, Tarako, Batagan-sya, 27 April 1917, S. Sasaki s.n. (**lectotype,**
 948 **designated here**: TAIF [accession no. 11810!]; isolectotype: TAIF [accession no. 11811!]).
 949 = *Photinia daphniphylloides* Hayata, Icon. Pl. Formosan. 7: 30. 1918. = *Photinia serrulata* f.
 950 *daphniphylloides* (Hayata) H.L.Li, Lloydia 14(4): 234. 1951. = *Photinia serrulata* var.
 951 *daphniphylloides* (Hayata) K.C.Kuan, Fl. Reipubl. Popularis Sin. 36: 222. 1974.
 952 Distribution: China (Taiwan).
 953

954 **23d. *Photinia serratifolia* var. *lasiopetala* (Hayata) H.Ohashi, J. Jap. Bot. 63(7): 234. 1988.**
 955 毛瓣石楠 (Chinese name); pinyin (spelled as sounds in Chinese): mao ban shi nan
 956 Type: CHINA. Taiwan: Nantou, 1 April 1916, B. Hayata s.n. (holotype: TAIF [accession no.
 957 11814!]; isotype: PH [barcode PH00067378!]).
 958 = *Photinia lasiopetala* Hayata, Icon. Pl. Formosan. 6: 17. 1916. = *Photinia serrulata* var. *lasiopetala*
 959 (Hayata) K.C.Kuan, Fl. Reipubl. Popularis Sin. 36: 222. 1974. = *Photinia serratifolia* var.
 960 *lasiopetala* (Hayata) H.Ohashi, J. Jap. Bot. 63(7): 234. 1988. = *Pyrus lasiopetala* (Hayata)
 961 M.F.Fay & Christenh., Global Fl. 4: 110. 2018.
 962 Distribution: China (Taiwan).
 963

964 **24. *Photinia stenophylla* Hand.-Mazz., Symb. Sin. Pt. 7(3): 480, pl. 15, f.3. 1933.**
 965 窄叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): zhai ye shi nan
 966 Type: CHINA. Guizhou, Sandjio, H. Handel-Mazzetti 10827 (lectotype, designated by Pathak et al.
 967 (2021: 41): WU [barcode 0059446!]). Sanhoa (= Sandu), Yao-ren-shan, Y. Tsiang 6374
 968 (syntypes: A [barcode 00026800!], NY [barcode 00436117!]). Image of lectotype available
 969 from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.wu0059446>

970 ≡ *Pyrus stenophylla* (Hand.-Mazz.) M.F.Fay & Christenh., Global Fl. 4: 122. 2018.

971 Distribution: China (Guangxi and Guizhou).

972

973 **25. *Photinia taishunensis* G.H.Xia, L.H.Lou & S.H.Jin, Nordic J. Bot. 30(4): 439. 2012.**

974 泰顺石楠 (Chinese name); pinyin (spelled as sounds in Chinese): tai shun shi nan

975 Type: CHINA. Zhejiang: Taishun County, Yangxi Village, C.S. Ding 4116 (holotype: ZJFC

976 [barcode 00030313!]; isotype: ZJFC [barcode 00030312!]).

977 Distribution: China (Zhejiang).

978

979 **26. *Photinia tushanensis* T.T.Yu, Acta Phytotax. Sin. 8(3): 229. 1963.**

980 独山石楠 (Chinese name); pinyin (spelled as sounds in Chinese): du shan shi nan

981 Type: CHINA. Guizhou, Dushan, Lipo Exped. 1296 (holotype: PE [barcode 00020611!]; isotype: PE

982 [barcode 01498407!]).

983 ≡ *Pyrus tushanensis* (T.T.Yu) M.F.Fay & Christenh., Global Fl. 4: 124. 2018.

984 Distribution: China (Guangxi and Guizhou).

985

986 **27. *Photinia wardii* C.E.C.Fisch., Bull. Misc. Inform. Kew 1936(4): 281. 1936.**

987 长叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): chang ye shi nan

988 Type: INDIA. Assam, Chibaon, Delei Valley, F.K. Ward 8042 (holotype: K [barcode K000758348!];

989 isotypes: K [barcode K000758349!, K000758350!]). Image of holotype available from

990 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758348>

991 Distribution: India (Assam).

992

993 ***Stranvaesia* Lindl., Edwards's Botanical Register 23: t. 1956. 1837.**

994 红果树属 (Chinese name); pinyin (spelled as sounds in Chinese): hong guo shu shu

995 Type: Lectotype, designated by Liu et al. (2019: 686): *Crataegus glauca* Wall. ex G.Don (=

996 *Stranvaesia nussia* (Buch.-Ham. ex D.Don) Decne.)

