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Systematics

A New Species of Bark Beetle, *Dendroctonus mesoamericanus* sp. nov. (Curculionidae: Scolytinae), in Southern Mexico and Central America

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ABSTRACT The bark beetle *Dendroctonus mesoamericanus* sp. nov. is described from a population in Parque Nacional Lagunas de Montebello, La Trinitaria, Chiapas, Mexico. This species belongs to the *D. frontalis* complex, which includes *D. adjunctus* Blandford 1897, *D. approximatus* Dietz 1890, *D. brevicomis* LeConte 1876, *D. frontalis* Zimmermann 1868, *D. mexicanus* Hopkins 1905, and *D. vitei* Wood 1975. The new species can be distinguished from closely related species *D. frontalis*, *D. mexicanus*, and *D. vitei* by four diagnostic morphological characters: the presence of striations on the preepisternal area of the prothorax (anterolateral pronotum) in both sexes, seminal rod with an approximately linear posterior margin of the dorsal process (in lateral view), irregularly sized ornamentations on the distal edge of squamiform plates present on the eighth abdominal tergite in females, and an inconspicuous pronotal callus in females. Furthermore, the karyotype of *D. mesoamericanus* sp. nov. (5AA+Xyp / XX) differs from that of its sister species *D. frontalis* (7AA + Xyp / XX). *Dendroctonus mesoamericanus* sp. nov. is distributed in Belize, Guatemala, El Salvador, Honduras, Nicaragua, and in the Michoacán, Oaxaca, and Chiapas states in Mexico. In these countries, this species has been collected at elevations above from 311 to 2600 m on six pine species, and it commonly occurs in syntopy with *D. frontalis*.

KEY WORDS bark beetle, *Dendroctonus mesoamericanus*, seminal rod, spermatheca

Bark beetles of the genus *Dendroctonus* Erichson, 1836 are major natural disturbance agents of Holarctic conifer forests and include some of the most economically significant forestry pests in the world. They attack species in the genera *Larix* Mill., *Picea* A. Dietr., and *Pseudotsuga* Carrière, but occur in greatest diversity in *Pinus* L. They complete their life cycle within the bark of their host trees where attacking adults pair, oviposit within a single gallery excavated in the inner bark, and both the parent adults and developing larvae feed on phloem tissue (Wood 1982). They generally attack and kill trees that are prostrate or weakened by age, drought, disease, mechanical damage, or other factors. However, during very high populations associated with epidemics, healthy trees can be colonized, causing significant tree mortality and economic losses in the forestry sector (Billings 2011).

In the first monograph of the genus *Dendroctonus*, Hopkins (1909) recognized and integrated 24 valid species arranged in divisions, subdivisions, sections, subsections, series, and subseries according to morphological characteristics. Due to the high intra- and interspecific morphological variation of these species, the genus was subject to taxonomic revisions (Wood 1963, 1982). Some species were synonymized (Wood 1963, 1974; Lanier and Wood 1968) and new species or subspecies were described (Thomas and Bright 1970; Furniss 2001).

The genus currently includes 19 valid species (Wood 1982), one of them with two subspecies (Furniss 2001, Ruiz et al. 2009), arranged into five to six groups or species complexes supported by morphological, behavioral, ecological, chromosomal, and molecular characteristics (Hopkins 1909; Wood 1963, 1982; Lanier 1981; Kelley and Farrell 1998; Zúñiga et al. 2002).

The *Dendroctonus frontalis* complex is composed of six species: *D. adjunctus* Blandford 1897, *D. approximatus* Dietz 1890, *D. brevicomis* LeConte 1876, *D. frontalis* Zimmermann 1868, *D. mexicanus* Hopkins 1905, and *D. vitei* Wood 1974 (Wood 1982, Lanier et al. 1988). Three species within the complex—*D. frontalis*, *D. mexicanus*, and *D. vitei*—are particularly problematic, because they are very similar morphologically (Wood 1974, 1982; Vité et al. 1974, 1975; Lanier et al. 1988) and their populations may coexist in space and time in pine forests of Mexico and Central America (Zúñiga et al. 1995, 1999; Salinas-Moreno et al. 2004; Moser et al. 2005; Armendáriz-Toledano et al. 2014a,b).

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From early 2000 to 2002, >25,000 ha of mature pine stands in the Mountain Pine Ridge Forest Reserve of Belize were devastated by an outbreak of what was initially identified as *D. frontalis* (Haack et al. 2000, Macías-Sámano et al. 2001, Billings et al. 2004). During studies of this outbreak, Midtgaard and Thunes (2002) collected a second, apparently undescribed *Dendroctonus* species from infested trees that these authors called the "caribbean pine beetle." The caribbean pine beetle species was distinguished from *D. frontalis* by the presence in both sexes of fine ridges on the preepisternal area of the prothorax (anterolateral pronotum) *sensu* Hopkins (1909, Fig. 17) oriented roughly parallel to the anterior margin, and by the width of the epistomal process, which appeared to be wider in caribbean pine beetle than *D. frontalis* (Thunes et al. 2005, 2011). These authors assigned the name "*Dendroctonus woodi*" to identify caribbean pine beetle (Thunes et al. 2005, 2011); however, according to the International Code of Zoological Nomenclature (ICZN 1999), this *binomen* is a *nomen nudum*, because a formal description of the species was not published.

Because insufficient biological data supported separation of the *D. frontalis* and caribbean pine beetle into two species, Sullivan et al. (2012) and Armendáriz-Toledano et al. (2014a) carried out studies to clarify the taxonomic status of this bark beetle using crossing experiments as well as biochemical, morphological, karyological, and molecular data. These studies consistently supported the separation of these species. Therefore, in this paper we describe *Dendroctonus mesoamericanus* sp. nov., which corresponds to "*D. frontalis* morphotype B" from Sullivan et al. (2012) and Armendáriz-Toledano et al. (2014a), and to caribbean pine beetle from Midtgaard and Thunes (2002).

Materials and Methods

Specimens. A total of 289 adult *Dendroctonus* sp. nov. were examined from 40 collection sites (Table 1). Specimens reported by Armendáriz Toledano et al. (2014a) corresponding to *Dendroctonus* sp. nov. (i.e., *D. frontalis* morphotype B) were included in the analyses. Additionally, adult specimens of *Dendroctonus* sp. nov. were collected by the authors from naturally infested *Pinus sp*. or graciously loaned by the following institutions: Comisión Forestal del Estado de Michoacán, Morelia, Michoacán; El Colegio de la Frontera Sur, Tapachula, Chiapas (ECOSUR); Laboratorio de Variación Biológica y Evolución, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México; Colección Científica de Entomología Forestal, División de Ciencias Forestales, Universidad Autónoma Chapingo (UACH), Estado de México; United States Forest Service, Southern Research Station, Pineville, LA.

Morphology. Sex of specimens was determined by a combination of dimorphic characters: the size and abundance of large tubercles on the fronts; the stridulatory apparatus in males, and genitalia (Lyon 1958, Mendoza-Correa and Zúñiga 1991). Species identification of specimens within the *D. frontalis* complex was performed using the key of Lanier et al. (1988). Specimens of *Dendroctonus* sp. nov. were distinguished by means of diagnostic characters reported by Armendáriz-Toledano et al. (2014a) for *D. frontalis* morphotype B, i.e., the presence of striations on preepisternal area (PEA), the irregular size of ornamentations of the plates of the eighth tergite of females (AP), and the shape of seminal rod (SSR) (Armendáriz et al. 2014a, Fig. 1).

