Illustrated Key to Species of Genus *Dendroctonus* (Coleoptera: Curculionidae) Occurring in Mexico and Central America

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Subject Editor: Ted MacRae

Received 14 November 2016; Editorial decision 23 January 2017

Abstract

We provide an illustrated key of species of *Dendroctonus* Erichson from Mexico and Central America based on characters of the male genitalia and external morphology. The key incorporates newly identified diagnostic characters for this genus that enhance discrimination of particularly difficult sibling species.

Key words: seminal rod, anchor, club shape, sensillae, bark beetle

Species of the genus *Dendroctonus* Erichson, 1836 are among the most important agents affecting the ecology and health of conifer forests in the northern hemisphere. Generally, these species colonize and kill only trees weakened by drought, disease, or damage, thereby favoring the regeneration and succession of forests (Wood 1982). However, environmental and biological factors can promote population outbreaks of certain species which result in extensive mortality of healthy trees (Billings 2011), and these species are considered major natural disturbance agents. *Dendoctonus* spp. colonize trees predominantly in the genus *Pinus* L., but also include species of *Larix* Mill., *Picea* A. Dietr., and *Pseudotsuga* Carriére. Like other bark beetles, these insects feed and complete their life cycle within the phloem tissue and outer bark (and occasionally roots) of their host trees (Six and Bracewell 2015).

The taxonomy of the genus has been reviewed several times, and the status of species has frequently changed because of high intraand interspecific morphological variation of its members (Hopkins 1909; Wood 1963, 1982). Currently, the genus *Dendroctonus* includes 20 taxonomically valid species (Wood 1982, Armendáriz-Toledano et al. 2015), one with two subspecies (Furniss 2001, Ruíz et al. 2009), which are arranged into five to six groups or complexes supported by morphological, behavioral, ecological, chromosomal, and molecular characters (Hopkins 1909; Wood 1963, 1982; Lanier 1981; Lanier et al. 1988; Kelley and Farrell 1998; Zúñiga et al. 2002; Víctor and Zúñiga 2016).

The distribution of this genus is Holarctic, with 18 species distributed from Alaska to Nicaragua in America (Wood 1982, Salinas-Moreno et al. 2004, Armendáriz-Toledano et al. 2015) and two native species inhabiting Europe and Asia (Grégoire 1988); recently, one species, *D. valens*, was accidentally introduced into China (Yan et al. 2005). Thirteen *Dendroctonus* species occur in the region defined by the political boundaries of Mexico and Central America (Wood 1982, Furniss 2001, Armendáriz-Toledano et al. 2015): D. adjunctus Blandford, D. approximatus Dietz, D. brevicomis LeConte, D. frontalis Zimmermann, D. jeffreyi Hopkins, D. mesoamericanus Armendáriz-Toledano and Sullivan, D. mexicanus Hopkins, D. parallelocollis Chapuis, D. ponderosae Hopkins, D. pseudotsugae barragani Furnnis, D. rhizophagus Thomas and Bright, D. valens LeConte and D. vitei Wood.

Despite the abundance of biological and distributional information that has been generated for many of these species, principally those distributed in United States and Canada, their identification in Mexico and Central America has remained problematic, in particular for species belonging to the *D. frontalis* complex (Lanier et al. 1988). This is because they are morphologically very similar and their external morphological characters are highly variable (Wood 1982; Vité et al. 1974, 1975; Lanier et al. 1988; Armendáriz-Toledano et al. 2014a; Víctor and Zúñiga 2016). Compounding this difficulty is the fact that their populations may coexist in space and time on the same trees due to their wide distribution, overlapping elevation range and polyphagy (Zúñiga et al. 1995, 1999; Salinas-Moreno et al. 2004, 2010; Moser et al. 2005; Armendáriz-Toledano et al. 2015).

Since the taxonomic revision of Hopkins (1909) several keys for identification of *Dendroctonus* spp. have been published. These keys were based upon external morphological characters (e.g., Wood 1963, 1982; Bright 1976; Lanier et al. 1988; Cibrián-Tovar et al. 1995; Rykken and Hanson 1999), seminal rod morphology (e.g., Vité et al. 1975, Gutiérrez-Barba 1985, Lanier et al. 1988), or larval morphology (Thomas 1965). Some of these keys identified

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Fig. 1. Dorsal view of *Dendroctonus*. Adult showing the abdominal segments (tergites). Distal edge of seventh tergite (pr, propygidium) has a bifurcated process (bp) in males (left) and in females distal edge of this segment is entire (right).

Dendroctonus species across the entire range of the genus or within the Nearctic (Wood 1963, 1982), while others addressed specific regions or countries (e.g., Vité et al. 1975, Bright 1976, Gutiérrez-Barba 1985, Cibrián-Tovar et al. 1995, Jiménez-Martínez et al. 2008). Although these keys included some Mexican and Central American species, none included all known species of this geographical region or remain current. In addition, earlier keys often included characters that were ambiguous or insufficiently described and illustrated, and this has complicated the identification of these species.

Novel, integrative, and quantitative approaches applied to the study of morphological variation among *Dendroctonus* species have revealed new diagnostic characters (e.g., of the antennae and male genitalia) for their identification (Armendáriz-Toledano et al. 2014a,b, 2015). Therefore, in this study we provide an updated, illustrated key to all species of *Dendroctonus* occurring in Mexico and Central America, based on morphological characters of the male genitalia, antennae, and exoskeleton. Original data on species biology and geographical distribution are also included.

Materials and Methods

Examined material included more than 4,000 specimens of 13 *Dendroctonus* species occurring in Mexico and Central America (Vité et al. 1975, Wood 1982, Furniss 2001, Salinas-Moreno et al. 2004, Armendáriz-Toledano et al. 2015). For *D. jeffrey*i and *D. ponderosae*, because they have a limited distribution in this region, we examined less than 50 specimens per species from Baja California Norte and Chihuahua, Mexico, respectively. For the eleven remainder species, between 200 and 500 individuals from several localities representative of their distribution ranges in these regions were examined.

Sex of specimens was determined by the presence of the stridulatory apparatus in males (Lyon 1958, Mendoza and Zúñiga 1991). *Dendroctonus* males have a bifid stridulating process (*sensu* Hopkins 1909) located on the posterior margin of propygidium (seventh abdominal tergite) which is absent in females (Fig. 1).