997

998 **1. *Stranvaesia nussia* (Buch.-Ham. ex D.Don) Decne., Nouv. Arch. Mus. Hist. Nat. 10: 178.**
999 **1874.**

1000 红果树 (Chinese name); pinyin (spelled as sounds in Chinese): hong guo shu

1001 Type: NEPAL. Nilcunt [Nilkantha, Shading District, Bagmati Zone, Madhyamanchal, Nepal;

1002 coordinates 27.91/84.94]. *Francis Buchanan-Hamilton s.n.* (lectotype, selected by Vidal (1965:

1003 231), first step; second step, designated by Guo et al. (2020: 110): BM [barcode

1004 BM000522002!]). *Wallich 658* (syntype: L [barcode L0062739!, L0062740!], M [barcode M-

1005 0213869!]). *Wallich 658a* (syntype: M [barcode M-0210542!]).

1006 ≡ *Pyrus nussia* Buch.-Ham. ex D.Don, Prodr. Fl. Nepal. 237. 1825. ≡ *Photinia nussia* (Buch.-Ham.

1007 ex D.Don) Kalkman, Blumea 21(2): 429. 1973.

1008 = *Crataegus glauca* Wall. ex G.Don, Gen. Hist. 2: 598, descr. 1832. Type: Nepalia & Kumaon.

1009 1829, *Wallich 673* (**lectotype, designated here:** K [barcode K000758343!, excluding the

1010 infructescence]; isolectotypes: G [barcode G00437202!, excluding the infructescence,

1011 G00437203!], GZU [barcode GZU000283039!], K [barcode K000758344!, K001111566!], L

1012 [barcode L0019509!], LE [barcode LE00013505!], M [barcode M-0213867!, M-0213868!, M-

1013 0213872!], P [barcode P02143111!], PH [barcode PH00028193!]).

1014 = *Stranvaesia glaucescens* Lindl., Edwards's Bot. Reg. 23: t. 1956. 1837. nom. superfl.

1015 = *Eriobotrya ambigua* Merr., Publ. Bur. Sci. Gov. Lab. 35: 19. 1906. ≡ *Stranvaesia ambigua* (Merr.)
1016 Nakai, J. Arnold Arbor. 5: 72. 1924. Type: PHILIPPINES. Lamao River, Mt. Mariveles,

Province of Bataan, Luzon, March 1905, *R. Meyer* 2796 (lectotype, designated by Kalkman (1973: 429) ‘holotype’: K [barcode K000758366!]; isolectotypes: NY [barcode 00436214!], US [barcode 00097488!]). ibidem, March 1905, *H.N. Whitford* 1155 (syntype: K [barcode K000758368!]). ibidem, March 1905, *H.N. Whitford* 1168 (syntype: K [barcode K000758367!]). ibidem, June 1905, *H.N. Whitford* 1307 (syntype: K [barcode K000758365!]). = *Eriobotrya oblongifolia* Merr. & Rolfe, Philipp. J. Sci., C 3: 102. 1908. ≡ *Rhaphiolepis oblongifolia* (Merr. & Rolfe) B.B.Liu & J.Wen, Frontiers Pl. Sci. (Online journal) 10-1731: 11. 2020. Type: PHILIPPINES. Mindanao. Misamis: Mount Malindang, May 1906, *E.A. Mearns & W.J. Hutchinson* 4680 (lectotype, designated by Liu et al. (2020: 108): NY [barcode 00436215!]; isolectotype: US [barcode 00097490!]). = *Photinia harmandii* Cardot, Notul. Syst. (Paris) 3: 375. 1918. ≡ *Stranvaesia harmandii* (Cardot) Vidal, Notul. Syst. (Paris) 13: 301. 1948. Type: LAOS. Attopeu, 1877, *Harmand* 1366 (lectotype, designated here: P [barcode P02143112!]; isolectotype: P [barcode P02143113!]). Distribution: China (Tibet and Yunnan), India, Laos, Myanmar, Nepal, Philippines, and Thailand.

