

REHDERODENDRON TRUONGSONENSE (STYRACACEAE),
A NEW SPECIES FROM VIETNAM

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ABSTRACT

Rehderodendron truongsense, a new species from Vietnam, is described and illustrated. In the treatment of the Styracaceae for the *Flora du Cambodge, du Laos, et du Viêt Nam*, specimens of this species were recognized as *R. macrocarpum* Hu. These specimens clearly differ from *R. macrocarpum*, however, as well as from all other species of *Rehderodendron* (where these characters are known) by, e.g., an evergreen versus deciduous habit, fewer secondary veins of the leaf blade, shorter inflorescences and corolla lobes, large and conspicuous lowermost bracteoles, the presence of eight ovules per carpel, and a fruit with ca. 10 to 20 ribs that are indistinct. Phylogenetic analysis based on five chloroplast DNA regions (*clpP-psbB*, *ndhD-psaC-ndhE-ndhG*, *rpl22-rps19*, *rps18-rpl20*, and *psbI-trnS-GCU*) placed the new species as nested within *Rehderodendron* and sister to *R. gongshanense*. This new species is endemic to the Truong Son Mountain Range, from which the epithet is derived, and we assign it an IUCN Red List preliminary status as Near Threatened.

摘要

本文报道了越南安息香科木瓜红属一新种——长山木瓜红 **Rehderodendron truongsense**。在《柬埔寨、老挝、越南植物志》中，本种被错误的处理为木瓜红 *R. macrocarpum*。然而，长山木瓜红与木瓜红以及本属的其它种均明显不同；本种为常绿（其它种落叶），叶片侧脉较少，花序和花冠裂片较短，最下部的小苞片大而明显，每室有8个胚珠，果具10–20棱；因而区别明显。基于5个叶绿体基因片段 (*clpP-psbB*, *ndhD-psaC-ndhE-ndhG*, *rpl22-rps19*, *rps18-rpl20*, *psbI-trnS-GCU*) 的系统发育研究显示，长山木瓜红嵌套进木瓜红属，并为贡山木瓜红 *R. gongshanense* 的姐妹类群。本种为越南长山山脉的特有种，也即本种种加词的来源。根据IUCN物种红色名录的评价指标，本种初步评价为近危物种。

TÓM TẮT

Dưa Dừa Trường Sơn (**Rehderodendron truongsense**), loài thực vật mới được phát hiện và mô tả ở dãy núi Trường Sơn, Việt Nam. Các mẫu của loài này bị định loại nhầm là *R. macrocarpum* Hu trong Thực vật chí Đông Dương. Tuy nhiên loài mới khác với tất cả các loài trong

chi Đũa Đũa bởi những đặc điểm hình thái như: cây gỗ thường xanh, gân thứ cấp ít, trục cụm hoa và thùy tràng ngắn hơn, lá bắc lớn, noãn 8, và quả gồm 10–20 đường gờ nổi rõ. Kết quả phân tích 5 vùng gen lục lạp (*clpP-psbB*, *ndhD-psaC-ndhE-ndhG*, *rpl22-rps19*, *rps18-rpl20*, *psbI-trnS-GCU*) chỉ ra rằng loài *R. truongsongense* có quan hệ gần gũi với loài *R. gongshanense*, chúng hình thành một nhánh riêng biệt so với các loài trong chi. Loài đặc hữu của Việt Nam này được đánh giá ở mức độ gần nguy cấp dựa trên khung đánh giá bảo tồn của IUCN.

KEY WORDS: IUCN Red List, molecular phylogenetics, new species, *Rehderodendron*, Vietnam

INTRODUCTION

Rehderodendron Hu (Styracaceae) currently comprises eight species distributed in southern China, Myanmar, and Vietnam (Institutum Botanicum Kunmingense Academiae Sinicae Edita 1983; Hwang & Grimes 1996). The genus is easily distinguished from the rest of the Styracaceae by its dry nut-like and generally cylindrical-ellipsoid fruit with a short rostrum and an endocarp with rays intruding into the mesocarp from a central column. It is also distinguished by the combination of fertile shoots produced only laterally on the branchlets of the previous growth period, pedicels borne on an inflorescence axis, petals connate distinctly beyond the base, corolla lobes five or rarely six, ovary inferior, and ovules four per carpel in two axial rows with the lower two ovules descending and epitropous, and the upper two ascending and apotropous (Hwang & Grimes 1996; Fritsch et al. 2001; Fritsch 2004).

Three species of *Rehderodendron* have been recognized in Vietnam—*R. indochinense* H.L. Li, *R. kweichowense* Hu, and *R. macrocarpum* Hu—all distributed in the Northwest Region and Northeast Region of the country, with *R. macrocarpum* extending to the North Central Coast Region (Pham 1991; Svengsuksa & Vidal 1992; Hwang & Grimes 1996; Nguyen 2003; Atlanta Botanic Garden 2016). The plants from the North Central Coast were treated as *R. macrocarpum* by Svengsuksa and Vidal (1992) for the *Flore du Cambodge, du Laos, et du Vietnam* on the basis of two collections in the Paris Herbarium (P) from Bach Ma Mountain in Thua Thien-Hue province, i.e., *E. Poilane 29888* (P04514862; in fruit) and *J.E. Vidal 700A* (P04514864; sterile), both of which were cited in Svengsuksa and Vidal's treatment and which Svengsuksa annotated. These and other collections of *Rehderodendron* made by E. Poilane from Bach Ma Mountain and farther south in Lien Chieu district of Da Nang province and Nam Tra My district of Quang Nam province, both in the South Central Coast Region, are available for examination digitally on the P herbarium specimen portal (<https://science.mnhn.fr/institution/mnhn/search>). None of these are identified or annotated to species. They are in fruit except for one sterile collection, and two also have young inflorescences with flower buds; none have open flowers.

During field expeditions in 2013 and late 2018 to Bach Ma National Park in Thua Thien-Hue province and Vu Quang National Park in Ha Tinh province, several of the authors made what were thought to be collections of *Rehderodendron macrocarpum* in flower and fruit, some of which, along with images of the living plants, were distributed to other herbaria, including BRIT. After careful comparison of these specimens with others, Fritsch as well as Liao and his lab independently concluded that the specimens represent an undescribed species. On this realization, all authors agreed to combine their complementary data and observations on this new species and publish the results together; the new species is described herein. We consider that all collections of *Rehderodendron* from Thua Thien-Hue, Da Nang, Quang Nam, and Kon Tum provinces, either available for examination digitally on the P specimen portal or collected by the authors, belong to this new species, with *R. macrocarpum* having been misapplied to the two specimens cited by Svengsuksa and Vidal (1992). The morphology of the new species is compared to that of the other species of *Rehderodendron*, and its conservation status is assessed. Further, a molecular phylogenetic analysis that includes multiple accessions of five *Rehderodendron* species is conducted to assess the distinctness of the new species, its monophyly, and its placement relative to other members of the genus.

MATERIALS AND METHODS

We compared the morphological characters of our collections of the new species with those from Thua Thien-Hue, Da Nang, and Quang Nam provinces on the P specimen portal and those representing the other species of *Rehderodendron* available at BRIT, IBSC, KUN, and SYS and digitally through several online web sites, e.g.,

the Chinese Virtual Herbarium (CVH), the data portal of the New York Botanical Garden herbarium (NY), and types on JSTOR Global Plants, as well as through examination of species protologues and the descriptions in Pham (1991), Hwang and Grimes (1996), and Svengsuksa and Vidal (1992).