Some characters included in the key were carried over from previous keys (Wood 1963, 1982; Bright 1976; Lanier et al. 1988; Cibrián-Tovar et al. 1995) and taxonomic studies (Lanier and Wood 1968; Furniss and Campos-Bolaños 1985; Lanier et al. 1988; Pajares and Lanier 1990; Ruíz et al. 2009; Armendáriz-Toledano et al. 2014a,b, 2015, 2017; Víctor and Zúñiga 2016). Furthermore, specimens were thoroughly examined to elucidate novel characters potentially useful for species identification. The antennae, elytra, seventh tergite, and genitalia of some specimens of the 13 species were removed. The structures were cleared, mounted and examined following the protocols described by López et al. (2014) and Armendáriz-Toledano et al. (2015).

Terminology used for describing characters and states is adapted from Hopkins (1909) and Wood (1963, 1982) for external adult morphology; Payne et al. (1973), Dickens and Paine (1977), and López et al. (2014) for antennal anatomy; and Cerezke (1964) and Armendáriz-Toledano et al. (2014a,b, 2015) for morphology of male genitalia. Lastly, karyotype information and gallery patterns were obtained from the literature and field observations (Lanier 1981; Wood 1982; Lanier et al. 1988; Salinas-Moreno et al. 1994, 2010; Armendáriz-Toledano et al. 2015). In all species, geographic ranges are described by mountain systems, and summarized by states for the United States and Mexico and country for Central America, and abbreviated as follows: San Pedro Martir-SSPM, Sierra of Juarez-SJ, Sierra Madre Occidental-SMOC, Sierra Madre Oriental-SMOR, Trans Mexican Volcanic Belt-TMVB, Sierra Madre del Sur-SMS and Sierra de Chiapas-SCh, and Cordillera Central-CC.

Key for Dendroctonus spp. adults

– Lateral margins of the epistomal process narrower (less than 40% of distance between eyes), more than 80° deviation from the right–left axis (Fig. 2D); declivital interstria II conspicuously narrower than interstriae I and III (Fig. 2E); sculpture of declivital interstriae I–III in females ornamented by prominent uniseriate tubercles (Fig. 2E); seminal rod with a distal lobe possessing an ovate laminar shape in lateral view (Fig. 2F); length 4.4–7.0 mm. *D. pseudotsugae barragani* Furniss

- Frontal region of head with median groove extending from just above the epistomal process to upper level of eyes (Fig. 3F and G);



Fig. 2. Anatomy of head, elytral declivity and seminal rod of *Dendroctonus*: (A, D) ventral view of the head; (B, E) posterior view of elytral declivity; (C, F) lateral view of seminal rod. bs, body of seminal rod; cr, crenulations; dl, distal lobe; lm, lateral margins of epistomal process; ep, epistomal process; in I, interstria one; in II, interstria two; in III, interstria three; pu, puncture; sl, stria one; sll, stria two; slll, stria three; sv, seminal valve; tb, tubercles.



Fig. 3. Anatomy of head, pronotum and seminal rod of *Dendroctonus*: (A, F) ventral view of the head; (B, G) dorsal view of head-pronotum; (C, H) dorsal view of pronotum; (D, I) lateral view of head-pronotum; (E, J) lateral view of seminal rod. bs, body of seminal rod; fr, frons; mg, median groove; pc, pronotal callus; psv, prolongation of seminal valve; sv, seminal valve.



proximal

Fig. 4. Anatomy of elytral declivity and male genitalia of *Dendroctonus*: (A, D) posterior view of elytral declivity; (B, E) dorsal view of seminal rod; (C, F) dorsal view of anchor. bs, body of seminal rod; gr, granules; in I, interstria one; If, lateral folds of seminal valve; Ilb, lateral lobes of anchor seminal rod; sv, seminal valve.

I or III), with granulations and punctures confused (without defined

4. Punctures of pronotum large, deep, coarse and close (separated by one to three times the diameter of a single puncture; Fig. 5A); prolongation of seminal valve short and curved, length roughly one quarter of seminal rod body (Fig. 5B and C); seminal rod anchor with well-developed and rounded distal, lateral lobes (Fig. 5D); length 3.4–6.8 mm. *D. ponderosae* Hopkins

- Pronotal punctures small, shallow and dispersed, separated by more than twice diameter of single puncture (Fig. 5E); prolongation of seminal valve with broadened distal area forming a distal fold (Fig. 5F) which in dorsal view has a sickle-shape (Fig. 5G), length of





Fig. 5. Anatomy of pronotum and male genitalia of *Dendroctonus*: (A, E) dorsal view of pronotum; (B, F) lateral view of seminal rod; (C, G) dorsal view of seminal rod; (D, H) dorsal view of anchor. bs, body of seminal rod; df, distal fold; Ilb, lateral lobes of anchor seminal rod; psv, prolongation of seminal valve; pu, punctures, sv seminal valve.

prolongation almost half that of seminal rod body; seminal rod anchor with two poorly developed, rounded lateral lobes (Fig. 5H); length 4.6–6.8 mm. *D. jeffreyi* Hopkins

5. Lateral margins of epistomal process not elevated (Fig. 6A); female frons without median protuberance at upper level of eyes (Fig. 6A); anterior region of pronotum almost as wide as posterior (i.e., pronotum without an abrupt constriction), lateral margins almost parallel in dorsal view (Fig. 6B); declivital striae I-IV conspicuously impressed (Fig. 6C); seminal valve with a straight and short prolongation, length less than a quarter of the seminal rod's body (Fig. 6D) length 4.9–6.3 mm. *D. parallelocollis* Chapuis

6. Antennal club symmetrical, with four antenomeres of similar color and two distal antennomeres only slightly narrower than two proximal antennomeres (Fig. 7A); prolongation of the seminal valve short (almost as long as wide), length approximately a quarter of body of seminal rod (Fig. 7B); distal area of seminal rod anchor with poorly curved lobe in lateral view (Fig. 7C); length 5.3–8.3 mm. *D. valens* LeConte

