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The status of the mistletoe genus *Dufrenoya* Chatin (Amphorogynaceae) with a specific focus on Nepal

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ABSTRACT

The genus *Dufrenoya* Chatin (Amphorogynaceae) is a rarely collected and studied aerial parasite found of southeastern Asia. Our goal is to provide a modern treatment of the genus for Nepal where two species occur: *D. platyphylla* (the type of the genus), and *D. granulata*. Fresh, fixed, and dried material of the former species and herbarium material of the latter was examined and used to prepare morphological descriptions. In addition, the ITS rDNA region was sequenced and phylogenetic analyses conducted on five genera of Amphorogynaceae. Strong support for the sister relationship between *Dufrenoya* and *Phacellaria* was obtained. The complex nomenclatural history of *Dufrenoya* is reviewed and discussed in the context of intergeneric relationships in the family. The morphology and anatomy of flowers and fruits are photographically illustrated and discussed. Collections of both species plotted on a map of Nepal showing ecological zones and physiographic regions indicates *Dufrenoya* is primarily distributed in the Middle Mountains region.

1. Introduction

The most familiar mistletoe to Europeans is *Viscum album* (Zuber, 2004), but the mistletoe habit has actually evolved independently in five Santalales families: Misodendraceae, Loranthaceae, Santalaceae, Viscaceae, and Amphorogynaceae (Nickrent et al., 2010). The latter three families are all considered Santalaceae s. lat. by APG III (2009); however, here they will here be considered as distinct following Nickrent et al. (2010). Amphorogynaceae is sister to the economically important mistletoe family Viscaceae and is remarkable in that it contains plants with a wide range of trophic modes and habits. For example, the genera *Choretrum* and *Leptomeria* are root hemiparasites whereas some *Dufrenoya* and all *Phacellaria* are best referred to as mistletoes. Furthermore, *Dendromyza* is a stem parasitic liana (dendroparasite, Vidal-Russell and Nickrent (2008) see Fig. 4D) that attaches first to the host with a primary haustorium and then forms two kinds of shoots: leafy non-twining as well as squamate, twining, haustorial stems. Some *Dendrotrophe* species can be terrestrial shrubs or woody climbers that parasitize the roots of host plants whereas others are dendroparasitic climbers. But unlike *Dendromyza*, *Dendrotrophe* does not form stems with secondary haustoria. Species such as *Dendrotrophe buxifolia* and *D. varians* that can exist as either stem or root parasites are called amphiphagous (Der and Nickrent, 2008). The amphiphagous condition has also been reported for *Daenikera* (Stauffer, 1969) where the host is *Amphorogyne*, both endemic to New Caledonia. Because these are sister genera, this may represent a case of adelphoparasitism (parasite evolved from its host), rarely documented in flowering plant parasites.

The stem morphologies seen across all 11 species of *Dufrenoya* are actually quite varied such that some are mistletoes of the "*Viscum album*" type according to Stauffer (1969). In *Dufrenoya* the stems may be erect or pendulous and in species such as *D. papillosa*, *D. poilanei*, and *D. sessilis*, at least some twining stems can be seen. But unlike *Dendromyza*, these twining stems do not form secondary haustoria. This is contrary to the description in Kuijt (2015) as well as Danser (1940) who said (p. 142): "*Hylomyza* [*Dufrenoya*, see below] agrees, in its mode of growing, with the non-climbing *Cladomyza* species and also with *Phacellaria*."

The genus *Dufrenoya* was first proposed by Chatin (1860), but in fact the plant upon which this name is based had been discovered and described 35 years earlier. Plants now assigned to *Dufrenoya platyphylla* have previously been included in five

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different genera, and the complex and turbulent nomenclatural history is briefly summarized here. Francis Buchanan-Hamilton first collected *Dufrenoya* in 1802 in Nepal under the name *Viscum latifolium* Buch.-Ham ex Don (1825). This mistletoe was named *V. platyphyllum* by Sprengel in 1827 and *V. heteranthum* Wallich ex A.P. De Candolle in 1830. The Wallich collection (no. 488) from the Kathmandu district is the type for the species and genus. Not accepting placement in the genus *Viscum*, Joseph D. Hooker named this mistletoe *Henslowia heterantha* Hook. f. ex A.P. De Candolle (1857), within a genus of Santalaceae named in 1951 by Blume. Based on the Wallich specimen, Gaspard A. Chatin erected the genus *Dufrenoya* in 1860 (commemorating his former teacher Pierre-A. Dufrénoy), making the new combination *Dufrenoya heterantha* Chatin. Based on nomenclatural rules and differences in fruit structure, Benedictus Danser (1940) replaced *Henslowia* with *Dendrotrophe* and created three new genera to accommodate the remaining species: *Cladomyza*, *Dendromyza*, and *Hylomyza*. Citing all the previous names as synonyms, Danser named *Hylomyza platyphylla* (Sprengel) Danser based on *Viscum platyphyllum*. The combination *Dendrotrophe heterantha* Henry and Roy (1969) apparently went unnoticed by those who prepared the posthumous manuscript by Stauffer (1969). Here the genera segregated from *Hylomyza* by Danser were retained, but *Dufrenoya* was reinstated, thus making *Hylomyza* a synonym. The earliest name, *Dufrenoya latifolia*, could not be used because *V. latifolium* Buch.-Ham. was a later homonym for an illegitimate name (*V. latifolium* Swartz) and a synonym of *Phoradendron piperoides* (*V. latifolium* Lam.). The name *D. heterantha* Chatin could not be used because it is based on *V. heteranthum* Wall. which is a nomen nudum. Thus the correct new combination published was *Dendrotrophe platyphylla* (Sprengel) Stauffer. Finally, the most recent (unfortunate) nomenclatural activity on this taxon was the publication in the Flora of China of *D. platyphylla* (Sprengel) N.H. Xia et M.G. Gilbert.

Nepal is a global biodiversity hotspot that contains over 7000 species of vascular plants and efforts to document its flora are ongoing (Bista et al., 2001; Hara et al., 1978, 1982; Hara and Williams, 1979; Press et al., 2000). At present, Santalales have yet to be treated. In general, *Dufrenoya* is poorly studied and relatively few collections of this genus exist within and outside of Nepal. Moreover, prior to the photos taken for this project, no photographs of living *Dufrenoya* plants were available. The purpose of this paper is to assemble available information and report new observations on two species of *Dufrenoya* from Nepal, *D. platyphylla* and *D. granulata*, with the goal of clarifying their taxonomic status.