1a. *Stranvaesia nussia* var. *nussia*

红果树 (原变种) (Chinese name)

Distribution: China (Tibet and Yunnan), India, Laos, Myanmar, Nepal, Philippines, and Thailand.

1b. *Stranvaesia nussia* var. *angustifolia* (Decne.) C.K.Schneid., Ill. Handb. Laubholz. 1: 713. 1906.

狭叶红果树 (变种) (Chinese name); pinyin (spelled as sounds in Chinese): xia ye hong guo shu

≡ *Stranvaesia glaucescens* var. *angustifolia* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 178. 1874.

Distribution: India (Mt. Khasia).

2. *Stranvaesia oblanceolata* (Rehder & E.H.Wilson) Stapf, Bot. Mag. 149: sub t. 9008. 1924.

滇南红果树 (Chinese name); pinyin (spelled as sounds in Chinese): dian nan hong guo shu

Type: CHINA. Yunnan: forests around Szemao (Simao), alt. 1500-1600 m, *A. Henry* 11615 (lectotype, selected by Vidal (1965: 232), first step; second step, designated by Guo et al. (2020: 110): US [barcode 00097547!]; isolectotype: A [barcode 00038562!]). ibidem, *A. Henry* 11615a (syntype: A [barcode 00038566!], K [barcode K000758307!], PE [barcode 01432740!]).

ibidem, *A. Henry* 11615b (syntype: A [barcode 00038563!], K [barcode K000758306!], PE [barcode 01432741!], US [barcode 00429887!]). ibidem, *A. Henry* 11615e (syntype: A [barcode 00038564!], K [barcode K000758308!], PE [barcode 01432742!], US [barcode 00429888!]).

ibidem, *A. Henry* 11615f (syntype: A [barcode 00038565!], K [barcode K000758306!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00038562>

≡ *Stranvaesia nussia* var. *oblanceolata* Rehder & E.H.Wilson, Pl. Wilson. (Sargent) 1: 193. 1913. ≡

Pyrus oblanceolata (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4: 114. 2018.

Distribution: China (Yunnan), Laos, Myanmar, and Thailand.

3. *Stranvaesia lasiogyna* (Franch.) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 11. 2023.

倒卵叶红果树 (Chinese name); pinyin (spelled as sounds in Chinese): dao luan ye hong guo shu

Type: CHINA. Yunnan, in silvis montanis ad fauces San-tchang-kiou supra Hokin, alt. 2300 m., 22

May 1884, *J.M. Delavay* 732 (lectotype, designated by Pathak et al. (2021: 40): P [barcode

P02143141!]; isolectotypes: P [barcode P02143142!], US [barcode 00097489!], image A

[barcode 00026747! with plant material sampled from P02143141!]). Image of lectotype