External morphology of adults was exhaustively examined and photographed with a NIKON SMZ800 dissecting microscope and a Nikon DXM1200F digital camera. Body measurements were taken with this same microscope with a micrometer eye piece (at 20–63×). For some photos of the holotype and paratype 2 (Fig. 1), images were recorded at successive focal depths and automatically combined into a single sharp image (i.e., focus stacking) using CombineZM software (Hadley 2008). Morphological details of some specimens were photographed with an environmental scanning electron microscope ESEM (Evo 40 VP, Zeiss, Jena, Germany).

The elytra and genitalia from 100 specimens of both sexes were removed. These structures were cleared by incubating them at 50°C in 10% KOH for 120–180 min for elytra and for 10–15 min for male and female genitalia. After incubation, structures were immersed in 20% acetic acid solution to neutralize the KOH and subsequently rinsed with 100% ethanol. For both males and females, the elytra were cut into two parts (elytral disc and declivity) and then mounted on the same slide. The eighth abdominal tergite and spermatheca from individual females were mounted in the same slide, and the seminal rod and genital capsule of individual males were separated and mounted in the same slide.

All structures were mounted semipermanently in glycerol and observed at 100–400× with phase contrast microscopy. Elements of elytral sculpture (punctures, granules, crenulations) were measured and quantified with a phase contrast microscope with an ocular micrometer (400×). Photographs of male and female genitalia were taken with a Nikon DXM1200F digital camera mounted in a phase contrast microscope. Morphological details of genitalia were photographed with an ESEM (Evo 40 VP, Zeiss).

From the entire series ($n = 289$), 98 specimens from 26 geographic localities were selected to constitute the type series (Table 1). In the type series, six specimens used by Armendáriz-Toledano et al. (2014a) in the karyological analysis were included. The genitalia of the holotype, allotype, and 18 paratypes were extracted, photographed, and preserved in a glycerol-filled microvial affixed to the same pin as the respective specimen. Holotype was indicated with H1 label; allotype was indicated with A1 label; and individual paratypes were designated from P1 to P96.

Dendroctonus mesoamericanus Armendáriz-Toledano & Sullivan, new species

(Figs. 1–3)

Type Material. HOLOTYPE: male, Mexico, Chiapas, La Trinitaria, Parque Nacional Lagunas de

Table 1. Key, country, locality, coordinates, and host of the populations of *Dendroctonus mesoamericanus* sp. nov

C	Key	Localitie	Latitude N	Longitude W	Altitude (m)	Host
Mexico	MTO	Michoacán, Tancitaro, Ojo de Agua de los Sauces	19° 14′00″	102° 17′00″	1803	?
	MVB	Michoacán, Villa Madero, Balcones[a]	19° 15′0″	101° 1′48″	1813	*Pinus pringlei*
	MCV	Michoacán, Chinicuila, El Volantin[a]	18° 38′24″	103° 21′52″	1180	?
	OSM	Oaxaca, Santa María Albarradas, San Pablo Villa de Mitla	16° 59′33″	96° 11′15″	2106	*P. pringlei*
	OSY	Oaxaca, Santiago Yosondua, Santa Catarina Cuanana, Paraje la Guacamaya[a]	16° 48′49″	97° 24′55″	2142	*P. oocarpa*
	OHT	Oaxaca, Heroica Cd. de Tlaxiaco, Paraje Cerro Negro	17° 20′23″	97° 45′36″	2454	*P. ocarpa* & *P. pringleii*
	OPZ	Oaxaca, San Pedro Ayutla, Zacatepec Distrito Mixe	17° 07′12″	96° 44′56″	1770	*P. pringlei*
	CJM	Chiapas, Jitotol de Zaragoza, Ejido Las Maravillas[a]	17° 05′48″	92° 53′28″	1677	?
	CTT	Chiapas, Teopisca, Area Forestal de Teopisca[a]	16° 34′25″	92° 27′30″	2321	?
	CTC	Chiapas, Teopisca, Bienes Comunales de Teopisca[a]	16° 30′30″	92° 29′15″	1809	?
	CBS	Chiapas, Reserva de la Biosfera la Sepultura	16° 25′00″	93° 20′00″	598	?
	CCC	Chiapas, Comitan, Predio Santa Cruz[a]	16° 12′47″	92° 14′00″	1347	*P. oocarpa*
	CTP	Chiapas, La Trinitaria, PNLM[b]	16° 08′42″	91° 43′29″	1557	*P. oocarpa* & *P.maximinoi*
	CTPI	Chiapas, La Trinitaria, PNLM[a]	16° 06′45″	91° 43′56″	1497	*P.maximinoi*
Belize	BMP1	Cayo, Mountain pine ridge[a]	17° 1′	88° 18′	?	*P.caribaea*
	BMP2	Cayo, Mountain pine ridge[a]	16° 59′	88° 49′	901	*P. oocarpa*
	BMP	Cayo, Mountain pine ridge	16° 59′	88° 46′	928	?
	BMP3	Cayo, Mountain pine ridge[a]	17° 00′	88° 51′	857	*P. oocarpa*
Guatemala	GHC	Huehuetenango, Canselaj	15° 16′10″	91° 25′53″	2065	*P. oocarpa*
	GHM	Huehuetenango, Malacatacinto, Cacum	15° 15′09″	91° 42′03″	2067	*P. montezumae*
	GQQ	El Quiché, Santa Cruz del Quiché, Chinique de las Flores[a]	15° 1′	91° 8′	2024	*P. montezumae*
	GQS	Quetzaltenango, San Carlos Sija, Estancia de la Virgen[a]	14° 59′8″	91° 30′29″	2612	*P. oocarpa*
	GST	Sololá, Colonia Maria Tecun	14° 48′50″	91° 12′20″	2409	*P. oocarpa*
	GMC	Mixco, Club Campestre Alta montaña[a]	14° 47′9″	90° 55′22″	2410	*P. maximinoi*
	GCT	Chimaltenango, Tecpan, Carretera Interaméricana 13 km	14° 45′50″	90° 59′14″	2288	*P. maximinoi*
	GSS	Sololá, Finca Socorro	14° 45′10″	91° 08′20″	1771	*P.pseudostrobus*
	GSC	Sololá, Finca Chuchiya	14° 44′00″	91° 07′50″	2022	*P.pseudostrobus*
	GM	Guatemala, Mixco[a]	14° 38′0″	90°36′0″	1660	*P. maximinoii* & *P. oocarpa*
	GMS	Guatemala, Mixco, San Cristobal[a]	14° 36′14″	90° 35′40″	1582	*P. pseudostrobus*
Honduras	HYY	Yoro, Yorito, Luquigüe[a]	14° 59′00″	87° 36′00″	311	?
	HGA	Guaimaca	14° 32′08″	86° 49′00″	862	*P. oocarpa*
	HCS	Comayagua, Sihuatepeque[a]	14° 31′49″	87° 32′13″	1717	*P.oocarpa*
	HT	Distrito Central, Tegucigalpa[a]	14° 8′52″	87° 10′21″	1168	*P. oocarpa*
	HMT	Francisco Morazán, Tatumbla[a]	14° 0′58″	87° 6′16″	1374	*P. oocarpa*
ES	SSC	San Salvador, El Carmen[a]	13° 45′0″	89° 12′0″	561	*P. caribaea*
Nicaragua	NJP	Jalapa	13° 55′1″	86° 07′38″	697	*P. caribaea*
	NSF	Nueva Segovia, San Fernando[a]	13° 40′38″	86° 18′55″	734	*P. oocarpa*
	NMZ	Madriz, Somoto[a]	13° 25′14″	86° 34′49″	1366	*P.oocarpa*
	NEE	Esteli, Esteli[a]	13° 12′00″	86° 18′00″	1290	*P. oocarpa*
	NPT	El Picacho, Cerro Tomabu	13° 02′00″	86° 18′00″	1238	*P. oocarpa*

C, country; ES, El Salvador; PNLM, Parque Nacional Lagunas de Montebello.
[a] Localities included in the type series.
[b] Type locality.