The molecular dataset comprised 14 samples. New DNA sequence data were generated for nine of these. For the other five, the data are from Yan et al. (2018) and downloaded from GenBank (Table 1). The ingroup comprised 10 terminals from five species of *Rehderodendron*, including three samples of the presumed new species. Four species from four separate genera of the Styracaceae were employed as the outgroup, i.e., *Meliiodendron xylocarpum* Hand.-Mazz., *Perkinsiodendron macgregorii* (Chun) P.W. Fritsch, *Pterostyrax psillophyllus* Diels ex Perkins, and *Sinojackia microcarpa* T. Chen & G.Y. Li; *Meliiodendron* was used to root the tree, in accordance with the findings of Yan et al. (2018). Voucher specimens for all newly generated sequences were deposited at SYS with duplicates in several herbaria, and their DNA sequences were deposited in GenBank (Table 1).

Genomic DNA was extracted from silica-gel-dried leaves with the modified 2× CTAB procedure of Doyle and Doyle (1987). Based on the chloroplast genome data in Yan et al. (2018), we selected five highly variable chloroplast gene regions (*clpP-psbB*, *ndhD-psaC-ndhE-ndhG*, *rpl22-rps19*, *rps18-rpl20*, and *psbI-trnS-GCU*) for phylogenetic tree construction. Eleven primer pairs were designed to amplify the regions (Appendix 1). PCR amplification was performed as in Chen et al. (2016). Sequences were aligned with MEGA version 6.0 (Tamura et al. 2013) and gaps were treated as missing data. Phylogenetic reconstruction was performed with maximum likelihood (ML) and Bayesian inference (BI) analyses. ML was performed on the CIPRES Science Gateway web server (RAxMLHPC2 on XSEDE 8.2.9; Miller et al. 2010) with 1000 bootstrap replicates. BI was performed in MrBayes version 3.2.6 (Ronquist & Huelsenbeck 2003) with the GTR model as determined with jModelTest version 2.1.7 (Posada 2008; Darrriba et al. 2012). FigTree version 1.4.3 (available at: <http://beast.community/figtree>) was used to visualize and edit the resulting tree.

RESULTS

Rehderodendron truongsongense P.W. Fritsch, W.B. Liao, & W.Y. Zhao, **sp. nov.** (Figs. 1–5). TYPE: VIETNAM. Ha Tinh province: Vu Quang National Park, S of Khe Che Forest Station, 60 m, 18°22'30"N, 105°18'42"E, 9 Oct 2018 (fl), U. Swenson, D.V. Truong, H.M. Quyen, & S. Razafimandimbison 2131 (HOLOTYPE: VNMN!; ISOTYPES: BRIT!, MEL!, MO!, P!, SI, SYS211337!).

Haec species *Rehderodendroni macrocarpo* Hu simillima, sed ab eo plantis sempervirentibus, nervis laminae paucioribus, bracteolis majus, lobis corollae brevioribus, ovulis 8 in quoque loculo, striis fructus 10–20 nec regulariter dispositis nec distinctis differt.

Trees, evergreen, 8–20 m tall; trunk to 60 cm d.b.h. with inconspicuous longitudinal ridges, bark beige with closely spaced longitudinal shallow furrows. Trichomes stellate throughout. Old branchlets gray, glabrous, with continuous pith; young branchlets brown, sparsely pubescent, more densely so distally. Perennating buds with 2 caducous coriaceous outer scales covered with dense golden brown pubescence; vegetative buds axillary or pseudoterminal, narrowly conoid, 3.3–6.8 mm long, fertile buds axillary, superposed with vegetative buds or solitary, subglobose or compressed-globose, 1.0–2.4 mm long. Leaves spirally arranged; petioles in cross section rounded abaxially, concave adaxially, 7–17 × 1.0–1.4 mm, sparsely pubescent; leaf blades glossy bright green in vivo, dark green or dark olive green in sicco, elliptic, 5.8–13.0 × 4.2–7.0 cm, 1.8–2.4 times as long as wide, membranaceous to chartaceous, abaxially glabrous or very sparsely pubescent, more densely so along major veins and at base, glabrescent, adaxially glabrous except sparsely pubescent along midvein basally, glabrescent, midvein prominent abaxially, slightly sulcate adaxially, veins raised on both surfaces, secondary veins 4 to 7 on each side of midvein, tertiary veins reticulate to subparallel, quaternary veins reticulate, base broadly cuneate-attenuate, margin not or slightly revolute, obscurely serrulate with reddish brown minute glandular teeth that are often hidden underneath when margin is revolute (then margin appearing entire) with the teeth spaced an average of ca. 1–2 cm apart but more crowded toward apex, apex shortly attenuate. Inflorescences racemose, axillary, globose on initial expansion and enveloped by ca. 5 caducous suborbicular prophylls, 1.0–3.5 cm long, 2- to 10-flowered with flowers regularly spaced along rachis or more or less congested at end of peduncle; peduncle 2–11 mm long, with dense grayish green pubescence. Articulation present

TABLE 1. Voucher information and GenBank accession numbers for sequence data of *Rehderodendron* used in this study (sequences published here have the prefix MK).

Accession	Voucher	Location	<i>clpP-psbB</i>	<i>ndhD-psc-ndhE-ndhG</i>	<i>rpl22-rps19</i>	<i>rps18-rpl20</i>	<i>psbI-trnS-GCU</i>
<i>Rehderodendron indochinense</i> 1	W.Y. Zhao 1121 (SYS)	Daweishan, Pingbian, Yunnan, China	MK695917	MK695899	MK695908	MK695881	MK695890
<i>Rehderodendron indochinense</i> 2	W.Y. Zhao 699 (SYS)	Laojunshan, Wenshan, Yunnan, China	MK695921	MK695903	MK695912	MK695885	MK695894
<i>Rehderodendron trungsonense</i> 1	Q. Fan et al. 17349 (SYS, VNMN)	Kon Buon, Kon Tum, Vietnam	MK695920	MK695902	MK695911	MK695884	MK695893
<i>Rehderodendron trungsonense</i> 2	Q. Fan et al. 17321 (SYS, VNMN)	Bach Ma, Thua Thien-Hua, Vietnam	MK695924	MK695906	MK695915	MK695888	MK695897
<i>Rehderodendron trungsonense</i> 3	Q. Fan et al. 17329 (SYS, VNMN)	Bach Ma, Thua Thien-Hua, Vietnam	MK695925	MK695907	MK695916	MK695889	MK695898
<i>Rehderodendron kweichowense</i> 1	W.Y. Zhao 1162 (SYS)	Sitaipo, Malipo, Yunnan, China	MK695918	MK695900	MK695909	MK695882	MK695891
<i>Rehderodendron kweichowense</i> 2	W.Y. Zhao 1163 (SYS)	Sitaipo, Malipo, Yunnan, China	MK695919	MK695901	MK695910	MK695883	MK695892
<i>Rehderodendron gongshanense</i> 1	W.Y. Zhao 872 (SYS)	Qinlangdang, Gongshan, Yunnan, China	MK695922	MK695904	MK695913	MK695886	MK695895
<i>Rehderodendron gongshanense</i> 2	W.Y. Zhao 873 (SYS)	Qinlangdang, Gongshan, Yunnan, China	MK695923	MK695905	MK695914	MK695887	MK695896
<i>Rehderodendron macrocarpum</i>	C.-X. Zhao 201402 (HIB)	Nanyue Arboretum, Hunan, China		MG719844 (chloroplast genome)			
<i>Meliiodendron xylocarpum</i>	M.-H. Yan 201404 (HIB)	Wuhan Botanical Garden, Hubei, China		MG719837 (chloroplast genome)			
<i>Pterostyrax psilophyllus</i>	M.-H. Yan 201406 (HIB)	Wuhan Botanical Garden, Hubei, China		MG719838 (chloroplast genome)			
<i>Sinojackia microcarpa</i>	T. Chen 9511041 (IBSC)	Meicheng, Jiande, Zhejiang, China		MG719835 (chloroplast genome)			
<i>Perkinsiodendron macgregorii</i>	C.-X. Zhao 201407 (HIB)	Nanyue Arboretum, Hunan, China		MG719841 (chloroplast genome)			