– Antennal club asymmetrical, with two distal antennomeres distinctly narrower than two proximal antennomeres (Fig. 7D); seminal valve's prolongation long (twice as long as wide), length approximately half that of body of seminal rod (Fig. 7E); distal area of seminal rod anchor with strongly curved, hook-shaped lobe in lateral view (Fig. 7F); length 5.0–6.3 mm. *D. rhizophagus* Thomas and Bright

7. Male frons with median grove slightly defined and with or without small granules grouped into two slightly elevated summits on lateral areas of frontal groove but without frontal tubercles (Fig. 8A); sparse pubescence on elytral declivity, setae very long and homogeneous in size (Fig. 8B); seminal rod divided into distinct dorsal and ventral processes, with a lobe- or broadly triangular-shaped dorsal process and an elongate, spine-like ventral process more than half the total length of seminal rod's body) (Fig. 8C); length 3.0–5.5 m. *D. adjunctus* Blandford



Fig. 6. Anatomy of head, pronotum, elytral declivity and seminal rod of *Dendroctonus*: (A, E) lateral-dorsal view of head-pronotum; (B, F) dorsal view of pronotum; (C, G) anterior view of elytral declivity; (D, H) lateral view of seminal rod. bs, body of seminal rod; ep, epistomal process; mp, median protuberance; psv, prolongation of seminal valve; sl, stria one; sll, stria two; slll, stria three; psv, prolongation of seminal valve; sv, seminal valve.

9. Declivital pubescence uniformly short, setae shorter than width of an interspace (Fig. 9A); seminal rod long, four to six times length of seminal valve, in lateral view distal area of seminal rod distinctly narrower than central area (Fig. 9B); length 2.0–4.7 mm. *D. brevicomis* LeConte

– Declivital pubescence uniformly long (Fig. 9D), setae longer than width of an interspace, typically more than three times as long; seminal rod two to three times the length of the seminal valve, distal area of the seminal rod broadened in lateral view (Fig. 9E); length 4.5–7.0 mm. *D. approximatus* Dietz

– Dorsal process of seminal rod flattened dorsoventrally but in lateral view appears spine-shaped, with a concave distal margin in lateral view (Fig. 11C and D); ventral process consisting of a robust spine with tip possibly expanded laterally (*D. vitei*); seminal rod anchor with two lateral lobes in distal region (Fig. 11K and L). ... 12

11. Anterolateral regions of pronotum (preepisternal area) smooth, without fine, parallel ridges (Fig. 12C); female pronotal

callus conspicuously elevated; spine-shaped ventral process of seminal rod infrequently extending distally beyond dorsal process, dorsal process semicircular or bulbous in lateral view (Fig. 11A) and not laterally compressed when viewed dorsoventrally (Fig. 11E); seminal rod anchor horseshoe-shaped and similar thickness throughout, with distally fused lateral arms that do not narrow proximally (Fig. 11I); length 2.0–3.2 mm. *D. frontalis* Zimmermann

- Anterolateral regions of pronotum (preepisternal area) with fine parallel ridges (Fig. 12A); female pronotal callus weakly or not elevated; spine-shaped ventral process of seminal rod typically extending distally beyond dorsal process, dorsal process approximately triangular in shape in lateral view (Fig. 11B) and laterally compressed when viewed dorsoventrally (Fig. 11F); anchor thickened distally, with distally-fused lateral arms strongly narrowing proximally (Fig. 11J); 2.9–4.9 mm. *D. mesoamericanus* **Armendáriz-Toledano & Sullivan**

12. Antennal club with clusters of sensillae arranged in circular concavities resembling pit-craters on the anterior surface (Fig. 12D) setae of elytral declivity commonly with a split tip or saw-toothed outer surface; ventral process of seminal rod flattened dorsoven-trally, paddle-shaped and somewhat resembling a beaver's tail (Fig. 11G), distal margin of dorsal process straight to strongly concave in lateral view (Fig. 11C); dorsal process ovate in ventral view, shorter and broader than the ventral process (Fig. 11G); seminal rod anchor with small lobes distally and thin arms (Fig. 11K). 3.4–5.2 mm. *D. vitei* Wood.

– Antennal club without sensillae arranged in circular pits (Fig. 12B); setae of elytral declivity with undivided tip and smooth outer surface; ventral process of seminal rod not compressed dorsoven-trally (Fig. 11H), distal margin of dorsal process strongly concave in lateral view; dorsal process ovate in ventral view, similar in length of the ventral process (Fig. 11H); seminal rod anchor with strongly





Fig. 7. Anatomy of antennal club and male genitalia of *Dendroctonus*: (A, D) anterior view of antennal club; (B, E) dorsal and lateral view of seminal rod; (C, F) lateral view of anchor seminal rod. bs, body of seminal rod; lb, lobe of distal area of anchor seminal rod; lp, length of prolongation of seminal valve; sb1, sensorial band one; sb2, sensorial band two; sb3, sensorial band three; se1, antennal segment one; se2, antennal segment two; se3, antennal segment three; se4, antennal segment four; psv, prolongation of seminal valve; sv, seminal valve.

protuberant distal lobes and with thick, proximally narrowing arms (Fig. 11L); length 2.3–3.7 mm. *D. mexicanus* Hopkins

Dendroctonus pseudotsugae barragani Furniss, 2001

Length 4.4–7.0 mm, color of head and pronotum dark-brown to black, elytra reddish brown to black; frontal region of head with a conspicuous median impression, epicranial suture deeply impressed, central area of frons with crenulations forming concentric series of ridges around the median area of frons, lateral margins of epistomal process flat, and narrow (less than 40% of distance between eyes), almost perpendicular relative to right–left axis (more than 80°); median line on pronotum forming a carina separating a shallow depression on either side; declivital interstria II conspicuously narrower than the interstriae I and III; margin of strial punctures on elytra distinctly elevated, particularly on the anterior; females with prominent uniseriate tubercles on declivital interstriae I–III; seminal rod with a distal lobe, seminal rod anchor formed by two fused arms that converge in their distal area in a narrow lobe. Chromosome formula in females and males is 14 AA + XX and 14 AA + Xyp + S, respectively. *Dendroctonus pseudot-sugae barragani* is found across the SMOC (Chihuahua, and Durango), and SMOR (Coahuila, and Nuevo Leon) at elevations between 1,500 and 3,100 m. This species colonizes and kills Douglas-fir trees, *Pseudotsuga menziesii* variety *glauca* (Beissn.) E. Murray. The parental gallery is generally straight (i.e., aligned with the bole), with larvae mining singly and egg deposition into individual niches.