Montebello (CTP), 16° 08′42″ N, 91° 43′29″ W, 1800 m, 20-October-2011, on *Pinus maximinoi* H. E. Moore, A. Niño (A. N.) and F. Armendáriz-Toledano (F. A. T.) coll., in the Colección Nacional de Insectos del Instituto de Biología, Universidad Nacional Autónoma de México (CNIN).

ALLOTYPE: female from type locality; same coordinates, elevation, date, host, collectors, in CNIN.

PARATYPES: 96; 40 (P1-P40), type locality (CTP), (4♀, 3♂) 16° 08′42″ N, 91° 43′29″ W, 1587 m, 9-IX-2009, (15♀, 19♂) 16° 06′45″ N, 91° 43′56″ W, 1494 m, 20-X-2011, on *P. maximinoi*, A. N. and F. A. T. coll.; **nine** (P41-P49) (5♀, 4♂), Guatemala, Chimaltenango, Misco, Club Campestre de Alta Montaña (GMC), 14° 47′9″ N, 90° 55′22″ W, 2410 m, 26-VI-2011, on *P. maximinoi*, A. N. and F. A. T. coll.; **two** (P50-P51) (♂), Mexico, Chiapas, Teopisca, Area Forestal de Teopisca (CTT), 16° 34′25″ N, 92° 27′30″ W, 2321 m, 5-XI-2003, on ex *Pinus*, trapped J. Macías coll.; **two** (P52-P53) (♀), Mexico, Chiapas, Comitán, Predio Santa Cruz (CCC), 16° 12′47″ N, 92° 14′00″ W, 1801 m, 5-XII-2003, on *P. oocarpa* Schiede ex Schlechtendal, C. A. Gallegos coll.; **four** (P54-P57) (2♀, 2♂), Mexico Chiapas, Jitotol de Zaragoza, Ejido las Maravillas (CJM), 17° 05′48″ N, 92° 53′28″ W, 1677 m, 5-X-2005, trapped J. Macías coll.; **two** (P58-P59) (♂), Mexico, Oaxaca, Santiago Yosondua, Santa Catarina Cuanana, Paraje la Guacamaya (OSY), 16° 48′49″ N, 97° 24′55″ W, 2142 m, 2005, on *P. oocarpa*, J. Cruz coll.; **four** (P60-P63) (2♀, 2♂), Mexico, Michoacán, Chinicuila, El Volantin (MCV), 18° 38′24″ N, 103° 21′52″ W, 1180 m, 14-XI-2005, Comisión Forestal del Estado de Michoacán; **one** (P64) (♂), Mexico, Michoacán, Villa Madero, Balcones (MVB), 19° 15′0″ N, 101°

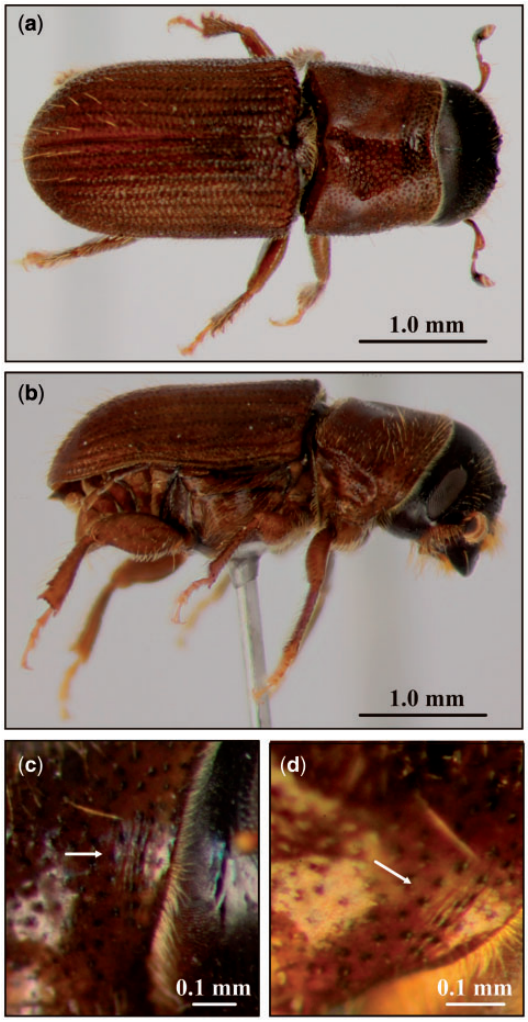

Fig. 1. *Dendroctonus mesoamericanus* sp. nov., male adult. Holotype, dorsal view (a), lateral view (b), preepisternal area (c); paratype one, preepisternal area (d). The arrows indicate the striations on preepisternal area.