2. Materials and methods

2.1. Molecular work

Genomic DNA was obtained from herbarium specimens using a 2X CTAB protocol (Doyle and Doyle, 1987) followed by a clean-up step using spin columns (Concert Rapid PCR Purification System, Life Technologies). A portion of the 5.8S rDNA and ITS-2 was PCR amplified using the ITS3 forward primer (White et al., 1990) and the AB102 reverse primer (Sun et al., 1994). Amplification utilized a standard PCR protocol with 5 M betaine added (20% of final volume). Thermal cycle parameters were 1 min 97 °C, 2 min 50 °C, and 3 min 72 °C for 40 cycles. Cycle sequencing followed the manufacturer's protocol (PerkinElmer Cetus) and the reactions were run on an ABI 377 automated DNA sequencer at the Royal Botanic Gardens, Kew. The six newly sequenced taxa and their Genbank accession numbers are: *Dendromyza ledermannii* (KP828443), *D. buxifolia* (KP828444), *Dendrotrophe varians* (KP828445), *Dufrenoya robusta* (KP828448), *Dufrenoya sessilis* (KP828447), and *Phacellaria rigidula* (KP828446). In addition to the above species, complete ITS sequences for three ingroup taxa were obtained from NCBI Genbank: *Dendromyza reinwardtiana* (DQ333870), *D. varians* (DQ333871), and *Leptomeria cunninghamii* (GU256865). The outgroups used were *Exocarpos cupressiformis* (HM116973), *E. sparteus* (GU256864) and *Santalum album* (JX856495). A manual alignment (available upon request) was made using SeAl (Rambaut, 2007). Maximum parsimony (branch and bound search) and bootstrap analyses were conducted with PAUP* (Swofford, 2002).

2.2. Field work

The site where *Dufrenoya platyphylla* was observed and collected is located near Kande village in the Western Region of Nepal (Table 1). One of us (MPD) made ten visits between February and September in 2010 as well as January and June 2012. Photographs, herbarium specimens, and alcohol fixed samples were obtained of flowering and fruiting plants. The host was a 12 m tall *Castanopsis indica* tree located at the margin of an agriculture terrace. Multiple mistletoe infections that measured from <50 cm to 1.5 m in diameter were observed on the host tree.

2.3. Herbarium work

Past collections of *Dufrenoya* in Nepal were examined and in some cases photographed by MPD. Two species are currently known from the country: *D. platyphylla* and *D. granulata*. Herbarium material was studied for both species whereas fresh material was available only for the former. The visited herbaria were Royal Botanic Garden Edinburgh (E), Natural History Museum in London (BM) and Royal Botanic Gardens Kew (K) from October to December, 2011, the National Herbarium in Kathmandu (KATH) in 2012 and 2015, and University of Tokyo Herbaria (TI) in September 2013. In addition to physical visits, virtual visits to the following online herbaria were made: B, BM, GH, Kew, P, L, E, and NY. Photos and metadata associated with these collections were assembled.

2.4. Anatomical work

Alcohol fixed material was used for dissection and photography using a stereomicroscope. Flowers and fruits were also prepared using standard paraffin embedding techniques, sectioned with a rotary microtome, and stained with saffranin and fast green. The slide were observed and photographed using an Olympus CH30 compound microscope fitted with an Olympus DP-20 digital camera.

2.5. Distribution mapping

Attempts to obtain coordinates for all *Dufrenoya* collections made in Nepal was made difficult because some herbarium specimen labels did not provide sufficient information to accurately locate the collection site. Moreover, some labels only indicated the overall excursion track taken by the botanical team. The Flora of Nepal website (http://padme.rbge.org.uk/floraofnepal/) was utilized to check place names, locations, and collectors. Latitude/longitude positions were in some cases inferred from the place name and elevation. Following this procedure, 12 discrete records of *D. platyphylla* and 8 records of *D. granulata* (Table 1) were plotted using Google My Maps. A map showing ecological zones and physiographic features for Nepal (Lillesø et al., 2005) was used as a layer in Adobe Photoshop and the dots from the Google map overlayed upon it.

Table 1
Collection information for the *Dufrenoya* species from Nepal examined in this study

Dufrenoya species	Collector	Number	Date	Region	Zone	District	Locality	Lat/long	Elevation
D. platyphylla	Wallich N.	488	1830	Central	Bagmati	Kathmandu	Pararil–Tokha Chandeswori	27 47 17.01N, 85 20 29.73E	1770 m
D. platyphylla	Malla S.B. & Rajbhandari S.B.	381	11 October 1960	Central	Janakpur	Dolakha	On way–Kalinchowk	27 42 01.14N, 86 01 06.25E	2500 m
D. platyphylla	Ohba et al.	8340419	27 August 1983	Central	Janakpur	Dolakha	Tamba Koshi–Malekhu–Kosikhet–Pikhuti	27 46 43.40N, 86 11 40.21E	900–1000 m
D. platyphylla	Manandhar N.P. & Adhikari M.K.	2040	3 June 1979	Central	Janakpur	Ramechap	Dhungre Bhanjayng, Sindhuli	27 16 03.01N, 85 56 59.02E	1275 m
D. platyphylla	Buchanan	s.n.	1802	Central	Narayani	Makwanpur	Bhimphedi	27 33 05.13N, 85 07 35.16E	1338 m
D. platyphylla	Stainton J.D.A.	5298	20 March 1966	Central	Narayani	Makwanpur	Trisuwan Rajpath, Daman	27 36 29.34N, 85 05 39.65E	2307 m
D. platyphylla	Long D.G. et al.	93	20 September 1991	Eastern	Koshi	Sankhuwasabha	Bhotebas to Chichila	27 27 06.07N, 87 13 19.81E	2100 m
D. platyphylla	Suzuki M. et al.	9263043	14 May 1992	Eastern	Mechi	Taplejung	Papung–Dongen–Mewa Khola bridge–Sawadin	27 28 22.21N, 87 37 55.04E	2000 m
D. platyphylla	Williams L.H.J.	982	27 June 1969	Eastern	Mechi	Taplejung	Yamphudin–Helok	27 24 00.00N, 87 54 00.00E	1676 m
D. platyphylla	Sayers C.D.	2387	10 April 1975	Western	Gandaki	Kaski	Between Landruk [Ghandruk] and Dhampus, NW of Pokhara	28 19 56.48N, 83 48 34.67E	1707 m
D. platyphylla	Devkota M.	475	30 June 2001	Western	Gandaki	Kaski	Kande village near Lumle	28 17 43.96N, 83 49 21.00E	1708 m
D. platyphylla	Stainton Sykes & Williams	5927	25 June 1954	Western	Gandaki	Lamjung	Pasgam	28 16 56.51N, 84 14 11.53E	1970 m
D. granulata	Ohba et al.	8530777	5 August 1985	Central	Janakpur	Ramechap	Patkare–Bhandar	27 34 06.55N, 86 21 14.76E	2080 m
D. granulata	Suzuki M. et al.	8840091	8 July 1988	Eastern	Koshi	Sankhuwasabha	Bhotebas–Gogane–Chichila	27 26 50.82N, 87 12 2.93E	1920 m
D. granulata	Beer L.W.	25710	5 November 1975	Eastern	Mechi	Ilam	Dongen	27 32 37.28N, 87 36 51.89E	2121 m
D. granulata	Hara H., Kanai H., Kurosawa S.	6301228	27 November 1963	Eastern	Mechi	Panchthar	Birwa (near Chyangthapu)	27 15 01.22N, 87 56 07.97E	2000 m
D. granulata	Hara H., Kanai H., Kurosawa S.	6301227	28 November 1963	Eastern	Mechi	Panchthar	Ghatte–Khebang	27 24 47.70N, 87 53 21.75E	2000 m
D. granulata	Kanai H. et al.	6301226	9 November 1963	Eastern	Mechi	Taplejung	Ila Danda–Solap	27 35 11.37N, 87 47 40.15E	2300 m
D. granulata	Suzuki M. et al.	9263134	23 May 1992	Eastern	Mechi	Taplejung	Thakpa Bazaar–Suketar (Tamur bridge)–Ramsyang Pati	27 32 57.80N, 87 46 04.94E	2300 m
D. granulata	Dawson G.	492	25 December 1975	Western	Gandaki	Kaski	Lumle, above Agricultural Centre	28 18 10.40N, 83 48 52.90E	1920 m