Dendroctonus pseudotsugae barragani specimens from SMOR and SMOC, Mexico show substantial genetic divergence coupled with morphological differences in body color, frons sculpture and pronotal vestiture-sculpture, suggesting that the isolation induced by mountain systems in north of this country have promoted its divergence. Additional studies must be performed to determinate the status of these populations.

Dendroctonus ponderosae Hopkins, 1902

Length 3.4-6.8 mm, dark-brown to completely black; median region of the frons round, without median groove; lateral margins of



Fig. 8. Anatomy of head, elytra and seminal rod of *Dendroctonus*: (A, D) ventral view of head; (B, E) lateral view of right elytron; (C, F, G) lateral view of seminal rod. bs, body of seminal rod; dp, dorsal process; ft, frontal tubercles; g, granules; mg, median groove; pb, pubescence; sv, seminal valve; vp, ventral process.



Fig. 9. Anatomy of elytra and male genitalia of *Dendroctonus*: (A, D) lateral view of right elytron; (B, E) lateral view of seminal rod; (C, F) dorsal view of anchor seminal rod. bs, body of seminal rod; dsc, elytral disc; ed, elytral declivity; sv, seminal valve.

epistomal process elevated and wide (approximately 50% of distance between eyes), approaching parallel to the right–left axis (less than 60°); punctures of pronotum large, deep, coarse, and close, separated by one to three times of diameter of a puncture; females with anteriolateral margins of pronotum straight or concave (like a "bottle-neck"), in dorsal view (without transverse elevated callus); first declivital interstria strongly elevated with uniseriate granulations, declivital interstria II almost as wide as interstriae I and III; females without uniseriate prominent tubercles on declivital interstriae I–III; seminal rod entire and with a short curved prolongation of the seminal valve, length of prolongation almost a quarter of length of body of seminal rod; in dorsal view the lateral folds of seminal valve oblique (approximately 40° with respect to antero-posterior edge of body of seminal rod); in dorsal view, anchor arms with two well-



Fig. 10. Lateral view, right elytron of *Dendroctonus*. dsc, elytral disc; ed, elytral declivity; lp, long pubescence; mp, medium pubescence; shp, short pubescense.

developed lateral-distal lobes. Chromosome formula in females and males is 11 AA + XX, and 11 AA + neo-Xy, respectively. *Dendroctonus ponderosae* is found from southwestern Canada, east Colorado to northern Baja California. In Mexico the only two collection records were from the SSPM in Baja California Norte at elevations between 2,300 and 2,400 m. In the United States and Canada, this species colonizes and kills *Picea engelmanni* Parry ex Engelmann, *Pinus albicaulis* Engelmann, *P. balfouriana* Greville et Balfour ex Murray, *P. contorta* Douglas ex Loudon, *P. coulteri* D. Don, *P. edulis* Engelmann, *P. flexilis* E. James, *P. lambertiana* Douglas, *P. monophylla* Torrey et Frémont, *P. monticola* Douglas ex D. Don in Lambert, *P. ponderosa* Douglas ex Lawson, and



Fig. 11. Anatomy of seminal rod (lateral and dorsal view) and anchor seminal rod (dorsal view) of *Dendroctonus*. (A, E, I) *Dendroctonus frontalis*; (B, F, J) *D. meso-americanus*; (C, G, K) *D. vitei*; (D, H, I) *D. mexicanus*. ar, arm of anchor seminal rod; da, distal area of anchor seminal rod; dl, distal lobe of anchor of seminal rod; dp, dorsal process; vp, ventral process.



Fig. 12. Anatomy of pronotum and antennae of *Dendroctonus*: (A, C) lateral view of pronotum; (B, D) anterior view of antennal club. pa, pre-episternal area; sb1, sensorial band one; sb2, sensorial band two; sb3, sensorial band three; se1, antennal segment one; scs, sensillae clustered in circular concavities like to pit-craters; se2, antennal segment two; se3, antennal segment three; se4, antennal segment four.

P. strobiformis Engelmann. The parental gallery is vertical, with larvae mining separately in the inner bark and egg deposition into individual niches.

Mexican specimens from Chihuahua show morphological differences in the antennae, anchor seminal rod, and seminal rod anatomy compared with insects from British Columbia (BC), Canada. Unfortunately, it was not possible to examine specimens from Baja California, Mexico or from other latitudes to compare these attributes.

Dendroctonus jeffreyi Hopkins, 1902

Length 4.6–6.8 mm, dark-brown to completely black; median region of the frons round, without median groove; external morphology similar to *D. ponderosae* except larger size and punctures of pronotum smaller, shallow and scarce, and separated by more than two times the diameter of a puncture. Seminal rod is entire and without a distal lobe, with a long-curved prolongation of the seminal valve, a distal area

broaden into a distal fold that in dorsal view has a sickle-shape, length of prolongation almost half the length of the seminal rod body; in dorsal view the lateral folds of seminal valve oblique (approximately 40° relative to antero-posterior axis of body of seminal rod); in dorsal view, anchor arms with two poorly developed, rounded lateral lobes. Chromosome formula in females and males is 11 AA + XX and 11 AA + neo-Xy + S, respectively. *Dendroctonus jeffreyi* is found from southern Oregon in the western United States to SJ and SSPM in Baja California, Mexico at elevations between 1,500 and 2,480 m. This species colonizes and kills *Pinus jeffreyi* Greville et Balfour in A. Murray. The parental gallery is parallel to the bole, with larvae in individual galleries and egg deposition into individual niches.