1′48″ W, 1813 m, 14-XI-2009, on *P. pringlei* G.R. Shaw ex Sargent, Comisión Forestal del Estado de Michoacán coll.; **two** (P65-P66) (♂), Mexico, Chiapas, Teopisca, Bienes comunales de Teopisca (CTC), 16° 30′30″ N, 92° 29′15″ W, 1809 m, 2003, on ex *Pinus*, trapped J. Macías coll.; **six,** Belize, Cayo, Mountain Pine Ridge (BMP1-3): (P67-P68) (1♀, 1♂) 17° 1′ N, 88° 18′ W, 9-VII-2013, on *P. caribaea* Morelet, B. T. Sullivan coll., (P69-P70) (1♀, 1♂) 16° 59′ N, 88° 49′ W, 901 m, 14-VII-2009, on *P. oocarpa*, S. R. Clarke coll., (P71-P72) (1♀, 1♂) 17° 00′ N, 88° 51′ W, 857 m, 16-VII-2009, on *P. oocarpa*, S. R. Clarke coll,; **two** (P73-P74) (1♀, 1♂), Guatemala, El Quiché, Santa Cruz del Quiché, Chinique de las Flores (GQQ), 15° 1′ N, 91° 8′ W, 2224 m, 4-VII-2013, on *P. montezumae* Lambert, P. Ortiz coll.; **two** (P74-P75) (1♀, 1♂), Guatemala, Quetzaltenango, San Carlos Sija, Estancia de la Virgen (GQS), 14° 59′8″ N, 91° 30′29″ W, 2612 m, 7-III-2007, *P. oocarpa*, P. Ortiz coll.; **two** (P77-P78) (1♀, 1♂), Guatemala, Mixco (GM), 14° 38′ N, 90° 36′ W, 1660 m, *P. maximinoi* and *P. oocarpa*, 25-I-2013, P. Ortiz coll.; **two** (P79-P80) (1♀, 1♂), Guatemala, Mixco, San Cristóbal (GMS), 14° 36′14″ N, 90° 35′40″ W, 1582 m, 23-IV-2013, on *P. pseudostrobus* Lindley, P. Ortiz coll.; **two** (P81-P82) (1♀, 1♂), Honduras, Yoro, Yorito, Luquigüe (HYY), 14° 59′00″ N, 87° 36′00″ W, 311 m, 31-V-2007, R. F. Billings coll.; **two** (P83-P84) (1♀, 1♂), Honduras, Comayagua, Sihuatepeque (HCS), 14° 31′49″ N, 87° 32′13″ W, 1717 m, 9-XI-2011, on *P. oocarpa*, R. F. Billings coll.; **two** (P85-P86) (1♀, 1♂), Honduras Distrito Central, Tegucigalpa (HT), 14° 8′52″ N, 87° 10′21″ W, 1168 m, 10-VIII-2011, on *P. oocarpa*, R. F. Billings coll.; **two** (P87-P88) (1♀, 1♂), Honduras, Francisco Morazán, Tatumbla (HMT) 14° 0′58″ N, 87° 6′16″ W, 1374 m, 8-VIII-2011, on *P. oocarpa*, R. F. Billings coll.; **two** (P89-P90) (1♀, 1♂), El Salvador, San Salvador, El Carmen (SCC), 13° 45′ N, 89° 12′ W, 561 m, 22-XI-2003, on *P. caribaea*, R. F. Billings coll.; **two** (P91-P92) (1♀, 1♂), Nicaragua, Nueva Segovia, San Fernando (NSF), 13° 40′38″ N, 86° 18′55″ W, 734 m, 12-III-2010, on *P. oocarpa*, R. F. Billings coll.; **two** (P93-P94) (1♀, 1♂), Nicaragua, Madriz, Somoto (NMZ), 13° 25′14″ N, 86° 34′49″ W, 1366 m, 13-III-2010, on *P. oocarpa*, R. F. Billings coll.; **two** (P95-P96) (1♀, 1♂), Nicaragua, Esteli, Esteli (NEE) 13° 12′ N, 86° 18′ W, 4-XII-13, on *P. oocarpa*, R. Billings coll.

Thirty-five paratypes were deposited in CNIN, México (P1-P7, P41- P44, P50, P52, P54-P55, P58, P60-P61, P64, P66, P68, P70, P72, P74, P76, P78, P80, P82, P84, P86, P88, P90, P92, P94, P96), 22 paratypes in the Museo de Historia Natural de la Ciudad y Cultura Ambiental, México (P18-P28, P45, P46, P49, P56, P62, P67, P73, P79, P85, P91, P95), 20 paratypes are in the Smithsonian National Museum of Natural History (P13-P17, P29-P34, P47, P51, P57, P63, P69, P75, P81, P87, P93), and 19 in the American Museum of Natural History (P8-P12, P35-P40, P48, P53, P59, P65, P71, P77, P83, P89).

Diagnosis. *Dendroctonus mesoamericanus* sp. nov. is distinguished from closely related species *D. frontalis* Zimmermann, *D. mexicanus* Hopkins, and *D. vitei* Wood by the presence of striations on the preepisternal area in both sexes running parallel to the anterior margin of the prothorax (Figs. 1c, d and 2j, k, m) which are absent in the other three species. It is also distinguished by the seminal rod, which has an approximately triangular-shaped, laterally compressed dorsal process with a nearly straight posterior margin in lateral view (i.e., arching inward or outward by less than approximately 15% of the length of the posterior margin; Figs. 2s and 3a, b). In *D. frontalis* the seminal rod in lateral view has a hemicircular or lobed dorsal process with a distinctly convex posterior margin; in *D. mexicanus* and *D. vitei* the dorsal process has a strongly concave posterior margin in lateral view and is not compressed laterally (Vité et al. 1975, Figs. 4–6; Armendáriz-Toledano et al. 2014a, Fig. 5a). In *D. mesoamericanus* females the squamiform plates