3. Results and discussion

3.1. Molecular phylogenetic results

The molecular phylogenetic investigation of (Der and Nickrent, 2008) sampled all genera of Amphorogynaceae and all intergeneric relationships were fully resolved. *Dufrenoya* is strongly supported was sister to *Phacellaria* using 18S rDNA, *rbcL* and *matK* and that clade was sister to another composed of *Dendromyza* and *Dendrotrophe*. In contrast to these relatively slowly evolving genes, the ITS region (internal transcribed spacers 1 and 2 plus 5.8S rDNA) is rapidly evolving, particularly in mistletoes (Ashworth, 2000; Molvray et al., 1999; Nickrent et al., 2004). Of the total 819 characters in this alignment of Amphorogynaceae, 252 (30%) are parsimony informative. In general, both ITS-1 and ITS-2 are significantly more variable than the 5.8S rDNA region and ITS-1 is more variable than ITS-2. Although, *Phacellaria* clearly shows sequence similarity to *Dufrenoya*, its rate of evolution is higher (more substitutions and insertion/deletion mutations). Such elevated rates are also seen in the dwarf mistletoes (*Arceuthobium*, Viscaceae), which like *Phacellaria* are also squamate indicating a convergent morphological and molecular evolutionary pattern.

Branch and bound analyses found one tree of length 810 (Fig. 1). Amphorogynaceae was strongly supported as monophyletic (99% BS). A *Dendrotrophe*/*Dendromyza* clade (67% BS support) is sister to another clade composed of *Dufrenoya*, and *Phacellaria* (100% BS support). These two clades were sister to *Leptomeria* (from Australia). That *Dufrenoya* and *Phacellaria* are closely related is also reflected in fruit and seed characters (Danser, 1940). Thus, the decision by Xia and Gilbert (2003) to lump *Dufrenoya* into *Dendrotrophe* was ill-advised, especially since they recognized the genus *Phacellaria* as distinct. *Dendrotrophe* and *Dendromyza* were not monophyletic. The Genbank sequence DQ333871 (voucher Calvin and Wilson B02-15) appears most closely related to *D. buxifolia*, thus the specimen could be misidentified. Clearly, more work is needed to determine whether *Dendrotrophe* and *Dendromyza* are distinct genera, a sentiment also expressed by Kuijt (2015) who provisionally lumped the former into the latter.

3.2. The genus Dufrenoya

In the posthumous publication by Stauffer (1969), no generic description was given, only citations of the original paper by Chatin (1860) and Danser (1940) who described the genus as *Hylomyza*. *Dufrenoya* can be distinguished from *Dendrotrophe* by the presence of umbellate vs. racemose male inflorescences. It differs from *Dendromyza* in fruit features such as an endocarp with apical chambers vs. a unilocular endocarp or with chambers at the base. Macklin (2000) provided detailed generic and specific descriptions for the 11 recognized species of *Dufrenoya*. Descriptions of the four species native to Thailand were given in Macklin and Parnell (2002). This information and novel observations were utilized in the following generic description.

3.2.1. Dufrenoya chatin

3.2.1.1 Type species: *Df. platyphylla* (Sprengel) Stauffer

Glabrous, aerially parasitic mistletoes with or without twining stems; stems spreading, erect or pendulous, if twining climbing but not forming secondary haustoria. Stem surface smooth or pustulate, juvenile and older stems distinctly different, bracteate at base. Bark on older growth with longitudinal fissures. Leaves alternate, simple, without stipules, petiolate, elliptic, obovate, or spatulate, coriaceous, venation basal actinodromous, with 3–11 primary veins. The genus is dioecious or in some species possibly gynodioecious. Male inflorescence an umbel of 5–7 flowers at the apex of a bracteate peduncle; peduncles of varying lengths, single or

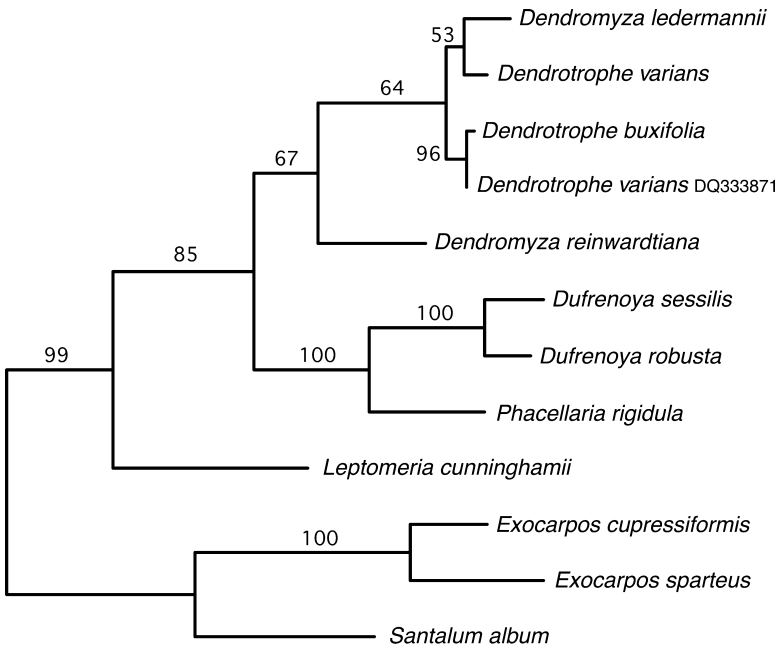

Fig. 1. Single tree (length 810) obtained from branch and bound analysis of ITS sequences from five genera of Amphorogynaceae. Maximum parsimony bootstrap consensus (1000 replications) values shown above nodes. Consistency index minus uninformative sites 0.6964, retention index 0.6531, rescaled consistency index 0.5177.

clustered in groups, arising from 1 to 2 year old stems, sometimes from brachyblasts; peduncles with tightly grouped bracts at the base and apex, apical bracts forming an involucre, also sometimes bearing bracteate lateral flowers. Male flowers in lateral position in axils of bracts, central flower ebracteate; calyx lobes absent, corolla lobes (petals) valvate, cuculate at apex, glandular hairs sometimes present on interior surface; stamens equal in number to petals, antipetalous, anthers dithecal, each theca with two locules (biocular, hence tetrasporangiate), locules isomerous or unequal with the posterior larger than the anterior, dehiscence transverse or longitudinal; nectary flat to concave, fleshy, smooth and scarcely 5-lobed; style rudiment variously developed. Female inflorescence pedunculate, 1-flowered. Female flower with 5 deltoid, valvate petals, staminodes present or not, disk flat, 5-lobed, ovary inferior, style short, cylindrical, style with 5 papilliform spreading stigmas, placenta convex, 5–6-lobed, placental column long, not twisted. Fruit an ellipsoid, ovoid or obovoid drupe borne singly at apex of peduncle; petals persistent at apex, erect or not; exocarp thin, mesocarp consisting of short or long membranous strands that wrap around the endocarp or do not; endocarp forming a 1-seeded pyrene, hard or not, if the latter then splitting easily, externally longitudinally grooved, internally 5–7 chambered at apex and base, incompletely so in central part; seed with same number of lobes as endocarp chambers.