Dendroctonus parallelocollis Chapuis, 1869

Length 4.9–6.3 mm, completely black; lateral margins of epistomal process flat (lateral margins not elevated) and wide (approximately

50% of distance between eyes), almost parallel with respect to the right-left axis (less than 60°), frontal region of the frons round, without median groove and females without a median protuberance at level of eyes; anterior region of pronotum almost as wide as posterior (i.e., without an abrupt constriction), in dorsal view lateral margins almost parallel, females without transverse elevated callus; declivital striae I-IV impressed with interstriae weakly elevated, first declivital interstriae not elevated (at the same height as interstriae II-III), declivital interstria II almost as wide as interstriae I and III, elytral declivity with confused granulations and punctures (not uniseriate and without tubercles); seminal rod entire with a short (less than a quarter of length of seminal rod body) and straight prolongation in seminal valve; in dorsal or ventral view, the lateral folds of seminal valve parallel to anteroposterior axis of seminal rod body; in dorsal view, anchor arms without two lateral lobes. Chromosome number formula in females and males is 14 AA+XX and 13 AA + Xyp, respectively. Dendroctonus parallelocollis extends from northern Mexico to Honduras. In Mexico, it has been found in the SMOC (Chihuahua, Durango, and Jalisco), SMOR (Nuevo Leon, and Tamaulipas), TMVB (Hidalgo, Michoacan, Mexico city, Morelos, and Puebla), SMS (Guerrero and Oaxaca), and SCh (Chiapas), and in Central America in the CC (Belize, Guatemala, Honduras, and Nicaragua). Its elevation range is between 800 and 4,000 m. This species is not aggressive, and it can be found in Pinus arizonica Engelmann ex Rothrock, P. devoniana Lindley, P. douglasiana Martínez, P. durangensis Martínez, P. hartwegii Lindley, P. leiophylla Schiede ex Schlechtendal et Chamisso, P. montezumae Lambert, P. oocarpa Schiede ex Schlectendahl, P. pringlei Shaw ex Sargent, P. pseudostrobus Lindley and P. teocote Schiede ex Schlechtendal et Chamisso. The parental gallery runs parallel with the host bole, with larval mining in individual galleries and egg deposition into individual niches.

Dendroctonus parallelocollis frequently is confused with D. appoximatus (in more than 90% of specimens examined, it has been identified as the latter species). These species can be reliably differentiated using characters of the frons (median grove and frontal tubercles absent in D. parallelocollis, but present in those of D. approximatus) and epistomal area (flat in D. parallelocollis, but elevated in D. approximatus). Integrative taxonomic analysis in progress supports that D. parallelocollis has strong phenotypic differences between geographical regions.

Dendroctonus valens LeConte, 1860

Length 5.3-8.3 mm, brown to reddish brown; lateral margins of epistomal process strongly elevated and wide (approximately 50% of distance between eyes), approaching parallel to the right-left axis (less than 60°), frontal region of the frons round, without median groove and females with an inconspicuous median protuberance at level of eyes; antennal club symmetric, with the four antenomeres of similar color, the last two antennomeres slightly narrower the first two; anterior of pronotum narrower than posterior in dorsal view (with an abrupt constriction anteriorly), females without transverse elevated callus; declivital striae I-IV impressed with interstriae not elevated, declivital interstria II almost as wide as interstriae I and III, elytral declivity with confused granulations and punctures (not uniseriate and without tubercles); seminal rod entire with a shortcurved prolongation, almost as long as wide, approximately a quarter of length of the seminal rod body; in dorsal or ventral view, the lateral folds of seminal valve parallel to anteroposterior axis of seminal rod body; in dorsal view, anchor with thin arms fused distally, distal area of anchor in lateral view with a weakly curved lobe. The

chromosome formula in males and females is 13 AA + Xyp and 14 AA+XX, respectively. Dendroctonus valens is distributed from Canada to Honduras. In Mexico and Central America, it has been found in SJ and SSPM in Baja California, SMOC (Aguascalientes, Chihuahua, Durango, Jalisco, Sinaloa, Sonora, and Zacatecas), SMOR (Coahuila, Nuevo León, San Luis Potosi, and Tamaulipas), TMVB (Colima, Hidalgo, Mexico city, Michoacán, Morelos, Puebla, Queretaro, Tlaxcala and Veracruz), SMS (Guerrero, and Oaxaca), SMCh (Chiapas), and CC (Belize, Guatemala, Nicaragua, and Honduras). Its elevational range is between 800 and 4,000 m. This species is not typically aggressive in its native range; however, in some locations in Mexico and Central America it has been found killing apparently healthy pine trees. It was inadvertently introduced into China where it has become more aggressive. In North and Central America it is found in Pinus arizonica, P. ayacabuite Ehrenberg ex Schlechtendahl, P. cembroides Zuccarini, P. devoniana Lindley, P. douglasiana, P. durangensis, P. engelmannii Carrière, P. greggii Engelmann ex Parlatore, P. hartwegii, P. herrerae Martínez, P. jeffreyi, P. leiophylla, P. lumholtzii B.L. Robinson et Fernald, P. maximinoi H. E. Moore, P. montezumae, P. oocarpa Schiede ex Schlectendahl, P. patula Schiede ex Schlectendahl et Chamisso, P. pringlei, P. pseudostrobus, P. quadrifolia Parlatore ex Sudworth, P. strobus L., and P. teocote. The parental gallery shape is variable, some as being cave shaped or linear, they are typically short and wide with communal larval galleries and egg oviposition in collective niches.

Integrative taxonomic analyses in progress show that specimens of *D. valens* from South Mexico and Central America (Guerrero, Oaxaca, Chiapas, Guatemala, Honduras) exhibit strong genetic divergence compared to northern population in three molecular markers and they have differences in body size, coloration of antennomeres, morphology of the seminal rod anchor, and seminal rod shape. Adults from these regions have the first two antennomeres darker, a long-curved prolongation of the seminal rod valve and seminal rod anchor with an intermediate shape between those of *D. rhizophagus* and *D. valens*.

Dendroctonus rhizophagus Thomas and Bright, 1970

Length 5.0-6.3 mm, dark reddish brown; females with an inconspicuous median protuberance at level of eyes; external morphology similar to D. valens except in antennal club shape and coloration. The antennal club in D. rhizophagus is strongly bilaterally asymmetrical, and the first two antennomeres are darker and distinctly wider than the third and fourth. The seminal rod is entire with a long, curved prolongation (twice as long as wide), equaling approximately half the total length of the seminal rod. In dorsal or ventral view, the lateral folds of the seminal valve are parallel to the anteroposterior axis of the seminal rod body; in dorsal view, seminal rod anchor with thin lateral arms fused distally, distal area of anchor in lateral view with a strongly curved, hook-shaped distal region. Chromosome formula in females and males is 14 AA+XX and 13 AA + Xyp, respectively. The range of D. rhizophagus extends from Chihuahua to northern Jalisco in Mexico. It has been found only in SMOC (Chihuahua, Durango, Jalisco, Sinaloa, and Sonora). Its elevation range is between 1,000 and 3,100 m. This species colonizes and kills seedlings and saplings of Pinus arizonica, P. ayacahuite, P. cembroides, P. durangensis, P. engelmannii, P. herrerae, P. leiophylla, P. lumholtzii, P. oocarpa, P.ponderosae, P. strobiformis, and P. teocote. The parental gallery typically encircles the root collar (commonly only one to two pairs colonize a single tree) with eggs

deposited into communal niches and communal larval galleries that extend downward into the taproot.