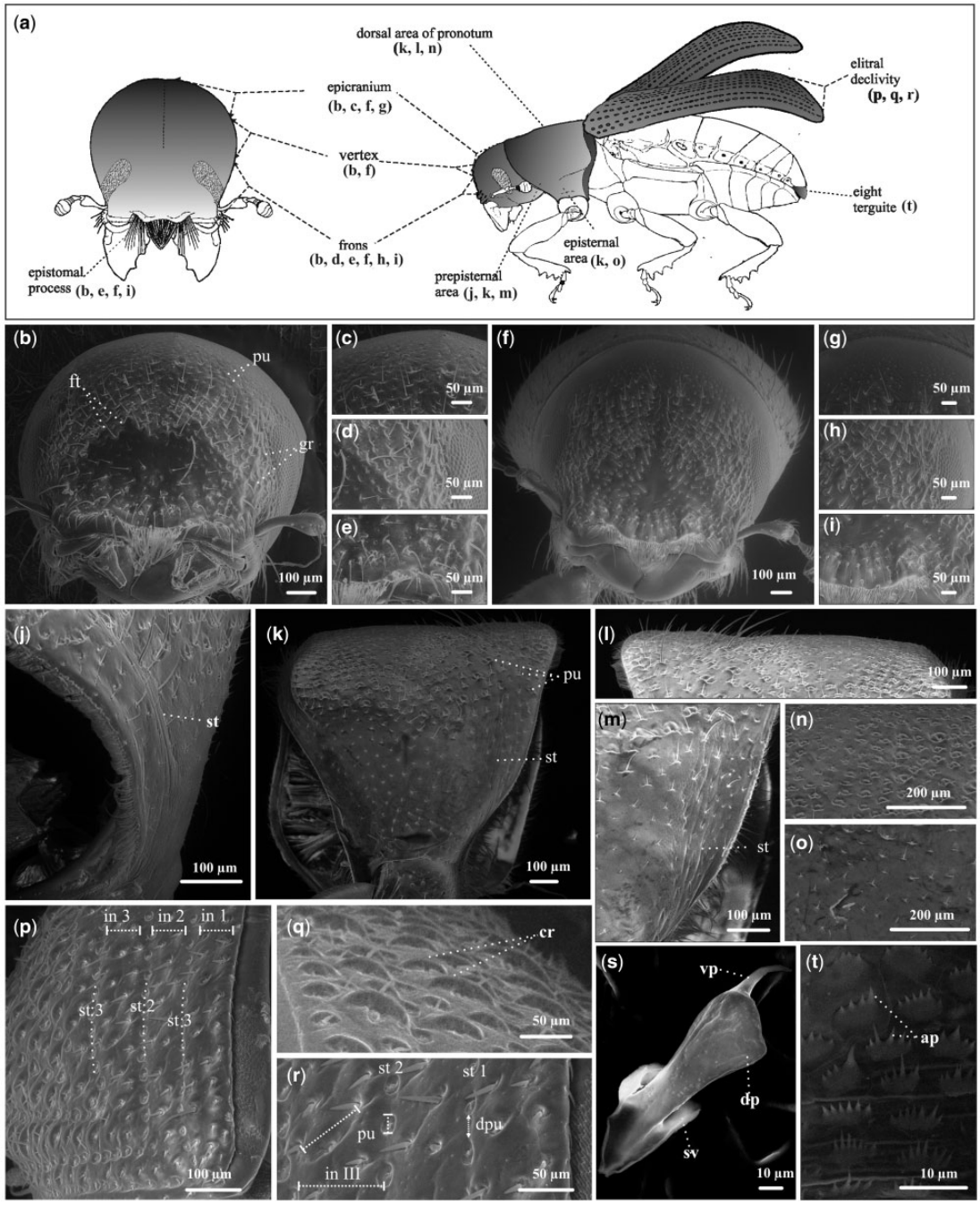

Fig. 2. *Dendroctonus mesoamericanus* sp. nov., adult. general anatomy (a), male head (b), male epicranial surface (c), male front surface (d), male epistomal process surface (e), female head (f), female epicranial surface (g), female front surface (h), female epistomal process surface (i), anterior view of preepisternal area (j), lateral surface of pronotum (k), dorsal surface of pronotum (l), preepisternal area (m), lateral posterior surface of pronotum (n), episternal surface (o), elytral declivity (p), three first interspaces on the distal area of elytral disc (q, r), lateral-dorsal view of seminal rod (s), plates on eight tergite in females (t). ap, acute projections; cr, crenulations; dp, dorsal projection; dpu, distance between punctures; ft, frontal tubercles; gr, granules; in 1, interspace one; in 2, interspace two; in 3, interspace three; pu, punctures; st, striations on preepisternal area; st 1, striae one; st 2, striae two; st 3, striae three; vp, ventral process. The letters in (a) indicate the figures in which the morphological structure is showed.

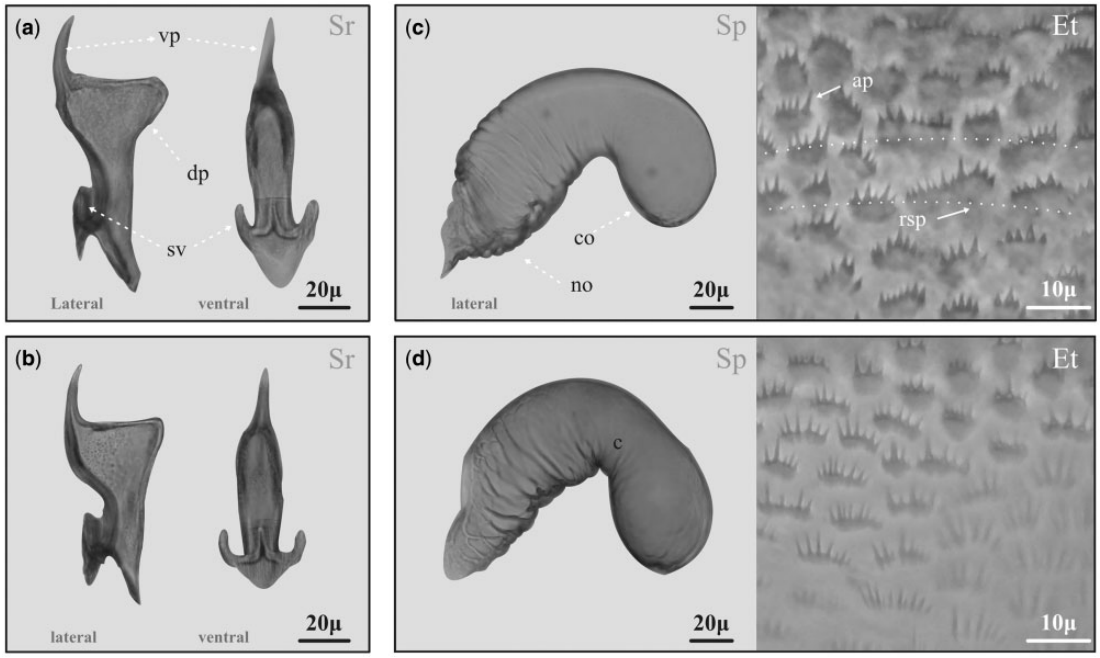

Fig. 3. *Dendroctonus mesoamericanus* sp. nov., genital organs. Male, seminal rod (Sr) in dorsal and lateral view: holotype (a), paratype one (b); female, spermatheca (Sp) and eight tergite (et): allotype (c), paratype six (d). ap, acute projections; co, cornu; dp, dorsal process; no, nodulus; rsp, ridges of squamiform plates; sv, seminal valve; vp, ventral process.

of the eighth tergite possess ornamentations along their distal edge of highly variable size (Figs. 2t and 3c, d) whereas in *D. frontalis* these ornamentations are uniformly short. In addition, females of *D. mexicanus* and *D. frontalis* can be readily distinguished from those of *D. mesoamericanus* sp. nov. by the inconspicuous pronotal callus in the latter (Fig. 1c, f in Sullivan et al. 2012). Further, it can be distinguished from its sister species *D. frontalis* by male meiotic formula 5AA+Xy_p (Fig. 6 in Armendáriz-Toledano et al. 2014a).

Holotype Male (Fig. 1a, b, c). Total length 4.1 mm (2.7–4.9 mm; $N = 50$); 2.7 times longer than wide; head, pronotum and elytra medium brown to black, with head darker than pronotum and pronotum darker than elytra.

Head. Length of head 0.7 mm, surface of epicranium and vertex covered with small punctures (Fig. 2b, c), vertex and frons truncated convex or completely convex (in lateral view). Frons armed by a pair of transverse elevations surrounded by eight prominent tubercles (paratypes 4–8 tubercles; $N = 50$) and granules just below upper level of eyes (Fig. 2b), length of highest frontal tubercles 0.04 mm (0.015–0.06 mm; $N = 50$); frontal tubercles separated by a median groove extending from just above epistomal process to upper level of eyes (Fig. 2b); surface of median groove is principally shining and smooth (some specimens with small granules between frontal transverse elevations); surface between eyes with punctures and granules distributed around median grove (Fig. 2b, d), punctures are less impressed in upper and lateral areas of epistomal process (Fig 2b, e); area immediately above epistomal process flat (some specimens flat or slightly concave), shining, finely granulate and with sparse small punctures (some specimens with or without punctures; Fig. 2b, e). Width of epistomal process 0.58 mm (0.33–0.75 mm; $N = 50$), 2/3 of distance between eyes (0.9 mm; 0.6–1.0 mm; $N = 50$), arms of epistomal process thick, elevated and oblique approximately 26° from horizontal (Fig. 2b, e), transverse midsection of the epistomal process absence or weak, separating the prominent arms by a space equal or larger than the length of the one arm, surface smooth and shining with small punctures, underside with a dense brush of conspicuous yellowish setae; pubescence of head yellowish, of three different sizes, sparse, distributed around frons, and less abundant on area immediately above epistomal process (Figs. 1b and 2b, d), shortest setae distributed on vertex; those of medium size on vertex and frons, and largest setae surrounding epistomal process.