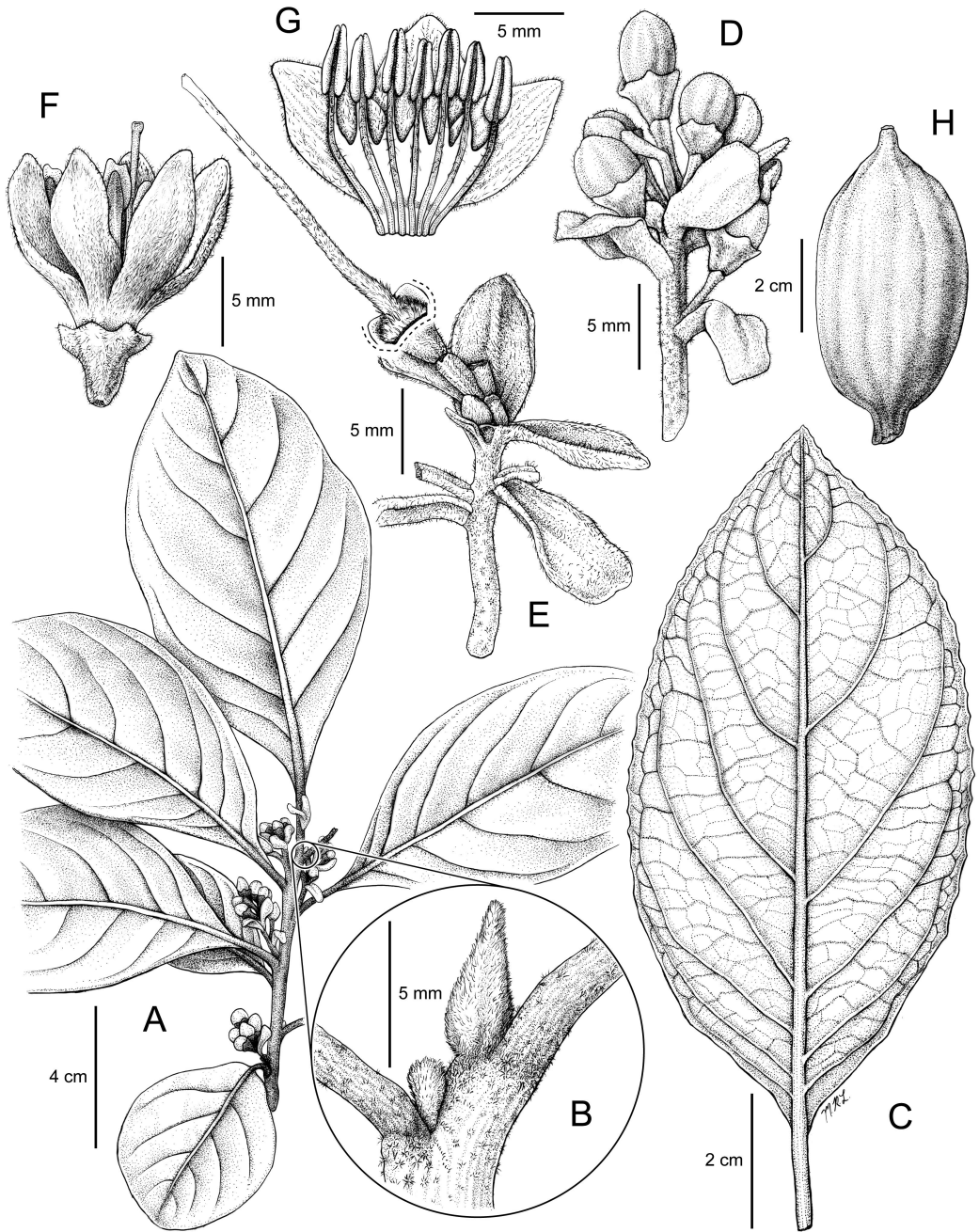


FIG. 1. *Rehderodendron truongsongense*. A. Flowering branchlet. B. Pseudoterminal vegetative (upper) and axillary fertile (lower) buds. C. Leaf, abaxial side. D. Inflorescence with flower buds. Note the large bracteoles subtending flowers toward base. E. Inflorescence with mostly fallen flowers showing remaining pedicels, and one flower with corolla, androecium, and calyx lobes removed (dotted line) showing ovary apex, style, and stigma. F. Flower. G. Corolla and androecium cut open to show three of the lobes and seven stamens. H. Fruit. A–G drawn from D.S. Penneys et al. 2095 (BRIT477286); H drawn from online image of E. Poilane 7561, P04458742.

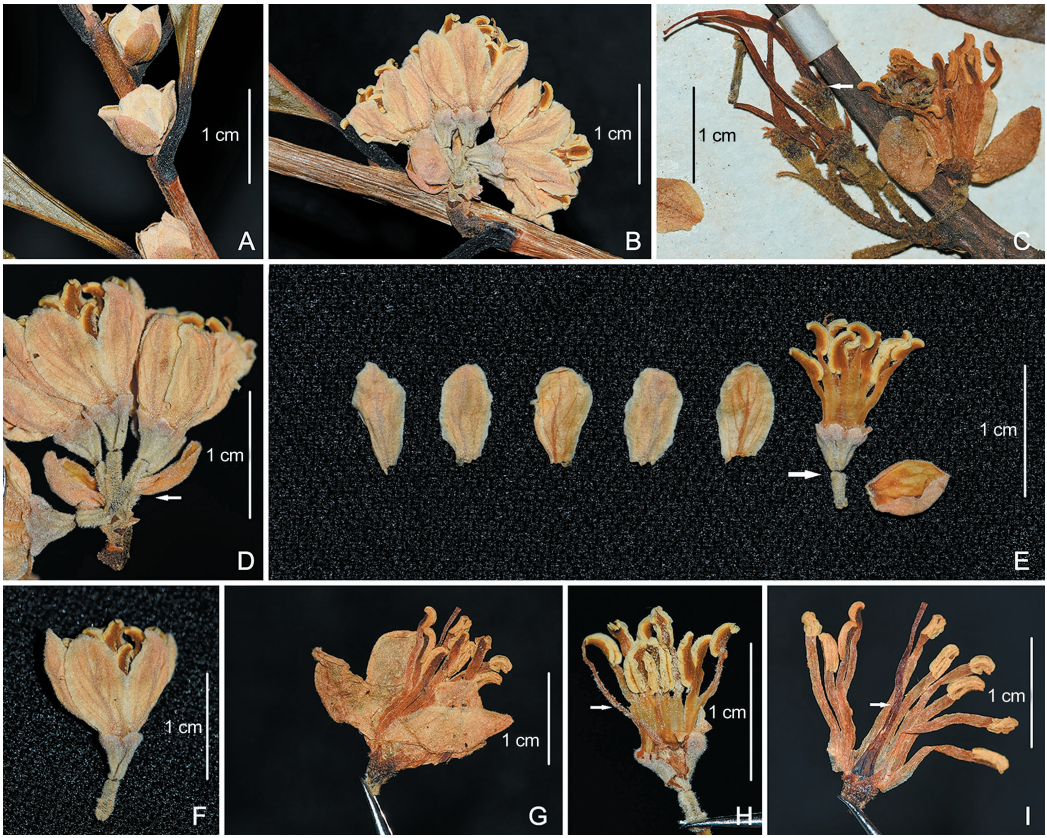


FIG. 2. Morphological characters of *Rehderodendron truongsense* (A, B, D, E, F, H) and *R. macrocarpum* (C, G, I). A. Expanding inflorescence buds of *R. truongsense*. B. Inflorescence of *R. truongsense*. Note suborbicular prophylls and bracteoles, and broadly deltoid calyx teeth. C. Inflorescence of *R. macrocarpum*. Note linear-lanceolate bracteole and (arrow) narrowly deltoid calyx teeth. D. Inflorescence of *R. truongsense*. Note cucullate bracteole inserted at base of pedicel (arrow). E. Bracteole and flower of *R. truongsense* with corolla divided into five parts corresponding to the lobes. Arrow indicates articulation of pedicel and hypanthium. Note filaments connate to above middle. F. Flower of *R. truongsense*. G. Flower of *R. macrocarpum*. H. Stamens, ventral view, and style of *R. truongsense*. Note pubescence on style (arrow) and filaments. I. Stamens, ventral view, and style of *R. macrocarpum*. Note glabrous style (arrow) and nearly glabrous filaments. Photographs of *R. truongsense* from isotype *U. Swenson et al.* 2131 (SYS211337); photographs of *R. macrocarpum* from *G.-H. Yang* 55171 (SYS136892).