Dendroctonus adjunctus Blandford, 1897

Length 3.0-5.5 mm, dark brown to black; lateral margins of epistomal process elevated and wide (approximately 50% of distance between eyes), approaching parallel to the right-left axis (less than 60°); median region of the frons concave with a median groove extending from just above the epistomal process to upper level of eyes (groove very weak in females), in males this region has small granulations arranged into two slightly elevated groups arranged laterally to the groove but without frontal tubercles; anterolateral regions of pronotum (pre-episternal area) with conspicuous, parallel ridges; female pronotum with an anterior elevated callus dorsally and transversally, anteriolateral margins of pronotum convex in dorsal view; declivital interstriae I-IV similar in width; stria I impressed with interstriae weakly elevated, elytral declivity with confused crenulations, granulations, and punctures (not uniseriate and without tubercles); pubescence of elytral declivity sparse, very long and homogeneous in size; seminal rod without a prolongation in the seminal valve and divided into dorsal and ventral processes; lobe-shaped dorsal process, broadly triangular in lateral view, and ventral process consisting of a long, narrow spine (more than half the length of seminal rod body); in ventral view seminal rod anchor with two thin, lateral arms which thicken distally and fuse to form an arch; distal margin of seminal rod anchor strongly rounded and without lobes, and in lateral view arms and distal lobe of anchor folded toward the seminal rod. Chromosome formula in females and males is 6 AA + XX and 6 AA + neo-Xy, respectively. The range of D. adjunctus extends from southwestern United States to Nicaragua (Wood 1982). In Mexico and Central America, it has been found in SMOC (Chihuahua, Durango, Jalisco, and Zacatecas), SMOR (Coahuila and Tamaulipas), TMVB (Hidalgo, Mexico city, Michoacán, Morelos, Puebla, Queretaro, Tlaxcala, and Veracruz), SMS (Guerrero, and Oaxaca), SCh (Chiapas) and CC (Belize, Guatemala, Nicaragua, and Honduras). Its elevation range is between 1,300 and 3,940 m. This species colonizes and kills Pinus arizonica, P. ayacabuite, P. douglasiana, P. durangensis, P. engelmannii, P. hartwegii, P. herrerae, P. leiophylla, P. maximinoi, P. montezumae, P. oocarpa, P. patula, P. pinceana Gordon, P. pringlei, P. pseudostrobus, and P. teocote. The parental gallery runs largely parallel to the host bole, is straight to slightly sinuous and typically L-shaped, with larvae mining separately and eggs deposited singly into individual niches.

Dendroctonus brevicomis LeConte, 1897

Length 2.0–4.7 mm, dark brown to black; epistomal region similar to *D. adjunctus*; frontal region of the frons concave with a median groove extending from above area of epistomal process to upper level of eyes, in males this region with prominent granules and numerous tubercles grouped into two strongly elevated summits positioned laterally to the groove; anterolateral region of pronotum (preepisternal area) smooth, females with a transverse, anterior, elevated callus, dorsally anteriolateral margins of pronotum convex; declivital interstriae I–IV impressed and similar in width; elytral declivity with confused crenulations, granulations and punctures (not uniseriate and without tubercles); declivital pubescence uniformly very short, shorter than the width of an interspace; seminal rod entire and long, body length of seminal rod from four to six times the length of seminal valve, in lateral view seminal rod body abruptly narrows distally; lateral arms of seminal rod anchor triangular and not fused distally; distal margin of each arm straight. Chromosome number in females and males is 5 AA + XX and 5 AA + neo-Xy, respectively. *Dendroctonus brevicomis* range extends from southwestern Canada to northern Mexico. In Mexico, it has been found in SMOC (Chihuahua and Durango) and SMOR (Coahuila, Nuevo Leon). Its elevation range is between 1,680 and 3,300 m. This species colonizes and kills *Pinus arizonica, P. ayacahuite, P. durangensis, P. engelmannii, P. leiophylla and P. teocote.* Parental gallery sinuous, with larvae mining separately and eggs deposited singly into individual niches.–

Integrative taxonomic analysis in progress supports that *D. brevicomis* has strong phenotypic differences between geographical regions in Mexico.

Dendroctonus approximatus Dietz, 1890

Length 4.5-7.0 mm, dark brown to black; epistomal, frontal and pronotal regions similar to D. brevicomis, declivital interstriae II-IV impressed and similar in width; elytral declivity with confused crenulations, granulations and punctures (not uniseriate and without tubercles); declivital pubescence uniformly very long, length typically more than three times width of an interspace; seminal rod entire and short, body length of seminal rod two to three times length of seminal valve, in lateral view seminal rod body is thick and rounded distally in lateral view; anchor with lateral arms triangular in shape and not fused distally, distal margin of each arm rounded. Chromosome number in females and males is 5 AA+XX and 5 AA + neo-Xy, respectively. Dendroctonus approximatus range extends from southwestern United States to Honduras. In Mexico and Central America, it has been found in SSPM (Baja California), SMOC (Chihuahua, Durango, Jalisco, and Zacatecas), SMOR (Coahuila, and Nuevo León), TMVB (Hidalgo, Mexico, Michoacán, Morelos, Puebla, and Querétaro), SMS (Guerrero, and Oaxaca), SCh (Chiapas) and CC (Belize, Guatemala, Nicaragua, and Honduras). Its elevation range is between 1,600 and 3,200 m. This species is not aggressive and can be found in Pinus arizonica, P. ayacahuite, P. devoniana, P. douglasiana, P. durangensis, P. engelmannii, P. hartwegii, P. herrerae, P. jeffreyi, P. leiophylla, P. lumholtzii, P. montezumae, P. oocarpa, P. patula, P. pseudostrobus, P. strobiformis, and P. teocote. The parental gallery is sinuous, with larvae mining separately and eggs deposited singly into individual niches.