Dufrenoya contains ca. 11 species distributed in northern India, Nepal, Bhutan, southern China, Myanmar, Thailand, Laos, Vietnam, Indonesia (Java, Sumatra) and Malaysia (peninsular and western Borneo).

3.3. *Dufrenoya* species in Nepal

Neither Danser (1940) nor Stauffer (1969) provided descriptions for the two species of *Dufrenoya* that occur in Nepal, only citing the original protologues. The first of the two species is *D. platyphylla* (Sprengel) Stauffer which also occurs in India, Bhutan, Myanmar, and Thailand (the latter a new record reported in Macklin, 2000). The second species, *D. granulata* (Hook. f.) Stauffer, is also found in India, Bhutan, and southern China. These mistletoes occur in submontane and montane regions, particularly in evergreen oak and oak-pine forests between 1500 and 2500 m elevation. The most frequent hosts are in Fagaceae (*Quercus*, *Castanopsis*, and *Lithocarpus*) and less frequently on other genera (e.g., *Rhododendron*, *Schima*, and *Symplocos*).

3.3.1. *Dufrenoya platyphylla (Sprengel) Stauffer*

Type: Wallich 488 (Holotype of *Viscum heteranthum* K!; Isotypes E!, L!, P!, TCD!) Nepal.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 70 (1969); Grierson et Long, Flora of Bhutan 1.1: 143 (1983); *V. platyphyllum* Sprengel, Linnaeus Systema Vegetabilium XIV (1824), Curae Posteriores: 47 (1827); DC Prodromus 4: 279 (1830); *V. latifolium* Buchanan-Hamilton ex D. Don, Prodromus Flora Nepalensis: 142 (1825); *V. heteranthum* Wall ex DC, Prodromus 4: 279 (1830); *H. heterantha* Hook. f. ex A.DC, Prodromus 14: 632 (1857); Kanjilal, Flora of Assam 4: 130 (1940); *D. heterantha* Chatin, Comptes rendus Acadamie Paris 51: 657 (1860); *H. platyphylla* Danser, Nova Guinea New Series 4: 145 (1940); *D. heterantha* Henry et Roy, Bulletin of the Botanical Survey of India 10: 274 (1969) syn. nov. *D. platyphylla* (Sprengel) N.H. Xia et M.G. Gilbert, comb. nov. Flora of China 5: 216 (2003).

A large shrub (mistletoe), up to 2 m in diameter; stems erect or pendulous, not twining, branched, often 3–4 from a single node, spreading on the trunks and branches of the host tree and attaching by means of a large network of epicortical roots. Juvenile stems terete, pustulate (verruculose), flattened towards the apex, slightly keeled, bracteate at the base at junction with older stem; older stems distinctly different, pale in color, with longitudinal fissures. Leaves coriaceous, (30–) 51(–97) × (15–) 31(–74) mm, elliptic, ovate, obovate, apex obtuse to sub-acute, base obtuse, attenuate or cuneate, margin entire, upper surface shiney, smooth, lower surfaces dull, primary veins 5–7, raised on the upper surface, secondary veins fine, arising at approximately right angles, opposite secondaries, percurrent; young leaves shiny dark brown; petiole angular, 8.0–10.0 × 1.5 mm. Male inflorescences in leaf axils and along internodes; peduncles up to 8 in a cluster, on juvenile stems and on short shoots arising from the older stems, terete, 2.0–6.0 × 0.5–0.7 mm, with a series of small bracts at the base, larger ones (ca. 1.0 mm) spiralling

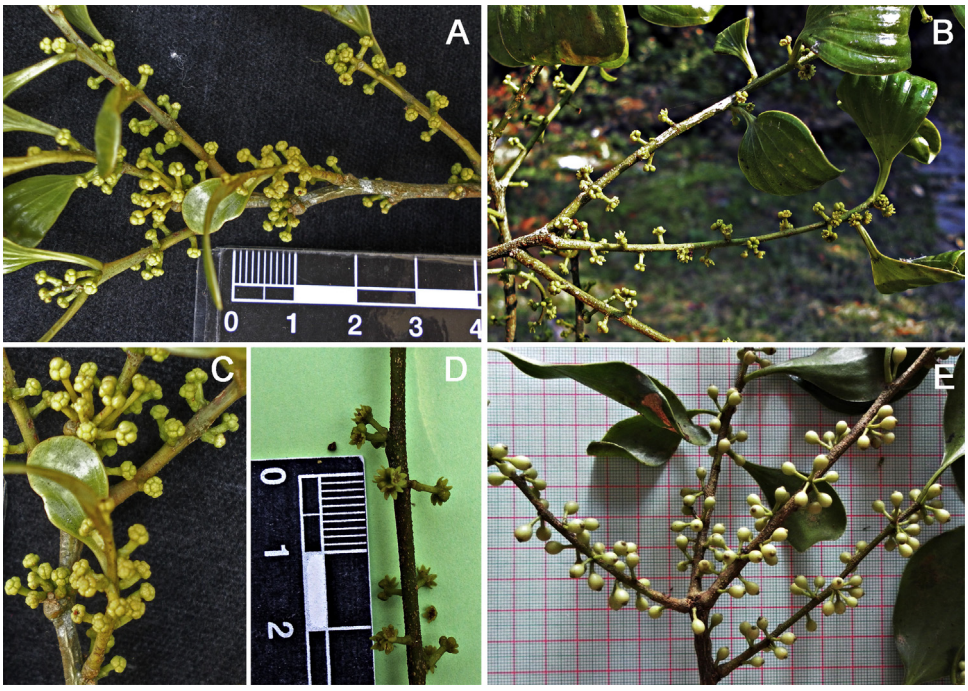

Fig. 2. Flowering and fruiting shoots of *Dufrenoya platyphylla*, all from Kande village, Kaski district, Ganddaki zone, Nepal (Devkota s.n.). A — shoot with unopened flower buds (January 2012); B — shoots with male flowers in full anthesis (April 2012); C — closer view of A showing the cluster of male flowers at the peduncular apex; D — shoot with male flower in full anthesis (April 2012); E — fruiting shoot.