at junction of pedicel and flower. Pedicel 2–9 × 0.4–0.7 mm with dense grayish green pubescence; bracteoles caducous, densely covered with grayish green pubescence on both sides or more sparsely adaxially, proximal bracteoles 5–9 × 2–5 mm, suborbicular, elliptic, or obovate, keeled, cucullate, with margin entire and apex obtuse to subrounded, distal bracteoles either becoming smaller toward apex of inflorescence and ultimately minute, or abruptly minute. Flowers ovoid to globose in bud, 11–17 mm long, pleasantly fragrant. Hypanthium obconoid, 1.4–3.5 × 1.2–3.0 mm, irregularly longitudinally ca. 5-ribbed ± in line with sinuses between calyx lobes, with dense grayish green pubescence. Free portion of calyx 1.2–1.9 mm long with dense grayish green pubescence, limb 0.8–1.5 mm long, lobes (teeth) 5 (to 7), broadly deltoid, 0.3–1.5 mm long with obtuse apex. Corolla white or light cream, campanulate, 8–11 mm long; tube ca. 1.5 mm, glabrous; lobes 5 (or 6), elliptic to obovate, 7–9 × 2.2–5.0 mm, densely pubescent abaxially, sparsely so adaxially, apex obtuse. Stamens 10 (or 12), exerted beyond corolla; tube glabrous, portion adnate to corolla ca. 1 mm long, free portion ca. 2.7–5.0 mm long, longer than filaments; filaments white to tinged orange, subequal (then 1–2 mm long), or of two different alternating lengths with longer five (outer) 4–6 mm and shorter five (inner) 1–2 mm, planar, abaxially

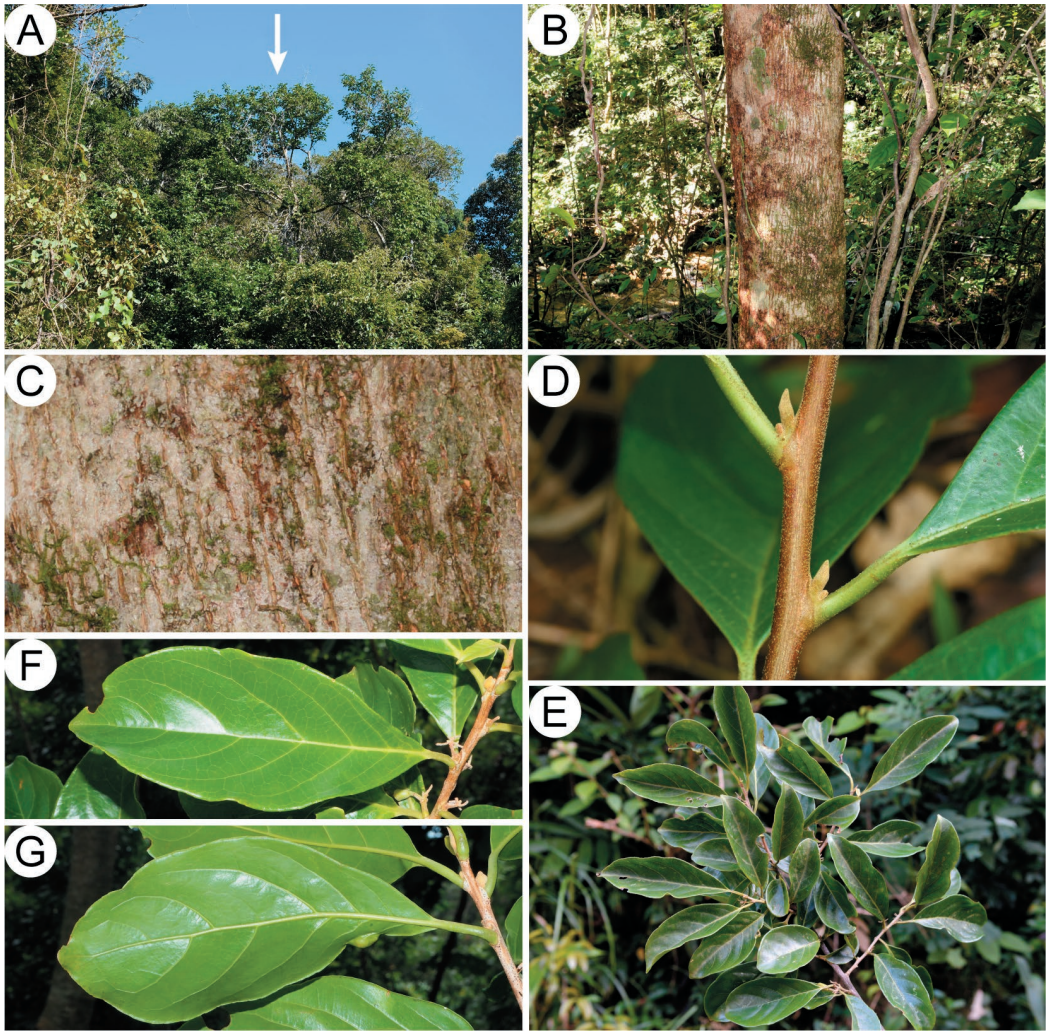


FIG. 3. Images of living *Rehderodendron truongsense*: vegetative characters. **A.** Tree habit (arrow) in evergreen broadleaved forest. **B.** Trunk. **C.** Bark. **D.** Branchlet. Note superposed conical vegetative and compressed globose fertile buds in each leaf axil. **E.** Branch with leaves. **F.** Leaf, adaxial side. **G.** Leaf, abaxial side. A–C, E, Q. Fan et al. 17322; photographs by Q. Fan. D, Q. Fan et al. 17349; photograph by W.-Y. Zhao. F, G, U. Swenson et al. 2108; photographs by U. Swenson.

glabrous, adaxially glabrous or bearing two types of trichomes, those with arms flattened and dull (common) and those with arms terete in cross section and glossy (rare); anthers oblong or narrowly deltoid, (1.5–)2.2–3.6 × 0.7–1.9 mm, connectives orange, thecae yellow, extending beyond connectives. Gynoecium 4-carpellate (one ovary sampled), incompletely 4-locular through distal attenuation of septa, apex densely pubescent; locules with abundant intra-ovarian trichomes; ovules 8 per locule, in two axial rows, lower 4 descending and epitropous, slightly longer than upper 4, upper 4 ascending and apotropous. Style filiform, 8–15 mm long, moderately pubescent, becoming glabrous distally; stigma truncate. Fruit nut-like, dry, indehiscent, 2- or 3-locular, green or yellowish green turning brown in vivo, dark olive brown in sicco, somewhat glossy, without spots, cylindrical-ellipsoid or (*E. Poilane 27700*) turbinate, short and broadly stalked and abruptly short-rostrate, 3.5–7.0 × 2.5–4.0 cm, irregularly ca. 10- to 20-ribbed, glabrescent except occasionally pubescent at maturity