available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143141>

- 1065 ≡ *Eriobotrya lasiogyna* Franch., Pl. Delavay. 225. 1890. ≡ *Photinia lasiogyna* (Franch.)
 1066 C.K.Schneid., Repert. Spec. Nov. Regni Veg. 3: 153. 1906. ≡ *Pyrus avalon* M.F.Fay &
 1067 Christenh., Global Fl. 4: 96. 2018. replacement name.
- 1068 = *Stranvaesia glaucescens* var. *yunnanensis* Franch., Pl. Delavay. 226. 1890. Type: CHINA.
 1069 Yunnan, in silvis supra Che-tong, prope Tapin-tze, May 18, 1885, *J.M. Delavay 1992*
 1070 (lectotype, designated by Idrees et al. (2022: 31): P barcode P02143161!; isolectotype: P
 1071 barcode P02143140!). Image of lectotype available from
 1072 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143161>
- 1073 = *Photinia mairei* H.Lév., Bull. Acad. Int. Géogr. Bot. 17: 28. 1916. Type: CHINA. rochers-brousse
 1074 des mont a Kiao-me-ti, May 1911-1913, *E.E. Maire s.n.* (lectotype, designated by Pathak et al.
 1075 (2021: 41): E [barcode E00011316!]; isotype: A [barcode 00038571!]). Image of lectotype
 1076 available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011316>
- 1077 Distribution: China (Fujian, Guangdong, Guangxi, Hunan, Jiangxi, Sichuan, Yunnan, and Zhejiang).
 1078
- 1079 **3a. *Stranvaesia lasiogyna* var. *lasiogyna***
 1080 Fig. 1D
 1081 倒卵叶红果树 (原变种) (Chinese name)
 1082 Distribution: China (Sichuan and Yunnan).
 1083
- 1084 **3b. *Stranvaesia lasiogyna* var. *glabrescens* (L.T.Lu & C.L.Li) B.B.Liu, Molec. Phylogen. Evol.**
 1085 **189-107914: 11. 2023.**
 1086 无毛倒卵叶红果树 (变种) (Chinese name); pinyin (spelled as sounds in Chinese): wu mao dao
 1087 luan ye hong guo shu
 1088 Type: CHINA. Jiangxi, Shangrao, 4 May 1972, *Jiangxi Exped. 1071* (holotype: PE [barcode
 1089 00336583!]; isotype: PE [barcode 00336582!]).
 1090 ≡ *Photinia lasiogyna* var. *glabrescens* L.T.Lu & C.L.Li, Acta Phytotax. Sin. 38(3): 278. 2000.
 1091 Distribution: China (Fujian, Guangdong, Guangxi, Hunan, Jiangxi, Sichuan, Yunnan, and Zhejiang).
 1092
- 1093 ***Weniomeles* B.B.Liu, Molec. Phylogen. Evol. 189-107914: 11. 2023.**
- 1094 楞木属 (Chinese name); pinyin (spelled as sounds in Chinese): luo mu shu
 1095 Type: *Weniomeles bodinieri* (H.Lév.) B.B.Liu ≡ *Photinia bodinieri* H.Lév.
 1096 Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Shaanxi,
 1097 Sichuan, Yunnan, and Zhejiang), Indonesia, and Vietnam.
 1098
- 1099 **1. *Weniomeles bodinieri* (H.Lév.) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 12. 2023.**
 1100 楞木 (Chinese name); pinyin (spelled as sounds in Chinese): luo mu
 1101 Type: CHINA, Kouy-Tchéou (now Guizhou): environs de Kouy-Yang, mont. du Collège, ca et là
 1102 autour des villages, 18 May 1898, *E. Bodinier 2256* (lectotype, designated by Liu et al. (2019:
 1103 686): P [barcode P02143207!]; isolectotypes: A [barcode 00045584!], E [barcode E00010998!],
 1104 P [barcode P02143208!, P02143209!]). Image of lectotype available from
 1105 <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143207>
- 1106 ≡ *Photinia bodinieri* H.Lév., Repert. Spec. Nov. Regni Veg. 4: 334. 1907. ≡ *Pyrus eureka* M.F.Fay
 1107 & Christenh., Global Fl. 4:103. 2018. replacement name. ≡ *Stranvaesia bodinieri* (H.Lév.)
 1108 B.B.Liu & J.Wen, J. Syst. Evol. 57(6): 686. 2019. ≡ *Stranvaesia bodinieri* (H.Lév.) Long
 1109 Y.Wang, W.B.Liao & W.Guo, Phytotaxa 447(2): 110. 2020. later homonym.
 1110 = *Photinia davidsoniae* Rehder & E.H.Wilson, Pl. Wilson. 1: 185. 1912. ≡ *Pyrus davidsoniae*
 1111 (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4:101. 2018. Type: CHINA, Western

Hupei (Hubei): near Ichang (Yichang), alt. 300–600 m., April 1907, *E.H. Wilson* 685 (lectotype, selected by Vidal (1968), first step “type”; second step, designated by Liu et al. (2019: 687): A [barcode 00038567!] excluding the fruits and seeds in the packet; isoelectotypes: BM [barcode BM000602130!], E [barcode E00011306! excluding the fruiting branch], GH [barcode 00045598! excluding the fruiting branch], HBG [barcode HBG511078! excluding the fruiting branch], US [barcode 00097494! excluding the fruiting branch]). *ibidem*, *E.H. Wilson* 685 (paratype: A [barcode 00038567, only the fruits and seeds in the packet, 00045599!], E [barcode E00011306, excl. the flowering branch!], GH [barcode 00045598, excl. the flowering branch!], HBG [barcode HBG511078, excl. the flowering branch!], US [barcode 00097494, excl. the flowering branch!]). CHINA, Hubei: south-west of Ichang, alt. 300 m, November 1907, *E.H. Wilson* 484 (paratypes: BM [barcode BM000946991!], HBG [barcode HBG511080!]). mountains south of Ichang, May 1900, *E.H. Wilson* 462 (paratypes: HBG [barcode HBG511079!], P [barcode P02143162!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00038567>
 = *Hiptage esquirolii* H.Lév., Repert. Spec. Nov. Regni Veg. 10:372. 1912. Type: CHINA, Kouy-Tchéou (now as Guizhou): Choui-Teou, route de Tin-Pan-Lo-Fou, alt. 900 m, 4 May 1900, *J Esquirol* 2097 (lectotype, designated by Liu et al. (2019: 687): E [barcode E00011307!]; isoelectotypes: A [barcode 00015103!, 00045102!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011307>
 Distribution: China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Shaanxi, Sichuan, Yunnan, and Zhejiang), Indonesia, and Vietnam.