upward to ca. half way up the peduncle, at its apex bearing a single involucre composed of ca. 6 quincuncially arranged, broadly ovate, ciliolate bracts, 0.8–1.0 × 0.8–0.9 mm, each bract bearing a flower at its base, apex terminated by a central flower. Male flowers greenish, subsessile, with receptacle gradually attenuate, becoming extremely narrow at base, lateral flower arising from pockets at the base of their subtending bracts; central flower ebracteate, globose, radially symmetrical, lateral flowers asymmetrical (by compression), turbinate; petals 5–6, deltoid, 1.4–1.5 × 1.0 mm, interior surface densely lined with hairs; filaments short, 0.2–0.3 × 0.1–0.2 mm, slightly dilated at the base, anthers basifixed, 0.2–0.3 × 0.4–0.5 mm, dithecal, lobes unequal in size, anterior shorter and broader than the posterior, dehiscence transverse; post-staminal hairs emanating from glandular cells on petal at base of filament, connecting (postgenitally) to anther; nectary disk 5–6 lobed, flat, apiculate in the center (a pistillode?). Female inflorescences sessile or shortly pedunculate. Female flowers green, buds distinctly turbinate, petals 5–6, elongate-ovate, apex acuminate, 1.0 × 0.6 mm, receptacle broad, 1.4 × 1.0 mm, staminodes present or absent, filaments 0.2 × 0.2 mm, anthers 0.3 × 0.4 mm, style short, broad, 0.3 × 0.3 mm, stigma 3–5 lobed, lobes fleshy, weakly papilliform. Fruit 3.8–5.0 × 3.0–4.0 mm, globose or slightly obovoid, persistent petals forming an apical mound, changing from green to pale yellow, to pink or purple upon ripening, exocarp smooth, thin, mesocarp composed of short, membranous, randomly oriented strands, endocarp hard, not splitting easily, globose or slightly obovoid, 2.1–2.5 × 1.6–1.8 mm, beaked at apex, apiculate at the base, distinctly 4–6 lobed, lobes rounded at the apex, internally 4–6 chambered at the apex and the base, incompletely so in the middle, bearing a crown of fibrovascular fibers at the apex.

3.3.2. *Dufrenoya granulata (Hook. f. et Thompson) Stauffer*

Type: Hook. f. (Holotype of *Henslowia granulata* K!; Isotypes E!, K!, L!, NY!, TCD!; P!) India (Sikkim, Khasia).

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 70 (1969); Grierson et Long, Flora of Bhutan 1.1: 142 (1983); *H. granulata* Hook. f. ex A.DC., Prodromus 14: 632 (1857); Hook. f., Flora of British India 5: 232 (1886); Kanjilal, Flora of Assam 4: 129 (1940); [*H. granulata* sensu Collett et Hemsley, Journal of the Linnean Society 28: 121 (1890)]; *Hylomyza granulata* Danser, Nova Guinea New Series 4: 145 (1940); *Dendrotrophe granulata* Tam, Flora Reipublicae Popularis Sinicae: 71 (1988) syn. nov.

Erect and pendant shrub (mistletoe), stems not twining. Juvenile stems angular, flattened, densely pustulate, bracteate at the base at junction with older stem; older branches terete, bark fissured. Leaves coriaceous, (14–) 27(–36) × (14–) 18(–20.0) mm, elongate-obovate, apex rounded, tip sometimes mucronate, base attenuate, upper surfaces weakly convex, smooth, shining, lower surface rough, dull, margins thin, undulating, completely smooth and flattened, primary veins 5–9, raised on the upper surface, secondary veins indistinct; petiole long, 2.0–3.5 × 1.5 rom, upper surface flattened, lower surface angular. Male inflorescences on juvenile shoots and those of second years growth, usually 2–3 in a cluster, 6-flowered, very shortly pedunculate, peduncles 0.5–0.6 × 1.0–1.2 mm, and involucre of 2–3 bracts at the base and a single involucre of 5, quincuncially arranged bracts at the apex, bracts large, broadly ovate, 1.0–1.5 × 1.0–2.0 mm, papyraceus, clearly divided into two areas, inner region thick, hard, margin thin and entire or sparsely ciliate. Male flower buds turbinate, green, tinged red, pedicel decurrent with receptacle, 0.8–1.5 × 0.8 mm, petals 5, broadly ovate, 1.0–1.2 × 1.4–1.6 mm, fleshy, apiculate on the inner surface at the apex, glandular hairs present, filaments long, narrow, 0.3 × 0.2 mm, anthers dorsifixed, large, broad, 0.3–0.4 × 0.6 mm, bithecate, lobes isomerous, dehiscence longitudinal, nectary disk flat, distinctly 5-lobed, lobes broad, pointed, style rudiment absent. Female flower unknown (description taken from fruiting specimen), tepals elongate — deltoid, 1.0–1.1 × 0.7–0.8 mm, apiculate on the inner surface at the apex, staminodes absent, stigma occupying the entire center of the flower, sessile, large, entire, weakly papillose, slightly