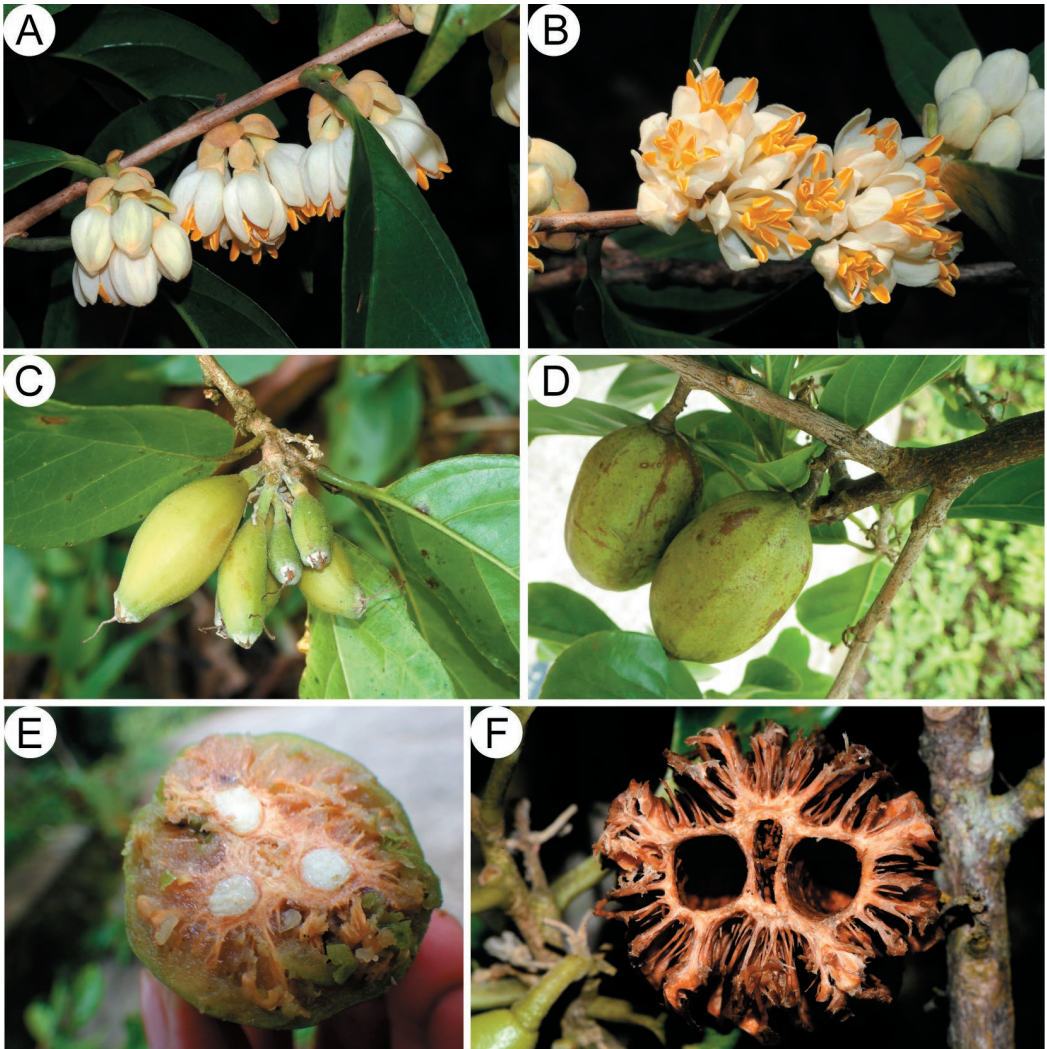


FIG. 4. Images of living *Rehderodendron truongsongense*: reproductive characters. **A.** Inflorescences showing bud scales, prophylls, bracteoles, and flowers in bud and at anthesis. **B.** Inflorescences showing flowers in bud and at anthesis showing stamens and styles. **C.** Branchlet with immature fruit. **D.** Branchlet with nearly mature fruit. Note indistinct ribs. **E.** Fruit cut transversely near middle showing three locules with one seed each. **F.** Old fruit showing endocarp tissue with radiating ribs and two locules separated by a central canal. A, B, U. Swenson *et al.* 2131; photographs by U. Swenson. C, F, Q. Fan *et al.* 17322; photographs by Q. Fan. D, E, Swenson *et al.* 2018; photographs by V.T. Do.

on beak, ribs indistinct, exocarp ca. 1.0–1.5 mm thick, mesocarp 5–8 mm thick, endocarp indurate, forming a column with a hollow central canal and irregularly radiating rays, at least some rays extending to fruit wall and separated by many lacunae (which are filled with mesocarp in vivo). Seeds 1 per locule, cylindrical-fusiform, 2.8–3.5 × ca. 0.4–0.5 cm; testa brown.

Distribution, Habitat, Ecology, and Common Names.—*Rehderodendron truongsongense* is endemic to the Truong Son Mountains in Vietnam and known from the North Central Coast, South Central Coast, and Central Highlands regions in the provinces of Ha Tinh, Thua Thien-Hue, Da Nang, Quang Nam, and Kon Tum. We suspect that it also occurs in neighboring Quang Ngai and Gia Lai provinces. The species occurs

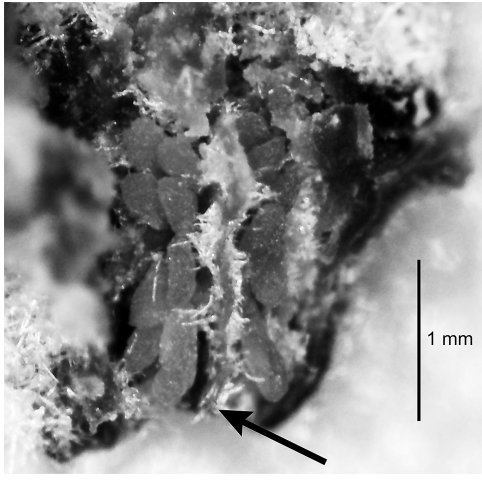


Fig. 5. Ovary of a flower bud from *Rehderodendron truongsongense* sliced longitudinally, exposing two locules. The floral axis is vertical with the ovary apex oriented top-ward. The bottom portion of the ovary has been cut away. The arrow points to the septum, in tangential view, that divides the locules. All eight ovules of one carpel are visible in the left locule, whereas six (of presumed eight; one of the lowermost has fallen off) are visible in the right locule. In the left locule, the four lower ovules are descending and epitropous and the four upper ovules are ascending and apotropous. Note the intra-ovarian stellate trichomes lining the septum. From *D.S. Penneys et al. 2095* (BRIT477286).

[digital image!]; summit of Bach Ma Mountain a little south of Hue, 1400–1500 m, 9 Sep 1938 (fl bud, fr), *E. Poilane 27700* (P05233152, P06614885, online images!); *ibid.*, (fr), *E. Poilane 27701* (P05586267, online image!); summit of Bach Ma Mountain near Hue, 1000–1200 m, 21 Apr 1939 (fr), *E. Poilane 29888* (P04514861, P04514862, online images!); Bach Ma National Park, along main road to summit, 1000 m, 16°11'50"N, 107°50'50"E, 6 Oct 2018 (fr), *U. Swenson et al. 2108* (BRIT!, MEL!, PI, SI, VNMNI!); Bach Ma, 1400 m, 16 Jun 1944 (st), *J.E. Vidal 700A* (P04514864).

Conservation Assessment.—We know of 15 collections of *Rehderodendron truongsongense*, all from Vietnam and together appearing to represent at least five distinct populations. One population is near and at the summit of Bach Ma Mountain, located in Bach Ma National Park of Thua Thien-Hue province, and another is from the mountainous north section of Lien Chieu district in Da Nang province within Bach Ma National Park. Another population is located in Nam Tra My district in Quang Nam province; the locality information is not specific enough to determine whether it is located in Ngoc Linh Nature Reserve, and thus may be in an unprotected area. A fourth population is in Vu Quang National Park in Ha Tinh province, and a fifth is in Kon Buon, an unprotected area of Kon Tum province. As estimated with GeoCAT (Bachman et al. 2011) from the five populations, the Extent of Occurrence (EOO) is ca. 22,986 km² and the Area of Occupancy (AOO) is 20 km²; three of these populations are known to occur in protected areas. On this basis, and in accordance with the IUCN Red List criteria (IUCN Standards and Petitions Subcommittee 2017), we categorize this species as Near Threatened (NT). The Endangered (EN) category could apply (B2a, AOO < 500 m² and number of locations ≤ 5), but it is uncertain as to whether there is a continuing decline in populations (Bb) or extreme fluctuations in the species (Bc). The fact that three populations occur in national parks, however, suggests that if declines and fluctuations are occurring, they are not extensive.