1a. *Weniomeles bodinieri* var. *bodinieri*

Fig. 1E, 7

楞木 (原变种) (Chinese name)

Distribution: China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Shaanxi, Sichuan, Yunnan, and Zhejiang), Indonesia, and Vietnam.

1b. *Weniomeles bodinieri* var. *longifolia* (Cardot) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 13. 2023.

长叶楞木 (Chinese name); pinyin (spelled as sounds in Chinese): chang ye luo mu

Type: CHINA, Kouei Tchéou (now as Guizhou Province): grande route Kouei Tchéou au Kuangsi (Guangxi Province), Kout’ong (now as Gudong Xiang, Pingtang County), 22 May 1899, *Beauvais J.* 175 (lectotype, designated by Liu et al. (2019: 687): P [barcode P02143211!]; isoelectotype: P [barcode P02143210!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143211>

≡ *Photinia bodinieri* H.Lév. var. *longifolia* Cardot, Notul. Syst. (Paris) 3: 374. 1918. ≡ *Stranvaesia bodinieri* var. *longifolia* (Cardot) B.B.Liu & J.Wen, J. Syst. Evol. 57(6): 687. 2019.

Distribution: China (Guizhou).

1c. *Weniomeles bodinieri* var. *ambigua* (Cardot) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 13. 2023.

尖瓣楞木 (Chinese name); pinyin (spelled as sounds in Chinese): jian ban luo mu

Type: CHINA, Su-Tchuen (Sichuan): Eul Se Yug, vallée du Yalory, alt. 2000 m, 5 May 1911, *Legendre* 834 (lectotype, designated by Jin et al. (2023a: 13): P [barcode P02143164!]; isoelectotype: P [barcode P02143165!]). Image of lectotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143164>

≡ *Photinia davidsoniae* var. *ambigua* Cardot, Notul. Syst. (Paris) 3: 374. 1918.

Distribution: China (Sichuan).

1d. *Weniomeles bodinieri* var. *pungens* (Cardot) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 13. 2023.

尖叶栲木 (Chinese name); pinyin (spelled as sounds in Chinese): ju jian luo mu

Type: CHINA, Hubei: Ichang, A. Henry 7174 (holotype: P [barcode P02143163!]). Image of holotype available from <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143163>

≡ *Photinia davidsoniae* Rehder & E.H.Wilson var. *pungens* Cardot, Notul. Syst. (Paris) 3: 374. 1918.

Distribution: China (Hubei).

2. *Weniomeles atropurpurea* (P.L.Chiu ex Z.H.Chen & X.F.Jin) B.B.Liu, comb. nov.

黑果栲木 (Chinese name); pinyin (spelled as sounds in Chinese): hei guo luo mu

Type: CHINA, Zhejiang: Taishun, Zuoxi, Lishuqiu, alt. 400 m, 3 May 2020, Z.H. Chen, Z.P. Lei & W.Y. Xie TS20050316 (holotype: ZM; isotype: ZM).

≡ *Photinia atropurpurea* P.L.Chiu ex Z.H.Chen & X.F.Jin, J. Hangzhou Univ., Nat. Sci. Ed. 20(4): 393. 2021.

Distribution: China (Zhejiang).