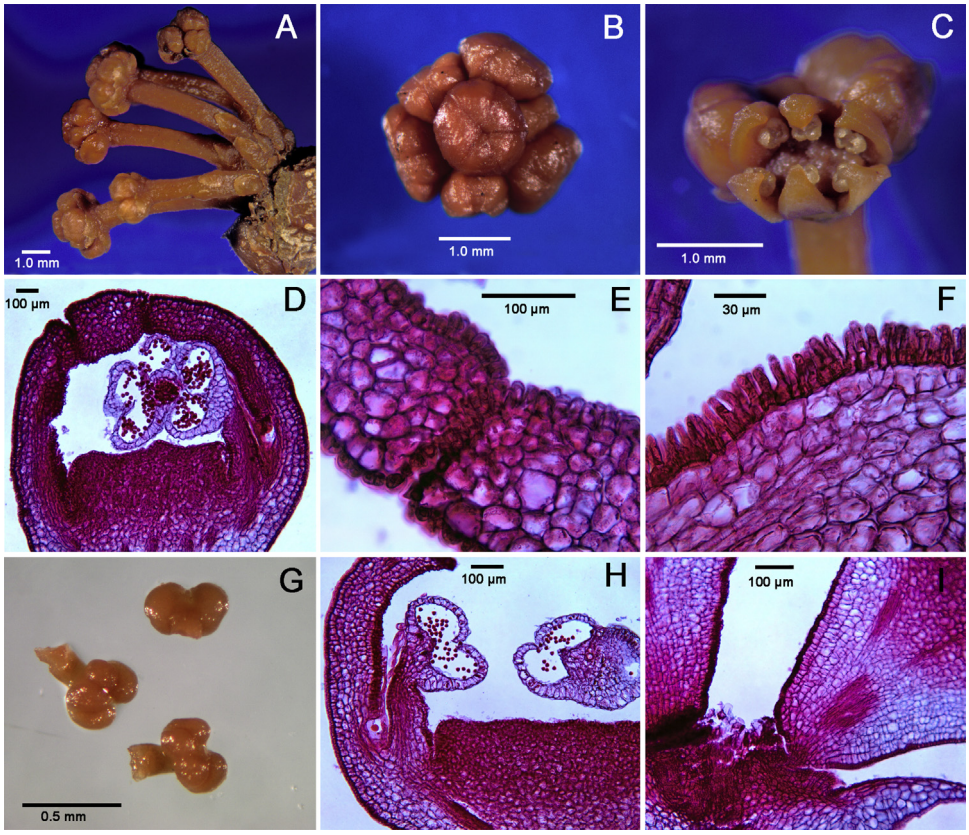

Fig. 3. Morphology and anatomy of male flowers from *Dufrenoya platyphylla*, all from Kande village, Kaski district, Ganddaki zone, Nepal (Devkota s.n.). All from alcohol fixed material. A — inflorescence showing cluster of pedunculate male umbels; B — top view of umbel showing globose central flower surrounded by compressed lateral flowers; C — open male flower showing six petals and dehiscing anthers; D — L.S. male flower bud showing interlocking valvate petal margins, stamen and central disk; E — closer view of valvate aestivation of petal margins, postgenitally coherent by their interlocking petal epidermal cells; F — hairs lining the inner surface of the petals; G — stamens removed from flower showing the dithecal anthers, each with two unequal thecae (posterior larger than the anterior); H — L.S. flower showing the post-staminal hairs, their basal portion of swollen, glandular cells as part of the perianth (cf. *Santalum album*, Fig. 18 in Rao, 1942), and the flat central disk; I — narrow pedicel where it enters the pit at the base of the involucral bract.

depressed in the center, nectary flat or convex, angular. Fruit 4.5–5.0 × 4.5–5.0 mm, globose, persistent petals erect, red to dark purple upon ripening, exocarp smooth, coriaceous, mesocarp composed of short, membranous, randomly oriented strands, endocarp splitting easily, obovoid, 2.7–3.0 × 1.8–2.0 mm, apiculate at the base and the apex, distinctly 5-lobed, internally 5-chambered at the apex and the base, incompletely so in the middle, not bearing a crown of fibrovascular bundles.

The following features can distinguish the two species of *Dufrenoya* found in Nepal. The leaves of *D. platyphylla* are significantly larger than *D. granulata* (average length 51 vs. 27 mm). Both species have variation in leaf shape (elliptic to obovate) but *D. platyphylla* also shows ovate leaves. The number of male inflorescence pedicels and their lengths are different between the two species (longer and more numerous in *D. platyphylla*). Male flowers are subsessile in *D. platyphylla* and pedicellate in *D. granulata*. Anther lobes are unequal with transverse dehiscence in *D. platyphylla* whereas in *D. granulata* they are isomerous with longitudinal dehiscence. The involucral bracts at fruiting time are larger in *D. granulata* and may be slightly accrescent. Finally, the endocarp of *D. platyphylla* has an apical crown of fibrovascular fibers whereas *D. granulata* lacks these. Additional floral and fruit features appear to show differences; however, more work is required to confirm them.

3.4. *Dufrenoya* morphology and anatomy

The arrangement of male flowers while still in bud is shown in fresh condition (Fig. 2A and C) and in fixed material (Fig. 3A and B). The globose central flower is surrounded by laterals that are distinctly flattened dorsally and compressed laterally against each other and the central flower. The term “fungiform” has been used to describe their shape, although here turbinate (top-shaped) was used. As described above, a male flower in *D. platyphylla* arises from a pocket formed at the base of its subtending bract, a feature apparently not previously described. The floral pedicel becomes extremely narrow at this point of entry (Fig. 3I). Because only one fruit is ever observed within one involucre (Fig. 4A), it is possible that these lateral flowers only serve as males and abscise soon after anthesis and pollen dehiscence. The valvate petals are interlocked at their margins by hairs (Fig. 3D and E). Open flowers (Figs. 2B and D, 3C) are minute, thus the aspect of the shoot in full anthesis differs little from when it is in bud stage. Given the flower size, color, presence of a glandular disk, and lack of a discernable smell, small insects are the likely pollinators. Indeed, small flies (at present unidentified) were seen visiting flowers at the Kande Village site by one of us (MPD).

The hairs often seen associated with stamens in Amphorogynaceae and related families are quite recognizable but have received various names. They have been called staminal hairs (Ewart, 1892), glandular hairs (Macklin and Parnell, 2002), and post-staminal hairs (Kuijt, 2015) and apparently exude a viscous, oily fluid. The post-staminal hairs seen in *D. platyphylla* (Fig. 3H) look remarkably similar those from *S. album* illustrated by Rao (1942) his Fig. 18, complete with a swollen basal portion containing a large nucleus. It should be noted that in *D. platyphylla*, the interior surface of the petals is lined with