Molecular phylogenetic data.—The assembled and aligned lengths of *clpP-psbB*, *ndhD-psaC-ndhE-ndhG*, *rpl22-rps19*, *rps18-rpl20*, and *psbI-trnS-GCU* are 2216, 1543, 847, 1448, and 581 bp in length and with six, four,

from 60 to 1500 m elevation. It is known to flower in August and October, and fruit in April and August to October. *Rehderodendron truongsongense* has been documented as occurring in submontane monsoon forest and secondary rain forest, in rocks and on clay soil derived from granite and schist. The common name in Vietnamese is “Đũa Đũa Trường Sơn.”

Etymology.—The specific epithet refers to the Truong Son Mountains in Vietnam, extending from the provinces of Nghe An to Kon Tum and to which the new species is endemic.

Paratypes.—VIETNAM. Da Nang. Lien Chieu near Tourane [Da Nang], 600 m, 16 Aug 1923 (fr), *E. Poilane 7561* (P04458741, P04458742, P05233109, online images!); *ibid.*, 650 m, 17 Aug 1923 (fl bud, fr), *E. Poilane 7584* (P04450962, P04450963, P05233113, online images!). Kon Tum. Kon Plong district, Kon Buon, 1034 m, 14°35'N, 108°15'E, 24 Dec 2018 (immature fr), *Q. Fan et al. 17349* (SYS!, VNMNI!). Quang Nam. Southwest of Tra My [Nam Tra My district], 18 February 1941 (immature fr), *E. Poilane 31350* (P06614884, online image!). Thua Thien-Hue. Phu Loc district, Bach Ma National Park, 1175 m, 16°11'N, 107°50'E, 21 Dec 2018 (immature fr), *Q. Fan et al. 17322* (SYS!, VNMNI!); *ibid.*, 1041 m, 16°11'N, 107°50'E, 21 Dec 2018 (st), *Q. Fan et al. 17321*; *ibid.*, 1169 m, 16°11'N, 107°51'E, 22 Dec 2018 (st), *Q. Fan et al. 17329* (SYS!, VNMNI!); Phu Loc district, Loc Tri, Bach Ma N.P., 1375 m, 16°11'38.7"N, 107°51'49.8"E, 26 Apr 2014 (immature fr), *D.V. Hai et al. 566* (NY02817951, online image!); Phu Loc district, Loc Tri, Bach Ma National Park, about 1 km from guesthouse on road to summit, 16°11'47.4"N, 107°51'18.8"E, 1300 m, 15 Aug 2013 (fl), *D.S. Penneys et al. 2095* (BRIT477286!, CAS1243169 [digital image!], HN, NY02852884

one, three, and three parsimony-informative characters, respectively. The aligned length of the chloroplast dataset used for phylogenetic analysis was thus 6635 bp. Individual ML and BI analyses produced identical topologies, so only the Bayesian tree is reported in Figure 6. The molecular phylogenetic results support the monophyly of *Rehderodendron* (BP = 100; PP = 1.0) as sister to *Perkinsiodendron* (BP = 100; PP = 1.0). The three accessions of the new species formed a clade (BP = 100; PP = 1.0) that is sister to *R. gongshanense* (BP = 100; PP = 1.0).

DISCUSSION

The new species is placed within *Rehderodendron* by its possession of floral and fruit characters that are all consistent with those diagnostic for this genus, especially the dry nut-like and generally cylindrical-ellipsoid fruit with a short rostrum and an endocarp with rays intruding into the mesocarp from a central column. Other characters that support its inclusion in *Rehderodendron* are fertile shoots produced only laterally on the branchlet of the previous growth period, pedicels borne on an inflorescence axis, petals connate distinctly beyond the base, corolla lobes five or rarely six, ovary inferior, and ovules arranged in two axial rows with the lower ovules epitropous and the upper ovules apotropous (Hwang & Grimes 1996; Fritsch et al. 2001; Fritsch 2004). Like other species of *Rehderodendron*, it also has the unusual occurrence of intra-ovarian trichomes, uncommon elsewhere in the flowering plants but also present in several other genera of the Styracaceae (Dickison 1993). Our molecular phylogenetic results also support the inclusion of the new species within *Rehderodendron*.

The treatment of *Rehderodendron* for the *Flora of China* (Hwang & Grimes 1996) treated the genus as consisting of five species, all of which are distributed in China (*R. gongshanense* Y.C. Tang, *R. indo-chinense*, *R. kwangtungense* Chun, *R. kweichowense*, and *R. macrocarpum*) and with only one occurring outside of China, i.e., in Myanmar and Vietnam.¹ However, three other species of *Rehderodendron* described in *Flora Yunnanica* (Institutum Botanicum Kunmingense Academiae Sinicae Edita 1983), i.e., *R. conostyle* C.Y. Wu, *R. membranifolium* C.Y. Wu, and *R. microcarpum* K.M. Feng, all from Yunnan Province, China, were inadvertently not treated in the *Flora of China*. These are incompletely documented taxa, e.g., the flowers are still unknown. *Rehderodendron truongsongense* differs from these eight species, insofar as their morphology is known, by an evergreen habit (versus deciduous; Hwang & Grimes 1996; linked to this, in the new species the flowers open well after the leaves expand, versus either prior to or with leaf expansion; Hwang & Grimes 1996); fewer secondary leaf veins [four to seven on each side of midvein versus (six to) seven to 13 (Hwang & Grimes 1996)]; shorter inflorescences [1.0–3.5 cm versus 4–10 cm (Svengsuksa & Vidal 1992; Hwang & Grimes 1996)]; larger lowermost bracteoles (5–9 × 2–4 mm long), suborbicular in shape (versus ca. 5.0 × 1.2 mm and linear-lanceolate; Hwang & Grimes 1996; pers. obs.); shorter corolla lobes [7–9 mm versus 13–25 mm (Hwang & Grimes 1996)]; stamen filaments connate to above middle [versus connate to below middle (“short connate,” Hwang & Grimes 1996)], adaxially with a mixture of glossy stellate trichomes with terete arms and dull stellate trichomes with flattened arms [versus all dull with flattened arms, or filaments glabrous (Fritsch et al. 2001)]; eight ovules per carpel [Fig. 5; versus four; Hwang & Grimes 1996]; and fruit that is ca. 10- to 20-ribbed with the ribs indistinct [versus three- to 12-ribbed with the ribs well defined (Hwang & Grimes 1996)].

Although some of the character states of the three species described in *Flora Yunnanica* are not known for the above characters, *Rehderodendron truongsongense* is still clearly distinguishable from them. From the original description and illustration of *R. conostyle*, and examination of digital images of specimens of the holotype K.M. Feng 4927 (KUN0246217, digital image!) and K.M. Feng 5126 (KUN1209627 and KUN1209628, digital

¹ Although Hwang and Grimes (1996) indicate that *Rehderodendron* is distributed in Myanmar, their treatment does not list an occurrence in Myanmar for any of the treated species. Moreover, Kress et al. (2003), in their Myanmar checklist, do not include the genus as recorded for the country. Nonetheless, we examined digital images of specimens from BM and E of two Myanmar collections of *Rehderodendron*, i.e., *F. Kingdon Ward 22086* (BM001194094 and E00663952, online images!) and *20738* (BM 001194090 and E00663951, online images!). These collections were only identified to genus by Kingdon Ward and not subsequently annotated to species, but appear to be *R. macrocarpum* as based on the glabrous leaves and brown unspotted fruit with well-defined ribs. Two other more recent Myanmar collections of *Rehderodendron* at NY, i.e., *K. Armstrong 2060* (NY 02653551, online image!) and *2902* (NY 02653967 and 02654008, online images!), appear to be correctly identified as *R. macrocarpum*, on the same characters.