Dendroctonus frontalis Zimmermann, 1868

Length 2.0–3.2 mm, light to dark brown; frontal region of the frons concave with a median groove extending from above epistomal process to upper level of eyes, in males with prominent granules and numerous tubercles grouped in two strongly elevated summits positioned laterally to the groove; anterolateral regions of pronotum (preepisternal area) smooth, females with prominently elevated anterior transversal callus, anterolateral margins of pronotum convex when viewed dorsally; declivital interstriae I-IV impressed and of similar width; elytral declivity with confused crenulations, granulations and punctures (not uniseriate and without tubercles); declivital pubescence of heterogeneous size (predominantly of two size classes, shorter setae much more abundant than longer setae, and long setae largely restricted to interstriae I and III); seminal rod divided into ventral and dorsal processes, ventral process of seminal rod consisting of a fine, sharp spine that rarely projects distally beyond dorsal process, dorsal process semicircular or bulbous with a distinctly convex distal margin in lateral view, laterally not compressed in ventral view; seminal rod anchor consisting of two lateral

arms fused distally with a horseshoe-like appearance and without distal lobes. Chromosome formula in females and males is 7 AA + XX and 7 AA + Xyp, respectively. The range of D. frontalis includes the entire southeastern United States (from New York to Texas) and from Arizona, United States to Honduras. In Mexico and Central America, it has been found in SMOC (Chihuahua, Durango, Jalisco), SMOR (Nuevo León, Tamaulipas, San Luis Potosi), TMVB (Hidalgo, Mexico, Michoacán, Morelos, Puebla, Queretaro), SMS (Guerrero, and Oaxaca), SCh (Chiapas), and the CC (Belize, Guatemala, Nicaragua, and Honduras). Its elevation range is between 311 and 2,612 m. This species is a highly aggressive primary bark beetle capable of killing healthy trees when population levels are elevated, and periodically forms outbreaks that cause widespread, catastrophic mortality. In some localities in Mexico and Central America it is commonly found in the same trees (syntopic) with D. mesoamericanus or D. mexicanus. When coexisting with D. mexicanus both species infest the entire length of the bole; when cohabiting trees with D. mesoamericanus, D. frontalis is concentrated in the mid to upper-bole with substantial overlap of both species in the bark. Hosts: Pinus caribaea Morelet, P. devoniana, P. douglasiana, P. greggii, P. lawsonni Roezl ex Gordon et Glendinning, P. leiophylla, P. maximinoi, P.montezumae, P. oocarpa, P. pringlei, P. pseudostrobus, and P. teocote. Parental galleries are sinuous and frequently intercross, with larvae mining separately and eggs deposited singly into individual niches.

Dendroctonus mesoamericanus Armendáriz-Toledano and Sullivan, 2015

Length 2.9–4.9 mm, pronotum and elytra medium brown to black, often with head darker than pronotum and pronotum darker than elytra; frontal region similar to D. frontalis but with frontal tubercles somewhat less prominent in males; anterolateral regions of pronotum (preepisternal area) with fine parallel ridges, females with weakly developed anterior transversal callus; declivital interstriae I-IV impressed; interstria II slightly narrower than interstriae I and III; elytral declivity with crenulations, granulations and punctures confused (not uniseriate and without tubercles); declivital pubescence of heterogeneous size (short and long, shorter setae much more abundant than longer setae, and long setae largely restricted to rows on interstriae I and III); seminal rod divided into both ventral and dorsal processes, ventral process of seminal rod consisting of a fine, sharp spine that typically projects distally beyond dorsal process, dorsal process approximately triangular-shaped (lateral view), laterally compressed (dorsal or ventral view); seminal rod anchor broad distally, composed of two lateral arms that narrow proximally and are fused distally (horseshoe-shaped) and without distal lobes. Chromosome formula in females and males is 5 AA+XX and 5 AA + Xyp, respectively. The range of D. mesoamericanus extends from the central Mexico to Honduras. In Mexico, it has been found in TMVB (Michoacán), SMS (Oaxaca) and SCh (Chiapas), and in Central America in the CC (Belize, El Salvador, Guatemala, Nicaragua, and Honduras). Its elevation range is between 600 and 3,200 m, preferring 2,000 and 2,500 m. The aggressiveness of D. mesoamericanus and its regional importance as a killer of pines has not been adequately established, although catastrophic mortality has been attributed to it in at least one report. Field observations suggest that D. mesoamericanus can initiate attacks on apparently vigorous trees in the absence of other bark beetle species. However, in most of its records it has been found in the same tree with D. frontalis. Attacks can occur throughout the bole, but when cohabiting trees with D. frontalis they are concentrated in the crown and

lower bole. Hosts: P. caribaea, Morelet, P. devoniana, P. hartwegii, P. oocarpa, P. maximinoi, P. montezumae, P. pringlei, and P. pseudostrobus. Parental gallery sinuate, with larvae mining separately and eggs deposited singly into individual niches.