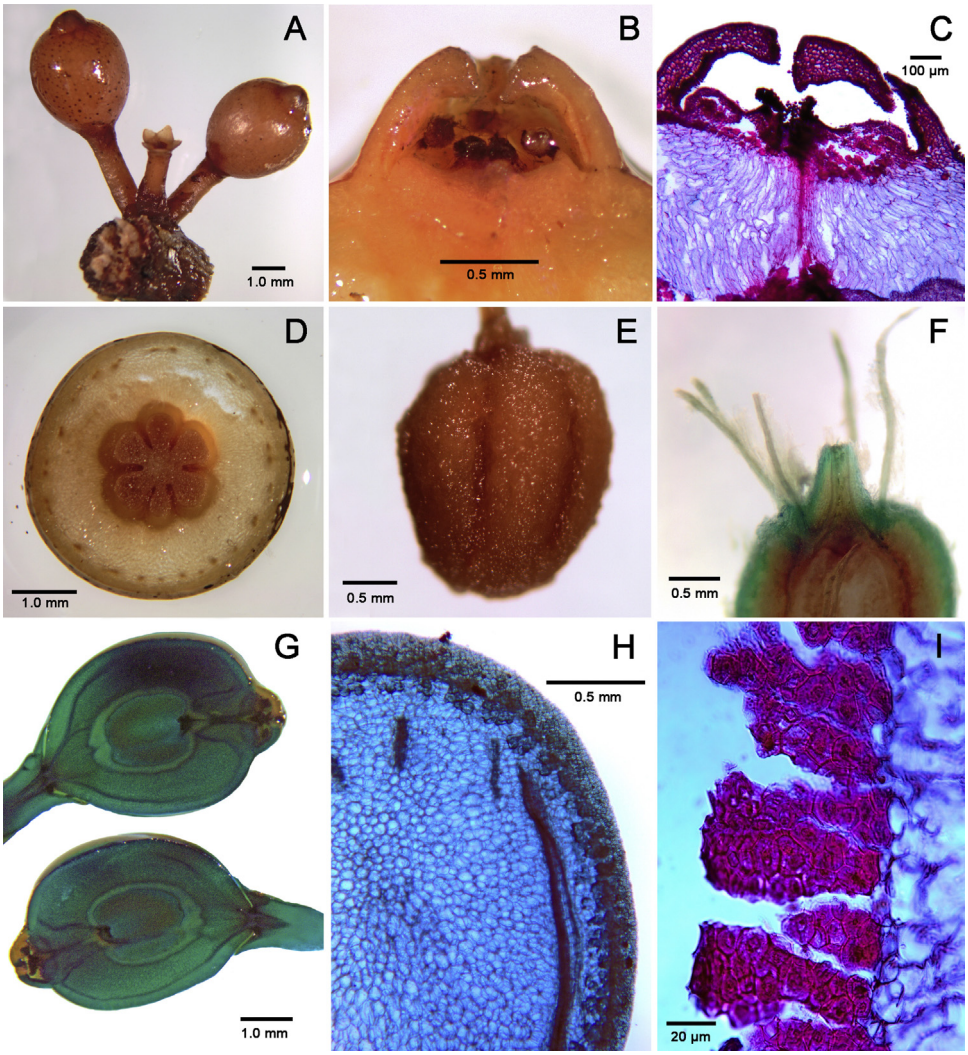

Fig. 4. Morphology and anatomy of fruits from *Dufrenoya platyphylla*, all from Kande village, Kaski district, Ganddaki zone, Nepal (Devkota s.n.). All from alcohol fixed material. A — fruits borne on peduncles, one fallen revealing subtending involucre; B — L.S. of fruit apex showing persistent petals, staminodes, and whithered papilliform stigma; C — L.S. of fruit apex showing glandular disk and the membranous mesocarp; D — fruit X.S. showing thin exocarp, fleshy mesocarp, 6-lobed endocarp enclosing the seed; E — endocarp dissected from fruit showing the longitudinal grooves; F — endocarp dissected from fruit, slightly stained with methylene blue, showing the apical beak and the crown of fibers attached to endocarp; G — fruit L.S. stained with methylene blue showing fiber structure; H — tangential section of fruit, stained with methylene blue, showing clusters of brachysclereids just below exocarp and fibers in the mesocarp below the sclerenchyma clusters; I — endocarp composed of brachysclereids (somewhat disrupted by microtomy).

hairs (glandular?) that are distinct from the post-staminal hairs (Fig. 3F).

The anther morphology in *Dufrenoya* varies between species. For *D. platyphylla* and six other species, the anterior lobes are smaller than the posterior and dehiscence is transverse (Fig. 3G). In three species (*D. oresitropha*, *D. poilanei*, and *D. robusta*), the lobes are equal in size and shape (isomerous) and dehiscence is longitudinal. Anther lobe type and dehiscence roughly correlates with pollen exine morphology where isomerous lobes that dehisce longitudinally have echinate pollen exines whereas unequal lobes with transverse dehiscence have rugulate pollen exines (Macklin, 2000). This correlation does not hold up for *D. granulata* and *D. papillosa* which have the inverse relationship.

Dufrenoya is usually described as being dioecious, but there is evidence that its sexual system is more complex. In Fig. 28 of Danser (1955) the flower of *D. oresitropha* (as *Hylomyza*) is labeled as "hermaphrodite (or pseudo-hermaphrodite)". Moreover, all descriptions of *D. granulata* indicate that female flowers are unknown; however, given that the isotype at K collected by Hooker and Thompson from Sikkim India bears fruits, these flowers could be bisexual. When observing fruits of *D. platyphylla*, some clearly have staminodes (Fig. 4B) whereas others apparently lack them (Fig. 4C), and these two fruit types came from the same individual. So in this case, the structures could be functional stamens or staminodes. If one individual bears fully functional bisexual flowers as well as female flowers and in the same population completely male individuals exist, this condition would be polygamodioecy. If the structures in some of the female flowers are staminodes, the sexual condition is dioecy but with those females being transitional between bisexual and unisexual.

The fruits in *Dufrenoya* and other Amphorogynaceae are the most complex in the sandalwood order, and their functional morphology is still incompletely understood. Substantial interspecific variation exists in fruit characters such as the persistence of the petals at the apex, mesocarp morphology, endocarp shape, lobing and hardness, and the presence of an apical crown of fibers. Unfortunately, neither Danser (1940) nor Stauffer (1969) provided descriptions for the two species discussed here, thus information from Macklin (2000) and Macklin and Parnell (2002) was consulted. Among the 11 *Dufrenoya* species, it appears that only *D.*

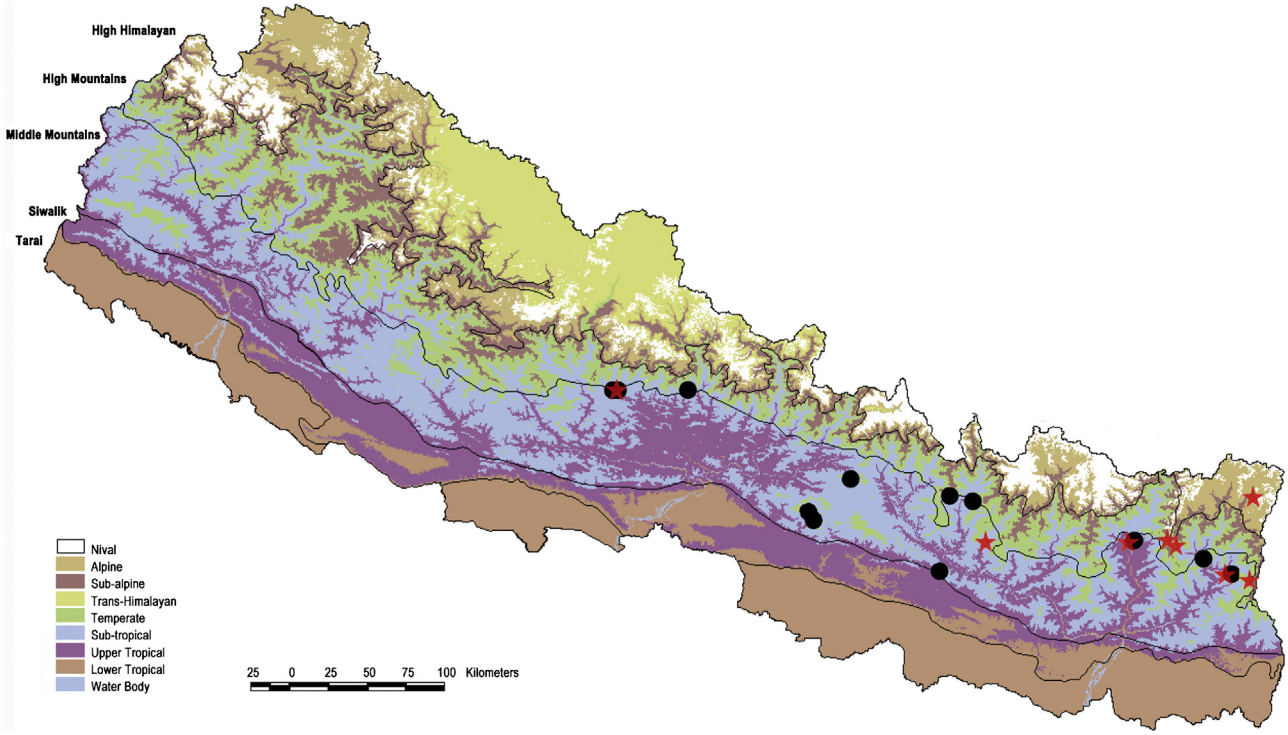

Fig. 5. Distribution of *Dufrenoya platyphylla* (dots) and *D. granulata* (stars) in Nepal. Map from Lillesø et al. (2005), used with permission.

platyphylla has an endocarp crowned by fibrovascular fibers (Fig. 4F), sharing this feature with *Dendromyza* (s. lat., including *Cladomyza*). These fibers ascend to the apical portion of the mesocarp where they then join fibers that descend to the base of the fruit, running just inside the clusters of brachysclereids (Fig. 4G and H). These fibers have been called "apical tails" in the literature, but are here referred to as a "crown". The fruit mesocarp was described as having radially aligned, membranous fibers by Danser (1940), a description repeated by Kuijt (2015). The description in Macklin (2000) and Macklin and Parnell (2002) indicate two forms exist among the *Dufrenoya* species: with long, membranous strands that wrap around the endocarp or with short, membranous strands that are randomly oriented. The latter type supposedly exists in *D. platyphylla* but was not seen in the fruits examined in this study. It is assumed that the fibrovascular fibers and mesocarp strands function as they do in *Dendromyza* where, after ingestion and excretion by the foraging bird, these structures help adhere the seed to the host tree branch.