Pronotum. Length 0.92 mm (0.64–1.3 mm; $N = 50$), width 1.5 mm (0.8–1.7 mm; $N = 50$), widest on posterior third, anterior region slightly constricted; dorsal surface with rather coarse, moderately deep, close punctures, and interspaces smooth and shiny (Figs. 1a and 2k, l, n). Punctures largest on anterior dorsal area, whereas those on preepisternal and episternal areas (lateral surfaces on anterolateral pronotum) shallower, less abundant, and reduced in diameter (Fig. 2o); surface of preepisternal area with a zone of striations running parallel to anterior margin of pronotum (Figs. 1c, d and 2j, k, m); pubescence yellowish; longer and more sparse on dorsal posterior area (Figs. 1b and 2l),

pubescence of preepisternal and episternal areas shorter and less abundant than dorsal area (Fig. 2k, m, o).

Elytra. Length 2.4 mm (1.6–2.7 mm; $N = 50$), 1.5 times longer than wide, 2.6 times longer than pronotum, sides straight on basal two-thirds, rather broadly rounded behind (Fig. 1a); declivity convex with striae weakly impressed (Fig. 2p); punctures of striations with a diameter ranging from 16 to 28 µm (Fig. 2p, r), surface between punctures smooth with a distance between punctures of 10 to 31 µm ($N = 15$); diameter of punctures roughly averaging size of interspaces (Fig. 2p); declivital interstria (measured at midinterstria) 2 narrower ($\overline{X} = 72$ µm; $N = 15$) than 1 ($\overline{X} = 93$ µm; $N = 15$) and 3 ($\overline{X} = 100$ µm; $N = 15$); declivital interstria 2 not constricted apically (mildly constricted or not; Fig. 2p); surface of interstriae with slightly marked rugae, punctures, and crenulations. Punctures on declivital interstriae less well defined, with some slightly larger than those of striae; average diameter of strial punctures 1.1 times diameter of punctures on interstriae (Fig. 2p, r); crenulations in interstriae of variable size, more defined and abundant toward anterior part (Fig. 2q); average width of crenulations on proximal area of elytral declivity 0.5 times width of interspaces. Setae in interstriae 1–3 of declivity originating from center of punctures; more than one size class setae, shortest about one-third length of longest, and longer ones show a gradual progression of sizes; color yellow to amber in mounted specimens (Fig. 1b).

Genitalia. Composed of four sclerotized structures: tegmen, spicule, penis, and accessory apparatus (seminal rod and anchor). General anatomy of tegmen, spicule, and penis similar to *Dendroctonus ponderosae* Hopkins (= *D. monticolae* Hopkins) (Cerezke 1964).

Anchor consisting of a tubular bag supported by two anchor branches and located within penis. Seminal rod consisting of a sclerotized structure connected to ejaculatory duct and situated within anchor. Proximal region of seminal rod consisting of a seminal valve, with distal portion divided into dorsal and ventral processes (Figs. 2s and 3a,b). Ventral process consisting of an acute, spine-shaped projection forming an approximately 90° angle with posterior margin of dorsal process. Dorsal process consisting of a laterally compressed, broadly triangularly shaped projection with ventral process forming a continuation of ventral side of triangle (Figs. 2s and 3a,b). Ventral process extends further from seminal valve (i.e., more distally) than dorsal process; dorsal process somewhat narrower than dorsal process in ventral view; and posterior margin of ventral process varies only slightly from straight in lateral view (Fig. 3a, b).

Allotype Female. Total length 4.2 mm (2.2–4.6 mm; $N = 48$); 2.8 times longer than wide; body color similar to male.

Head. Length 0.6 mm; surface of epicranium and vertex covered with small punctures (Fig. 2f, g) less abundant and smaller than in male; shape of vertex and frons in lateral view similar to male. Frons with slight, transverse elevations covered with small granules, tubercles much less prominent than those on male (Fig. 2f); transverse elevations separated by a median groove extending from just above epistomal process to upper level of eyes (Fig. 2f); median groove weak varying from scarcely perceptible to distinct only occasionally stretching all the way from vertex to epistoma, mainly visible between elevations, surface of median groove shining and largely impunctate; punctures and granules distributed around of median grove less abundant and smaller than in male (Fig. 2f, h), distribution of punctures and granules between eyes is similar to males (Fig 2d, h); area immediately above epistomal process flat (some specimens concave), shining, less granulate and with more sparse and smaller punctures than in males (some specimens without punctures) (Fig. 2f, i); epistomal process (width 0.52 mm, 0.33–0.69 mm; $N = 48$) narrower than males, 3/4 the distance between eyes (0.7 mm; 0.48–0.97 mm; $N = 48$), arms of epistomal process elevated, oblique, and about 21° from horizontal (Fig. 2f, i), surface smooth and shining with punctures less abundant and smaller than in male; arms of the epistomal process continuous or nearly so (not clearly separated as in male); underside with a less dense brush of setae than in male, pubescence of head slightly more abundant (Fig. 2f, i, g).

Pronotum. Length 1.0 mm (0.7–1.2 mm; $N = 48$), width 1.5 mm (0.9–1.8 mm; $N = 48$), widest on posterior third, anterior region slightly constricted; pronotal constriction possessing a transverse callus that is visible but very inconspicuous both laterally and dorsally; vestiture and sculpture of pronotum similar to males.

Elytra. Length 2.5 mm (1.0–2.9 mm; $N = 48$), 1.6 times longer than wide, 2.3 times longer than pronotum; sides parallel on basal two-thirds, rather broadly rounded behind; declivity convex with striae weakly impressed; vestiture and sculpture of elytral declivity similar to males.

Eighth Tergite. Structure characterized by an oval distal edge and two oval proximal lateral edges converging on an anterior median line. Distal surface of tergite is covered by abundant setae of two different sizes. Length of large setae 0.12 times width of tergite and two times longer and wider than small setae. Eighth tergite displays 18 parallel lines of squamiform plates of sclerotized cuticle (13–22; $N = 20$; Fig. 3c, d). Lines better defined in anterior area and fade in posterior area. Squamiform plates possess acute distal projections of variable size (Figs. 2t and 3c, d).

Spermatheca. Reniform and divided into two parts, nodulus and cornu. Nodulus transversely covered by 18 striae (10–23) becoming confused in proximal region of nodulus. Cornu is longer than width of middle constriction, displaying an oval shape in lateral view (Fig. 3c, d).

Variation. Despite wide morphological variation of *D. mesoamericanus*, this species has characters in addition to those in the diagnosis, which produce good (but less reliable) discrimination from sibling species. These include body measurements, sculpture of elytral declivity and female terminalia.

Body proportions can be used for discrimination between *D. mesoamericanus* sp. nov. and *D. frontalis*

when long series are available. Numerous body measurements are on average greater in *D. mesoamericanus*: epistomal process width (EPW $0.51 \pm SE_{\bar{X}}$ 0.01 mm), distance between eyes (DE 0.83 ± 0.1 mm; $N = 289$), eye width (WE 0.24 ± 0.003 mm; $N = 289$), width of pronotum at widest point (PW 1.39 ± 0.03 mm; $N = 289$), pronotum length (PL 0.97 ± 0.014 mm; $N = 289$), and elytral length (EL 2.26 ± 0.07 mm; $N = 289$); in contrast, these measurements in *D. frontalis* are: EPW 0.38 ± 0.05 mm; $N = 289$, DE—0.67 ± 0.006 mm; $N = 289$, WE—0.2 ± 0.001 mm; $N = 289$, PW—1.18 ± 0.01 mm; $N = 289$, PL—0.81 ± 0.01 mm; $N = 289$, EL—2.0 ± 0.01 mm; $N = 289$. Of these, epistomal process and eye width have the lowest overlap in $SE_{\bar{X}}$ between species, and consequently size of these features are better characters than other external measurements for separating these two species by size (EPW and WE are 30% and 20% respectively larger in *D. mesoamericanus* sp. nov.). Frontal tubercles are relatively more prominent in male *D. frontalis* than in male *D. mesoamericanus* sp. nov.