Dendroctonus vitei Wood, 1975

Length 3.4-5.2 mm, head black, pronotum and elytra medium brown to black; frontal region of the frons concave with a median groove extending from above epistomal process to upper level of eyes, frons sculpture with shallow punctures, scarce granulations on lateral areas of epistomal process, frons in males with prominent tubercles grouped in two elevated summits positioned laterally of median groove; anterior side of antennal club with sensillae clustered into circular concavities resembling pit-craters on the third antennal segment and the sensorial band between the third and fourth antennal segments; anterolateral regions of pronotum (preepisternal area) smooth, females with a slightly elevated anterior transversal callus; declivital interstriae II-IV impressed; interstria II slightly wider than interstriae I and III; elytral declivity with confused crenulations, granulations, and punctures (not uniseriate and without tubercles); declivital pubescence of heterogeneous size (at least three different size classes in the same specimen, rows of long setae in interstriae I and III less distinctive); in majority of specimens setae of elytral declivity with split tip or saw-toothed outer surface; seminal rod divided into distinct ventral and dorsal processes, dorsal process spine-shaped in ventral view and lobed in dorsal view; ventral process of seminal rod spine-shaped in lateral view but broadened dorsally, paddle-shaped, somewhat resembling a beaver tail; distal margin of dorsal process straight to strongly concave in lateral view, dorsal process ovate, shorter and wider than ventral process in ventral view; seminal rod anchor with thin arms and poorly developed distal lobes. Chromosome formula in females and males is 5 AA + XX and 5 AA + Xyp respectively. The range of D. vitei extends from northeastern Mexico to Guatemala. In Mexico, it has been found in SMOr (Nuevo León, and Tamaulipas), east of TMVB (Veracruz), SMS (Guerrero and Oaxaca), and SCh (Chiapas), and in Central America it has been found in the CC (Guatemala). Its elevation range is between 1,000 and 2,500 m, preferring from 1,000 to 1,500 m. The importance of D. vitei as a tree killer has not been sufficiently evaluated; however, in Oaxaca we have observed this species killing apparently healthy trees. Outbreaks of D. vitei in Mexico have not been recorded. Hosts: Pinus maximinoi, P. michoacana Martínez, P. montezumae, P. oocarpa, P. pseudostrobus, P. teocote. Parental gallery is sinuous, with larvae mining separately and eggs deposited singly into individual niches.

Dendroctonus mexicanus Hopkins, 1905

Length 2.3-3.7 mm, head black, pronotum typically darker than elytra, pronotum and elytra light brown to black; frontal surfaces similar to D. vitei except frons sculpture with deeper punctures and prominent granules abundant on lateral areas of epistomal process, male frontal groove with prominent lateral tubercles; anterolateral surfaces of pronotum (preepisternal area) smooth, females with a prominent elevated anterior transversal callus; declivital interstriae II-IV impressed and similar in width; elytral declivity with confused crenulations, granulations and punctures (not uniseriate and without tubercles); declivital pubescence is of heterogeneous size (at least three different size classes, long/medium setae not restricted to interstriae I and III or arranged in conspicuous rows); the pubescence of elytral declivity with an undivided tip and smooth outer surface; seminal rod divided into ventral and dorsal processes, ventral process of seminal rod consisting of a thick, robust spine; seminal rod in lateral view with distal margin of dorsal process concave, in ventral

view dorsal process ovate, similar length as the ventral process; seminal rod anchor entire with protuberant distal lobes and distally thickened arms. The chromosome formula in females and males is 5 AA + XX and 5 AA+Xyp, respectively. Its geographic range extends from Arizona, United States to Oaxaca, Mexico. In Mexico, it has been recorded in SMOC (Aguascalientes, Chihuahua, Durango, Jalisco, Sinaloa, and Zacatecas), SMOR (Coahuila, Nuevo Leon, Tamaulipas, and San Luis Potosi), TMVB (Colima, Hidalgo, Mexico city, Mexico, Michoacan, Morelos, Puebla, Queretaro, Tlaxcala, and Veracruz), and SMS (Guerrero, and Oaxaca). Its elevation range is between 800 and 3,650 m, preferring 2,000 and 2,500 m. This species is a highly aggressive primary bark beetle capable of killing healthy trees when population levels are elevated, and periodically forms outbreaks that cause widespread, catastrophic mortality. It has commonly been found cohabiting trees with D. frontalis. Hosts: Pinus arizonica, P. ayacahuite, P. cembroides, P. devoniana, P. douglasiana, P. durangensis, P. engelmannii, P. greggii, P. hartwegii, P. herrerae, P. lawsonni, P. leiophylla, P. lumholtzii, P. maximinoi, P. montezumae, P. oocarpa, P. patula, P. pinceana, P. pseudostrobus, and P. teocote. The parental gallery is sinuous, with larvae mining separately and eggs deposited singly into individual niches.

Dendroctonus mexicanus distribution has been recorded from Arizona, United States (Moser et al. 2005) to Honduras (Wood 1982, Wood and Bright 1992, Cibrián-Tovar et al. 1995, Salinas-Moreno et al. 2004). However, based on the revision of seminal rod anchor morphology and seminal rod shape, we cannot verify the occurrence of this species south of the Isthmus of Tehuantepec, which agree with Lanier et al. (1988). The southern records of this species are in Sierra Norte and Sierra Sur, Oaxaca, Mexico.

Notes for Observing Characters

The specimens and morphological structures must be placed in the same position that shows their respective figures. Most characters included in the key can be observed on pinned or alcohol preserved specimens with an average quality dissecting microscope, but some of them must be examined on structures previously cleared and mounted on slides at $100-400 \times$.

For observation of body sculpture and vestiture in pinned or alcohol preserved specimens, the use light filters and powerful lighting at magnifications higher than 30 x is recommended. In some characters such as pronotal ridges of *D. mesoamericanus* (Fig. 12A) and elytral punctures is recommended to use fluorescent light at $50 \times$.

The characters related with antennal club pubescence, surface of pubescence on elytral declivity, in *D. mexicanus* and *D. vitei*, morphology of seminal rod anchor and seminal rod shape, must be observed in clarified structures preferably on slides at $100-400\times$; however, with some experience, these can be evaluated at $63\times$ with a high quality dissecting microscope, particularly the male genital structures can be appreciated under these conditions with unseparated seminal rod anchor and seminal rod. The olfactory pits on the antennal clubs of *D. vitei* are the best observed on slides. However using powerful lighting in cleared specimens, these structures can be observed such small black holes under a dissecting microscope at $63\times$.

Acknowledgments

We are grateful to Brian T. Sullivan, Miguel Angel Barrios, Jorge Macias Sámano, David Cibrián, Gerardo Cuellar, Guillermo Sánchez and two anonymous reviewers for their comments and suggestions on this manuscript. We thank Jazmin García Roman, Victoria Araiza, Osiris Valerio, León Cerrillo who collaborated in using preliminary versions of the key and provide observations for its improvement. This study was funded by the Secretaría de Investigación y Posgrado del Instituto Politécnico Nacional (IPN) (20161790). F.A.T. was a member of Programa de Becas de Estímulo Institucional de Formación de Investigadores - IPN (BEIFI-IPN) and of Consejo Nacional de Ciencia y Tecnología (CONACyT) fellow (267436).

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