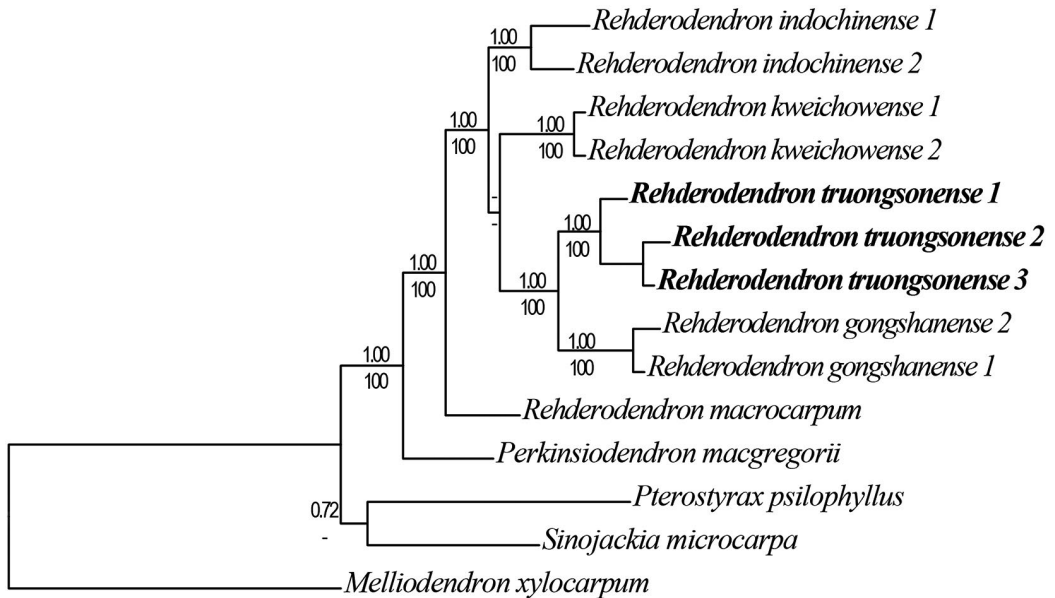


FIG. 6. Bayesian inference (BI) majority-rule tree of *Rehderodendron* based on five chloroplast gene regions, with other members of the Styracaceae as outgroup. A separate maximum likelihood (ML) analysis yielded an identical topology. BI posterior probabilities > 0.70 (above) and ML bootstrap values > 50% (below) are shown along the branches. The new species is shown in bold.

images!), all annotated by C.Y. Wu, as well as images on the CVH, i.e., an isotype of *K.M. Feng 4927* (PE00857454, online image!) and *K.M. Feng 5126* (WUK0207099, online image!), the new species is similar to *R. conostyle* in its fertile buds that appear to be enveloped by either prophylls or bracteoles (or both) that are suborbicular, but it is distinguished by its glossy leaf blades (versus dull or slightly glossy) with four to seven secondary veins on each side of the midvein (versus 10 to 15) and abaxially dark green or dark olive green in sicco (versus green to light brown). The fruit of the holotype of *R. conostyle* appears to have indistinct ribs but the two KUN specimens of *K.M. Feng 5126* clearly have well defined ribs, and the description states that the species has 10 faint ribs. The similar shape of the expanding fertile buds suggests a close relationship to *R. truongsongense*; however, at least *R. indochinense* also appears to have this character (e.g., P04514849, online image!) and the morphology of bud expansion needs critical examination for all species. From the original description and illustration of *R. membranifolium*, and examination of digital images of the holotype *S.K. Wu 60-3596* (KUN1209634, digital image!) and isotype (KUN1209635, digital image!), the new species is distinguished from *R. membranifolium* by its leaf blades abaxially dark olive green in sicco (versus pale green abaxially and green adaxially), obscurely serrulate leaf margin (versus distinctly so) shortly attenuate leaf apex (versus long-acuminate), and fruit ca. 10- to 20-ribbed with indistinct ribs (versus fewer but well defined). Finally, from the original description and illustration of *R. microcarpum*, a treatment of this species in Fritsch and Garrison (2010), and examination of a specimen of this species (*Gaoligong Shan Biodiversity Survey 32557*, CASI090267!) and digital images of the holotype (KUN1209632, digital image!) and an isotype (KUN1209633, digital image!), the new species is distinguished from *R. microcarpum* by its leaf blades with four to seven secondary veins on each side of the midvein (versus eight to 13), abaxially dark olive green in sicco (versus bright green or greenish brown) and glabrous or very sparsely pubescent abaxially (versus sparsely to moderately pubescent), and fruit generally larger (ca. 6.5–7.5 × 3.3–3.5 cm) with the ribs indistinct (versus 5.3–5.6 × 1.7–2.2 cm and well defined ribs).

Three characters of the new species appear to be rare or unique in the Styracaceae. The lowermost two bracteoles are large (5–9 × 2–4 mm long), whereas bracteoles in the rest of the family are described as minute

[Hwang & Grimes 1996; ca. 5×1.2 mm (pers. obs.)], although rarely they are notably larger, e.g., in *Styrax bracteolatus* Guillaumin with bracteoles 3.6–7.2 mm long (Li & Fritsch 2018). The new species also has stamen filaments possessing (when not glabrous) a mixture of glossy stellate trichomes with terete arms and dull stellate trichomes with flattened arms. This deviates from the filaments of other species of *Rehderodendron*, which exclusively have trichomes with flattened and dull arms (or else are glabrous; Fritsch et al. 2001). The stamen filaments of the other genera of the Styracaceae either have glossy trichomes with terete arms, i.e., *Bruinsmia* Boerl. & Koord., *Huodendron* Rehder, *Sinojackia* Hu, and *Styrax* L., or dull trichomes with flattened arms, i.e., the rest of the genera except for *Alniphyllum* Matsum., which has glossy trichomes with flattened arms (Fritsch et al. 2001). Finally, *R. truongsongense* has eight ovules per carpel in two axial rows, with the four lower ovules epitropous and four upper ovules apotropous (Fig. 5). *Rehderodendron* is otherwise reported to have four ovules per carpel in two axial rows, with the two lower ovules epitropous and the two upper ovules apotropous (Hwang & Grimes 1996), although this has not been examined in species whose flowers are still unknown. The other genera of Styracaceae either have the same ovule number, arrangement, and orientation as in the other species of *Rehderodendron*, or else are all apotropous in two or more axial rows with various ovule numbers (Dickison 1993; Hwang & Grimes 1996; Fritsch et al. 2001).

Variation in the above bud, stamen filament, and ovule characters have all been used to delimit genera in the family, and the presence of these unique features on morphology alone could leave some doubt as to the placement of the new species in *Rehderodendron*. In this regard, a unique combination of morphological characters supported by molecular phylogenetic data has demonstrated the paraphyly of *Halesia*, with *H. macgregorii* placed as sister to *Rehderodendron* (Fritsch et al. 2001; Yan et al. 2018), and on this basis the new genus *Perkinsiodendron* was designated by Fritsch et al. (2016). Nonetheless, in the case of the new species, the fruit characters are diagnostic and our molecular phylogenetic data place it as nested within the *Rehderodendron* clade.