3.5. Generic circumscriptions

Given the above results, it is necessary now to critique some recent taxonomic works, specifically their generic circumscriptions. In the treatment of Santalaceae for Flora of China (Xia and Gilbert, 2003), *Dufrenoya* was included within *Dendrotrophe*. The rationale for this decision was not explained; however, this action resulted in a combined generic description that did not adequately encompass *Dufrenoya*. For example, all five species are referred to as "woody vines", but neither of the two included *Dufrenoya* species (*D. platyphylla* and *D. granulata*) twine, thus they are best described as erect or pendulous shrubs (mistletoes). The number of ovules given is three, but no published data about ovule number in *Dufrenoya* could be located. Both Danser (1940) and Stauffer (1969) relied heavily upon features of the fruit and seed to differentiate genera in Amphorogynaceae. The description of the fruit and seed by Xia and Gilbert (2003) appears to be a combination of features from *Dendrotrophe* and *Dufrenoya*, none of which would appear together in any one species. From the molecular phylogenetic work and morphological data reported here, it is clear that *Dufrenoya* is distinct from *Dendrotrophe*. Separate generic status is also supported by morphological characters differences. For example, *Dendrotrophe* has a fleshy mesocarp and a tuberculate endocarp with chambers at the apex and the base as well as transverse chambers. The mesocarp in *Dufrenoya* consists of membraneous strands and its endocarp is smooth with chambers but no transverse chambers.

3.6. Distribution of Dufrenoya in Nepal

Nepal has traditionally been divided into three physiographic regions (Tarai, Hills and Mountain), but more recently this has been further divided into Terai (13.7% of Nepal, <500 m), Siwaliks (12.8%, 300–1500 m), middle-Mountains (from 29.2%, to 300–3000 m), high Mountains (from 20.3%, to 1000–5500 m) and the high Himalayas (23.9%, 2000–8500 m). Furthermore, ecological zones comparable to Holdridge life zones can be designated: lower tropical, upper tropical, sub-tropical, temperate, subalpine, and trans-Himalayan (Lillesø et al., 2005). Nearly all of the administrative districts of Nepal have a wide range of ecological zones, e.g., Kaski with upper tropical to trans-Himalayan.

The printed version of the Flora of Nepal (Hara et al., 1982) lists both *D. platyphylla* and *D. granulata* as does the online version of the Annotated Checklist of the Flowering Plants of Nepal (Press et al., 2000). From our herbarium investigations, 12 discrete localities were recorded for *D. platyphylla* and 8 localities for *D. granulata* (Table 1, Fig. 5). The distribution of *Dufrenoya* in Nepal is strongly associated with physiographic region. With the exception of three *D. granulata* collections, all were located in the middle Mountain region or near its border with the high Mountains region. The Beer (5 November 1975) and Suzuki (23 May 1992) collections were mapped to the high Mountains region; however, in neither case was label information precise plus the locations are very near

the border with the middle Mountains region. The Kanai et al. (9 November 1963) collection of *D. granulata* from Ila Danda, Taplejung District was mapped to the high Himalayan region, but in a narrow river valley at 2300 m. All *Dufrenoya* collections examined occur in the eastern half of the country, but this may be simply an artifact of collecting. Suitable habitat in the middle Mountains region is present, thus future field work may locate this mistletoe in the mid-Western and far-Western regions. In at least three districts (Kaski, Sankhuwasabha and Taplejung), collections of both *D. platyphylla* and *D. granulata* have been made within close proximity, thus it can be deduced that these species are sympatric over a portion of their respective ranges.

3.7. Protection status

Relatively few *Dufrenoya* collections have been made in Nepal and most herbarium specimens are old: the mean year for all collections examined for *D. platyphylla* is 1950, for *D. granulataem* > 1975. Most examined collections fall outside of protected areas. The type location for *D. platyphylla* (Wallich 488) may have been collected within what is currently designated the Shivapuri Nagarjun National Park. In Kaski District, one collection of *D. granulata* (Dawson 492) and two collections of *D. platyphylla* were made just south of the border of the Annapurna National Park, thus it is possible these taxa occur within the park confines. It appears that the Kanai et al. collection of *D. granulata* from Taplejung district occurs within the Kanchenjungha conservation area. The middle Mountain region is undergoing rapid change with the conversion of natural ecosytems into human-dominated landscapes through forestry, farming, and settlement expansion. As an aerial parasite, *Dufrenoya* is dependent upon intact populations of compatible host trees, thus it is very susceptible to deforestation. Protection of suitable habitats for biodiversity conservation in general and *Dufrenoya* in particular must include the East Himalayan Oak-Laurel forests in temperate zones and the Schima-Castanopsis forest in sub-tropical zones. Because many regions of Nepal have not received floristic inventories, it is difficult to estimate the number and size of *Dufrenoya* populations within the country. But because of modifications of the middle Mountain region landscapes, fragmentation of mistletoe populations is likely. Thus, we estimate that both species of *Dufrenoya* should receive the IUCN classification of vulnerable.

4. Conclusions

Two well-defined species of *Dufrenoya*, *D. granulata* and *D. platyphylla*, occur in Nepal, mostly restricted to the middle Mountain region in the eastern half of the country. The genus is important because it is on a clade representing one of the five cases of independent evolution of the mistletoe habit. The nomenclatural history of *Dufrenoya* is complex, complicated by varying generic concepts and incomplete taxonomic descriptions. Previous molecular work and the ITS phylogeny reported here clearly show that *Dufrenoya* is distinct from *Dendrotrophe* and *Dendromyza* and is most closely related to another mistletoe, *Phacellaria*. Although, the genus is generally reported to be dioecious, evidence exists that more complex sexual systems may be in place. Further study is required to determine the sexual systems and floral visitors/pollinators occurring in populations of the 11 species in the genus. The apical crown of fibrovascular fibers is known only from *D. platyphylla*, a feature shared with *Dendromyza*. The functional role such morphological and anatomical structures play requires elucidation, as well as field studies to document details of seed dispersal. We estimate that both species of *Dufrenoya* in Nepal should receive the IUCN classification of vulnerable because of human alteration of natural ecosystems where its host trees occur.

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