Strial punctures of the elytral declivity of *D. mesoamericanus* sp. nov. are larger (diameter, $D = 17.2 \pm 1.2$ µm; $N = 40$) and more sparse (distance between punctures $D_{BP} = 26.4 \pm 1.1$ µm; $N = 40$) than in *D. frontalis* ($D = 15.0 \pm 0.5$ µm; $N = 40$, $D_{BP} = 18.7 \pm 0.6$ µm; $N = 40$). In some specimens the number of granules (G) and punctures (P) on the interstriae 3 of the elytral declivity is apparently greater in *D. frontalis* ($G = 26.7 \pm 4.2$; $N = 100$, $P = 14.7 \pm 1.7$; $N = 100$) than *D. mesoamerianus* sp. nov. ($G = 21.3 \pm 2.0$; $N = 100$, $P = 12 \pm 2.0$; $N = 100$). Because the variation in the number and size of these structures is wide in both species, these characters are not recommended for identification.

The eighth tergite in *D. mesoamericanus* sp. nov. has on average a greater number of rows of squamiform plates than *D. frontalis* (18 vs. 16, respectively). The spermatheca of *Dendroctonus mesoamericanus* sp. nov. has the edge of the cornu ovate, striations covering more than half of the spermatheca body, and conglomerate striations in the proximal region of nodulus. The spematheca of *D. frontalis* females tend to has the edge of the cornu round, striations covering one fourth of the spermatheca body, and a nodulus with conglomerate striations in the proximal region.

Although the seminal rod shape varies intraspecifically associated to the evagination of the posterior margin of the dorsal process and in the relative size of ventral process (Fig. 4), this structure can be used reliably for discriminating *D. mesoamericanus* sp. nov. and *D. frontalis*. In *D. mesoamericanus* sp. nov., the posterior margin of the dorsal process is either straight (Fig. 3a, b) or slightly convex or concave (e.g., Fig. 4, populations MTO, OHG, GMS, NPT). Additionally the ventral process is invariably longer than the dorsal one (see Fig. 1a in Armendariz-Toledano et al., 2014b), in all specimens. In contrast *D. frontalis* has a dorsal process that is strongly convex and is equal to or greater than ventral process in length (Fig. 5. in Armendáriz-Toledano et al. 2014a). The overall shape of the dorsal process in *D. frontalis* is semicircular or bulbous whereas in *D. mesoamericanus* sp. nov. it is broadly triangular.

Distribution. The type locality is the Parque Nacional Lagunas de Montebello, La Trinitaria, Chiapas, Mexico, which is part of the Sierra de Chiapas. The climate of this region is temperate and humid with rain all seasons, and the dominant vegetation is mixed pine-oak and sweetgum (Comisión Nacional de Áreas Naturales Protegidas [CONANP] 2007). Six pine species are present in this locality: *Pinus caribeae*, *P. leiophylla*, *P. maximinoi*, *P. montezumae*, *P. oocarpa*, *P. pseudostrobus*, and *P. tenuifolia* (= *P. maximinoi*) (González-Espinosa et al. 1997); however, *Dendroctonus mesoamericanus* has been recorded in this area only in *P. maximinoi* and *P. oocarpa*.

Identifications based on seminal rod shape, the presence of striations on the preepisternal area, and identification based on DNA sequencing indicate that *D. mesoamericanus* occurs within Nicaragua, Guatemala, El Salvador, Honduras, Belize, and states of Chiapas, Oaxaca, and Michoacán in Mexico. Within this geographical area, the distribution of this species appears to be entirely sympatric with *D. frontalis*.

Biology. *Dendroctonus mesoamericanus* has been observed at elevations above 311 m on *P. caribaea*, *P. devoniana*, *P. hartwegii* (= *P. rudis*), *P. oocarpa*, *P. maximinoi*, *P. montezumae*, *P. pringlei*, and *P. pseudostrobus*. Generally this species has been encountered infesting hosts simultaneously with *D. frontalis* (i.e., occurring in syntopy). In this situation, *D. mesoamericanus* colonizes primarily the bottom 1–3 meters of the stem whereas *D. frontalis* is concentrated in the mid- to upper-bole. However, there is extensive spatial overlap by these species in the bark, and *D. mesoamericanus* brood have been reared in at least small numbers from the entire length of the bole as well as the crown of co-infested trees (Moreno 2008). Midtgaard and Thunes (2002) likewise observed that this species can colonize the entire bole. All brood stages appear to be present at any time of year (as with *D. frontalis*).

The aggressiveness of *D. mesoamericanus* and its regional importance as a killer of pines has not been adequately established. Midtgaard and Thunes (2002) reported this species to be the major mortality agent during the catastrophic *Dendroctonus* outbreak in Belize in 2000–2002. However, we have only occasionally observed *D. mesoamericanus* initiating attacks on apparently vigorous trees in the absence of other bark beetle species. Furthermore, its habit of colonizing predominantly the basal portions of host trees coinfested with another species is a behavior typical for secondary (i.e., relatively less aggressive) bark beetles (Wood 1982). In trees colonized by both *D. frontalis* and *D. mesoamericanus*, the authors have always observed the former species greatly outnumbering the latter. *D. mesoamericanus* has not been observed infesting downed trees.

Pitch tubes of *D. mesoamericanus* are conspicuously larger than those of *D. frontalis*. Parent galleries are S-shaped, frequently intercross, and cannot be readily distinguished from those of *D. frontalis* (as displayed in Wood 1982, Fig. 60G). As with *D. frontalis*, larvae