The molecular phylogenetic results strongly support monophyly for *Rehderodendron truongsongense*, thus corroborating the evidence for new species status based on morphology. These results also yielded a sister-species relationship of the new species with *R. gongshanense*. This relationship may be supported by shared golden brown trichomes on vegetative buds and a pubescent style. However, sampling for these and other characters is incomplete owing to the lack of knowledge of the flowers of several species, and increased species- and population-level sampling will be needed for a more complete understanding of species relationships and character evolution within the genus.

Rehderodendron truongsongense is the only species of *Rehderodendron* endemic to Vietnam. Two other species of *Rehderodendron* are documented from Vietnam in Pham (1991) and Svengsuksa and Vidal (1992), i.e., *R. indochinense* and *R. kweichowense*. In addition to the characters mentioned above, the new species is distinguishable from *R. indochinense* by its dark olive brown fruit without pale brown spots (versus reddish brown with prominent pale brown spots). From *R. kweichowense* it is easily distinguishable by nearly glabrous leaves abaxially (versus densely tomentose) and glabrous mature fruit (versus densely tomentose). Because the new species would key best to *R. indochinense* in the key of Hwang and Grimes (1996), we tabulate the taxonomically relevant character states separating *R. truongsongense* from *R. indochinense*, and also from *R. macrocarpum*, with which the new species has been confused (Table 2). The segregation of *R. truongsongense* from *R. macrocarpum* results in a geographic range of the latter that is now restricted to southwestern China and probably also far northwestern Vietnam (see below). In China, *R. macrocarpum* occurs in Guangxi, Sichuan, and Yunnan provinces (Hwang & Grimes 1996).

Although the reason why Svengsuksa and Vidal (1992) did not recognize the collections of *Rehderodendron* from central Vietnam as representing an undescribed species is unclear, it is possibly because open flowers were unavailable for examination at the time. Their description of *R. macrocarpum* is more consistent with the features of *R. macrocarpum* sensu stricto rather than those of the new species. For example, the number of secondary leaf veins (seven to 13 on each side of the midvein) corresponds with that in *R. macrocarpum* described by Hwang and Grimes (1996) in the *Flora of China* rather than the four to seven that we have

TABLE 2. Morphological comparison of *Rehderodendron truongsongense*, *R. indochinense*, and *R. macrocarpum*.

Character	<i>R. truongsongense</i>	<i>R. indochinense</i>	<i>R. macrocarpum</i>
Habit	Evergreen	Deciduous	Deciduous
Number of secondary leaf veins on each side of midvein	4 to 7	6 to 9	7 to 13
Inflorescence length (cm)	1.0–3.5	≤ 5	4–5
Lowermost bracteoles shape and size (mm)	Suborbicular, elliptic, or obovate, 5–9 × 2–4	Linear-lanceolate, minute (ca. 5.0 × 1.2)	Linear-lanceolate, minute (ca. 5.0 × 1.2)
Calyx lobes	Broadly deltoid	Narrowly deltoid	Narrowly deltoid
Corolla lobe length (mm)	7–9	12–14	15–18
Stamen filament connation	To above middle	To below middle	To below middle
Stamen filament surface	Glabrous or with a mixture of glossy stellate trichomes with terete arms and dull stellate trichomes with flattened arms	With trichomes all dull stellate with flattened arms	Glabrous or with trichomes all dull stellate with flattened arms
Style base	Pubescent	Pubescent	Glabrous
Ovule number per carpel	8	4	4
Fruit color	Olive brown without pale brown spots	Reddish brown with pale brown spots	Brown or reddish brown without pale brown spots
Fruit rib number and definition	10 to 20, indistinct	6 to 8, well defined	8 to 10, well defined

observed in *R. truongsongense*. It thus appears likely that Svengsuksa and Vidal used material of *R. macrocarpum* from outside of the study area for their treatment of the species, perhaps from China, because two specimens in the Paris herbarium of *R. macrocarpum* from Sichuan Province are annotated by Svengsuksa as *R. macrocarpum* (T.H. Tu 730, P04514859, online image! and W.P. Lang 2663, P04514860, online image!). Similarly, the entry for *R. macrocarpum* in *An Illustrated Flora of Vietnam* (Pham 1991) apparently includes the new species, because the text states that the species is distributed in “Sapa and Bach Ma.” However, the fruit depicted in that work has well defined ridges, unlike that of *R. truongsongense*, as well as fewer ribs than the new species. Thus, this entry might be based solely on *R. macrocarpum* s.s. collected from Sapa in the Northwest Region of Vietnam (see below), with *R. truongsongense* either not represented or confused with *R. macrocarpum* s.s.

There appears to be some uncertainty as to the occurrence and number of *Rehderodendron* species in the Northwest and Northeast regions of Vietnam. We have not seen specimens of *R. macrocarpum* from Vietnam, and therefore it may be that all prior documentation of Vietnamese *Rehderodendron* has been based on specimens that are now identified as *R. truongsongense*. However, *R. macrocarpum* has been reported from the Northwest Region of Vietnam near the Chinese border (Atlanta Botanic Garden 2016; the area of the pass on Fan Xi Pan mountain, northwest of Sapa), and the photograph of an individual of *Rehderodendron* accompanying the report clearly possesses leaf blades with more than seven veins on each side of the midvein, sharply serrulate leaf blade margins, and an elongate inflorescence without large bracteoles, all consistent with *R. macrocarpum* and generally unlike *R. truongsongense*. It thus appears that *R. macrocarpum* does occur in Vietnam but well to the north of *R. truongsongense*. Furthermore, several U.K.-based expeditions conducted subsequent to Svengsuksa and Vidal’s (1992) treatment have returned with accessions identified as *R. indochinense*, *R. kwangtungense*, *R. kweichowense*, and *R. macrocarpum* [live-plant images on Crug Farm Plants, North Wales, U.K. web site (<https://www.mailorder.crug-farm.co.uk>)]. These collections require careful reassessment in the light of our new findings.

Several species of *Rehderodendron* are yet poorly documented both taxonomically and phylogenetically. Future work on the genus should include documenting the floral characters of the Yunnan endemics described in *Flora Yunnanica*, assessing the morphological and geographical limits of these species and those that extend into northern Vietnam and Myanmar, and tracing the evolution of characters with phylogenetic data. We thus advocate a detailed phylogenetic analysis and taxonomic revision of *Rehderodendron*.

APPENDIX 1

Primers used in this study, in the format: name of chloroplast gene region. Primer name (5' to 3') //primers (F, forward; R, reverse).

clpP-psbB. clpP_P2//F-GCAGATGAAGTGAAGAGA and R-CAAGAGGTTGATAGCGAGAT, clpP_P3//F-TGACGCTGAAGTGGACTC and R-GGTTGGCTTGATTGGACTAA, clpP_P4//F-CTCGCTATCAACCTCTTGG and R-CATCATAGAAGGACCTATTTCG, clpP_P5//F-GTCCATCAAGCCAACCA and R-CACAACAGTATGAACACGAT

ndhD-psaC-ndhE-ndhG. ndhD_psaC_ndhE_P1//F-GTCCATCTACTCTAATCTCC and R-CTCTCTAAGTCAATCCAGAA, ndhD_psaC_ndhE_P2//F-AGGCGGATTCACATCTCT and R-GCTATTGACTGGCTATTGT, ndhD_psaC_ndhE_P3//F-CAGACGAATCAATGAGTTACC and R-GACTGTTGGAGATGAATTAC

rpl22-rps19. rpl22_P1//F-GCCAGAGGATATTCTCATATTC and R-TCTTCGTCGCCGTAGTAA

rps18-rpl20. rps18_rpl20_P1//F-GACACAATACGCTAATCG and R-AGGTGCTCATTCAAGACTTA, rps18_rpl20_P2//F-GTTGACCACTAGAACTACTG and R-GCAAGAACGGACTAACAGS

psbI-trnS-GCU intergenic spacers. trnS_psb1//F-TCTTGAGATTGTGTAATGC and R-TATCTGTGATTCGTTGGAAC

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