Conclusion

In summary, our study addresses the long-standing deficiency of the comprehensive phylogenetic backbone in the apple tribe Maleae, primarily stemming from limited taxon and marker sampling in prior research efforts. Our phylogenomic investigations conclusively identified three major clades within the tribe, and through a meticulous integration of nuclear phylogenetic data with morphological and chromosomal evidence, we present an updated infra-tribal taxonomic system, introducing subtribe Malinae Reveal, subtribe Lindleyinae Reveal, and subtribe Vauquelininae B.B.Liu (subtr. nov.). Notably, our plastid phylogenetic analysis underscored the monophyly of most genera, albeit with exceptions such as *Amelanchier*, *Malus*, *Sorbus* sensu lato, and *Stranvaesia*. Furthermore, we contribute a comprehensive taxonomic synopsis of *Photinia* and its morphological counterparts in the Old World, recognizing and delineating 27 species along with ten varieties within *Photinia*, three species and two varieties within *Stranvaesia*, and two species paired with three varieties within *Weniomeles*. Additionally, our study makes a valuable contribution by lectotypifying 12 names and making two new combinations, thereby aiding in clarifying nomenclatural ambiguities.

Overall, this research represents a significant milestone in the field of botanical science by effectively bridging longstanding gaps in our comprehension of the evolutionary history of the Maleae tribe. By providing a comprehensive and carefully analyzed phylogenetic framework, this study not only sheds light on the intricate relationships among the various species and genera within the tribe but also offers a foundation upon which future botanical investigations can be built. This refined taxonomic framework, meticulously constructed through a synthesis of plastid data, morphological analyses, and chromosomal evidence, stands as a cornerstone for the scientific community, serving as a valuable resource for guiding taxonomic revisions and clarifying the classification of diverse plant species within the Maleae tribe. Its utility extends beyond the present research, offering researchers and conservationists a crucial tool for informed decision-making, species conservation, and the preservation of biodiversity in the ever-evolving botanical landscape.

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1210 Additional information

1211 Conflict of interest

1212 The authors have declared that no competing interests exist.

1213 Ethical statement

1214 No ethical statement was reported.

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1220 Author contributions

1221 B.B.L conceptualized and led the project, with collaborative supervision from G.N.L and S.H.J. The
1222 data assembly and phylogenomic analysis were carried out by H.W, X.Y.L, Y.J, and Y.Z. C.X was
1223 responsible for conducting the experimental work. The initial draft of the manuscript was skillfully
1224 prepared by H.W, X.Y.L, Y.J, Y.Z, D.K.M, and Z.T.J. B.J.G examined and detailed the fine structure
1225 of the species represented in the study. T.W contributed by providing fresh samples essential for
1226 analyzing the fine structure. B.L offered valuable insights and feedback on the Chinese names
1227 proposed in the research. All the authors approved the final manuscript.

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1242 Data availability

1243 All of the data that support the findings of this study are available in the main text or Supplementary
 1244 Information.

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Figure legend:

- Figure 1. Phylogenetic tree of the apple tribe Maleae estimated by Maximum Likelihood (ML) algorithm using RAxML, based on a concatenated 426 nuclear single-copy genes (SCNs) supermatrix (**A**). Inset in the upper left corner (**B**): A segment of the RAxML tree focusing on *Photinia* and its allies, inferred from concatenated 78 plastid coding sequences (plastid CDSs). (Adapted from Fig. 1 in Jin et al. (2023)). **C** *Photinia serratifolia* (Zhejiang, China: Bin-Bin Liu); **D** *Stranvaesia lasiogyna* (Yunnan, China: Bin-Bin Liu); **E** *Weniomeles bodinieri* (Yunnan, China: Bin-Bin Liu); **F** *Pourthiaea magnoliifolia* (Zhejiang, China: Bin-Bin Liu).
- Figure 2. A comprehensive phylogenetic backbone of the apple tribe Maleae, including 563 plastomes across 370 species and 26 genera, estimated by IQ-TREE2 based on the whole plastome dataset. Each of the 26 genera is represented by a unique color for clear distinction. Owing to the extensive scope of the tree, it is segmented into four distinct groups (labeled Group A, B, C, and D), each depicted in separate images. The interconnections among these subgroups are denoted by branch connectors labeled α , β , γ , δ , ϵ , and ζ .
- Figure 3. Fine structure of *Photinia griffithii*. **A B & C** infructescence branch **D** longitudinal section of fruit **E** fruit, viewed from above **F** cross-sections of fruit. Yan-Li Wen collected all the specimens on 7 October 2023 from Kunming Institute of Botany, Chinese Academy of Sciences. Subsequently, Bin-Jie Ge (Chenshan Botanical Garden) dissected and photographed each of these samples.
- Figure 4. Fine structure of *Photinia integrifolia*. **A C & D** infructescence branch **B** fruit, viewed from above **E** longitudinal section of fruit **F** cross-sections of fruit. Yan-Li Wen collected all the specimens on 7 October 2023 from Kunming Institute of Botany, Chinese Academy of Sciences. Subsequently, Bin-Jie Ge (Chenshan Botanical Garden) dissected and photographed each of these samples.
- Figure 5. Fine structure of *Photinia lanuginosa*. **A C D & E** infructescence branch at different developmental stages **B** abaxial surface of leaf blade **F** fruit, viewed from above **G** cross-sections of fruit **H** longitudinal section of fruit **I** seed. Specimens A, B, and C were collected on October 7, 2023, while the remaining samples were gathered on November 29, 2023. Ting Wang was responsible for the collection of all fresh specimens at the Hangzhou Botanical Garden. Furthermore, Bin-Jie Ge (Chenshan Botanical Garden) dissected and photographed all the samples.
- Figure 6. Fine structure of *Photinia prunifolia*. **A C D & F** infructescence branch at different developmental stages **B** abaxial surface of leaf blade, showing the black glands **E** fruit, viewed from above **G** cross-sections of fruit **H** longitudinal section of fruit **I** seed. Specimens A, B, and C were collected on October 7, 2023, while the remaining samples were gathered on November 29, 2023. Ting Wang was responsible for the collection of all fresh specimens at the Hangzhou Botanical Garden. Furthermore, Bin-Jie Ge (Chenshan Botanical Garden) dissected and photographed all the samples.
- Figure 7. Comprehensive structural anatomy of *Weniomeles bodinieri*. **A** branch of the inflorescence **B** flowers **C & D** comparative top view of a single flower in both unopened and opened states **E** bottom perspective of an individual flower **F** longitudinal section through the ovary **G** stamens **H** cross-section through the ovary **I** detailed view of the pistil **J** dissected flower, illustrating internal structure **K** branch of the infructescence **L** cross-section of a young fruit **M** top view of