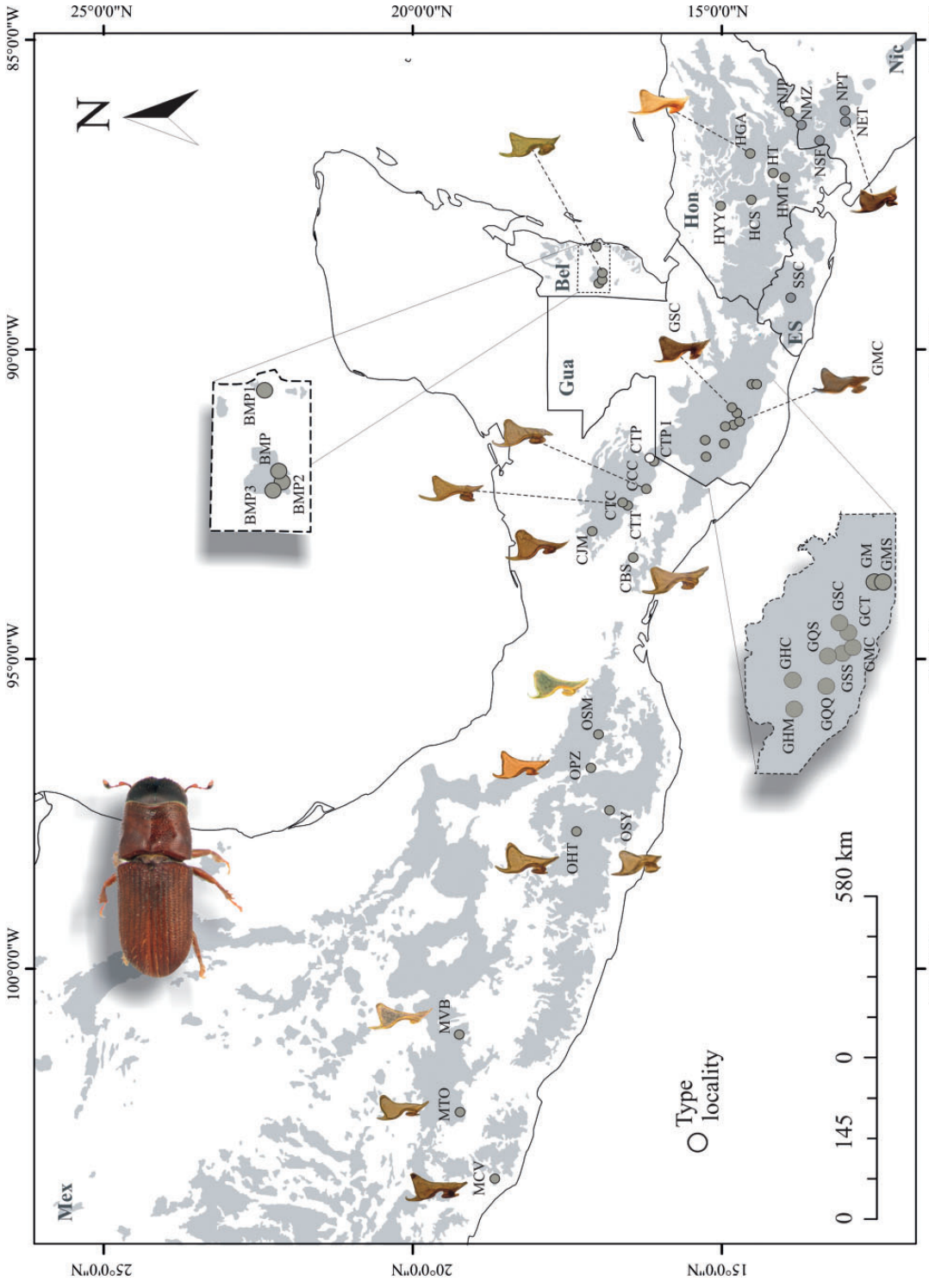

Fig. 4. Geographical distribution of *Dendroctonus mesoamericanus* sp. nov. The Keys of localities are showed in Table 1. Bel, Belize; ES, El Salvador; Gua, Guatemala; Hon, Honduras; Mex, Mexico; Nic, Nicaragua.

mine within the inner bark roughly perpendicularly to the parent gallery and form a progressively broadened, frass-filled feeding chamber typically one to a few centimeters distance from the parent gallery. Pupation occurs in the outer bark. Peak emergence of *D. mesoamericanus* from logs derived from coinfested trees occurs three to four weeks later than *D. frontalis*, although it is not known whether this is due to later attack by *D. mesoamericanus*, a longer development time for this species, or both factors.

D. mesoamericanus differs from other species in the *D. frontalis* complex in its pheromone and cuticular hydrocarbon compositions. A pheromone produced by *D. mesoamericanus* females strongly attracted conspecific males in a walking olfactometer while being largely unattractive to *D. frontalis* males (unpublished data). Additionally, synthetic trap lures that are highly attractive to flying *D. frontalis* catch very few *D. mesoamericanus* (Sullivan et al. 2012). Female *D. mesoamericanus* produce the combination of frontalin, *endo*-brevicomin, and ipsdienol (Sullivan et al. 2012), whereas this blend does not occurs in females of other species in the *D. frontalis* group that have so far been investigated (i.e., *D. adjunctus*, *D. brevicomis*, *D. frontalis*, and *D. vitei*; Renwick et al. 1975, Hughes et al. 1976, Byers et al. 1984). Additionally, the composition of the cuticular hydrocarbon blend of *D. mesoamericanus* differs significantly from that of *D. frontalis* (Sullivan 2012). In particular, the ratio of 5- to 9-methylheptacosane is a biochemical character that provides >99.9% reliable separation of *D. mesoamericanus* and *D. frontalis* specimens collected in Belize and Chiapas, Mexico.

Etymology. The specific epithet *mesoamericanus* is a substantive in genitive that refers to the geographic region called Mesoamerica. It is the region in the American continent that include the meridional region from Mexico, and the territories from Guatemala, El Salvador y Belize, the west of Honduras, Nicaragua, and a part of Costa Rica. This region was defined, delimited, and characterized by Kirchhoff (1943). This name was chosen for this species because all collections are in the central and southern region of Mesoamerica: Michoacán, Oaxaca, Chiapas, Guatemala, Belize, El Salvador, Honduras, and Nicaragua. The common name to propose for this species is Mesoamerican pine beetle (acronym MAPB).

Systematics and Affinities. The new species belongs to the *Dendroctonus frontalis* complex that includes *D. adjunctus*, *D. approximatus*, *D. brevicomis*, *D. frontalis*, *D. mexicanus*, and *D. vitei* (Lanier et al. 1988). The complex (Wood 1968, 1982), is characterized by a deep, narrow median groove on the frons of sexes; the frons at the level of the upper eyes protuberant and armed by tubercles (most noticeable in males) with the exception of *D. adjunctus* and a transverse elevated callus, inconspicuous, occurring laterally and dorsally on the anterior region of pronotum in females. These species, except *D. adjunctus*, were included in *Dendroctonus* species group I according to morphological, ecological, and biological characteristics (Wood 1963, 1982) or group VI based on the small chromosomal number that present these species within *Dendroctonus* genus, with karyotypes of six, seven, or eight pairs of chromosomes (Lanier 1981, Zúñiga et al. 2002).

Phylogenetic analysis of the *Dendroctonus frontalis* complex based on 786 base pairs of cytochrome oxidase I of mtDNA indicated that the species group of *D. mesoamericanus*, *D. frontalis*, *D. mexicanus*, and *D. vitei* is monophyletic, and further that *D. mesoamericanus* and *D. frontalis* are monophyletic within this species group (Fig. 7 in Armendáriz-Toledano et al. 2014a).

D. mesoamericanus and *D. frontalis* are sibling species (*sensu lato*) and share morphological similarities in male genitalia (Sullivan et al. 2012, Armendáriz-Toledano et al. 2014a). The seminal rod of these two species has a dorsal process that is laterally compressed and broadened in the sagittal plane (shape broadly triangular, hemicircular, or lobed) and an acute, spine-shaped ventral process (Fig. 5a, in Armendáriz-Toledano et al. 2014a). In contrast, *D. mexicanus* and *D. vitei* have a dorsal process that is broadened perpendicularly to the sagittal plane and has an invaginated posterior margin in lateral view (Vité 1975; Lanier et al. 1988; Armendáriz-Toledano et al. 2014 a,b). Geometric morphometric analyses of the seminal rods revealed quantitative differences among these four species (Armandáriz-Toledano et al. 2014a,b).

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