a developing fruit **N** mature fruits **O** longitudinal-section through a mature fruit **P** cross-section through a mature fruit **Q** cross-section through a mature seed **R** a fully matured seed. The inflorescence branches were collected on June 14, 2022, and the infructescence branches were gathered on December 15, 2023, by Bin-Jie Ge at the Chenshan Botanical Garden, Shanghai. Additionally, Bin-Jie Ge dissected and photographed all the samples.

1560 **Supplementary files**

1561 **Supplementary material 1**

1562 **Table S1**

1563 Authors: Hui Wang, Xiao-Ya Li, Yan Jiang, Yu Zhang, Ze-Tao Jin, Dai-Kun Ma, Bing Liu, Chao
1564 Xu, Bin-Jie Ge, Ting Wang, Qiang Fan, Shui-Hu Jin, Guang-Ning Liu, Bin-Bin Liu

1565 Data type: Tables

1566 Explanation note: Voucher and sequence information for taxon samples of the apple tribe used in this
1567 study.

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1572 credited.

1573 Link:

1574

1575 **Supplementary material 2**

1576 **Figure S1**

1577 Authors: Hui Wang, Xiao-Ya Li, Yan Jiang, Yu Zhang, Ze-Tao Jin, Dai-Kun Ma, Bing Liu, Chao
1578 Xu, Bin-Jie Ge, Ting Wang, Qiang Fan, Shui-Hu Jin, Guang-Ning Liu, Bin-Bin Liu

1579 Data type: Images.

1580 Explanation note: Phylogenetic tree of the apple tribe Maleae estimated through maximum
1581 likelihood analysis using IQ-TREE2, based on the whole plastome dataset. The numbers
1582 displayed above each branch represent the SH-aLRT support values and Ultrafast Bootstrap
1583 support percentages, respectively.

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1588 credited.

1589 Link:

1590

1591 **Supplementary material 3**

1592 **Figure S2**

1593 Authors: Hui Wang, Xiao-Ya Li, Yan Jiang, Yu Zhang, Ze-Tao Jin, Dai-Kun Ma, Bing Liu, Chao
1594 Xu, Bin-Jie Ge, Ting Wang, Qiang Fan, Shui-Hu Jin, Guang-Ning Liu, Bin-Bin Liu

1595 Data type: Images.

1596 Explanation note: Phylogenetic tree of the apple tribe Maleae estimated through maximum
1597 likelihood analysis using RAxML, based on the whole plastome dataset. The numbers displayed
1598 above each branch represent the Bootstrap support value.

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