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Taxonomy and systematics

Phylogeny of the weevil genus *Megalostylus* (Coleoptera: Curculionidae: Entiminae), endemic to Mexico

Filogenia del género de gorgojos Megalostylus *(Coleoptera: Curculionidae: Entiminae), endémico de México*

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Abstract

The first phylogenetic analysis of the weevil genus *Megalostylus* endemic to Mexico (Entiminae, Naupactini) is presented, based on a data matrix of 37 morphological characters of adults and 21 terminal taxa. The ingroup comprises 9 species, 4 varieties, and 5 specimens of *Megalostylus* whose identification at the species level is doubtful. The outgroup includes species representing closely related genera: *Pantomorus albosignatus*, *Naupactus cervinus*, and *Megalostylodes hirsutus*. The objectives were to test the monophyly of *Megalostylus*, to explore its species relationships, and to determine which synapomorphies allow its identification and differentiation from other genera. The analysis yielded a single cladogram of 61 steps, showing the following phylogenetic sequence: (*Pantomorus albosignatus* (*Naupactus cervinus* (*Megalostylodes hirsutus* (*Megalostylus rhodopus* (*M.* morpho 2 (*M. macrophthalmus* (*M. tomentosus* (*M. dilaticollis* (*M. albicans* (*M. brevipilis, M. fusiformis* (*M. splendidus - M. sturmi*))))))))))). The results support the monophyly of *Megalostylus* based on the following synapomorphies: protibia with a prominence opposite to mucro, elytra almost flat, sternite VIII subrhomboidal very elongated, and aedeagus smooth. They also support its sister-group relationship with *Megalostylodes*.

Keywords: Systematics; Naupactini; Morphology; New species; New varieties; *Megalostylodes*

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Resumen

Presentamos el primer análisis filogenético del género de gorgojos *Megalostylus* endémico de México (Entiminae, Naupactini) basado en una matriz de datos de 37 caracteres morfológicos de adultos y 21 taxones terminales. El grupo interno comprende 9 especies, 4 variedades y 5 especímenes de *Megalostylus* de dudosa identificación a nivel de especie. El grupo externo está formado por 3 especies representantes de géneros relacionados cercanamente: *Pantomorus albosignatus*, *Naupactus cervinus* y *Megalostylodes hirsutus*. Los objetivos fueron poner a prueba la monofilia de *Megalostylus*, explorar sus relaciones interespecíficas y determinar qué sinapomorfías lo identifican y diferencian de otros géneros. El análisis produjo un solo cladograma de 61 pasos, que muestra la siguiente secuencia filogenética: (*Pantomorus albosignatus* (*Naupactus cervinus* (*Megalostylodes hirsutus* (*Megalostylus rhodopus* (*M.* morpho 2 (*M. macrophthalmus* (*M. tomentosus* (*M. dilaticollis* (*M. albicans* (*M. brevipilis, M. fusiformis* (*M. splendidus - M. sturmi*))))))))))). Los resultados avalan la monofilia de *Megalostylus* con base en las siguientes sinapomorfías: protibias con una prominencia opuesta al mucro, élitros casi planos en vista lateral, esternito VIII subromboidal muy elongado y aedeago liso. También respaldan su estrecha relación con *Megalostylodes*.

Palabras clave: Sistemática; Naupactini; Morfología; Especie nueva; Variedades nuevas; *Megalostylodes*

Introduction

Megalostylus Schoenherr, 1840 (Entiminae, Naupactini) is a genus of broad-nosed weevils distributed in the Mexican states of Durango, Guanajuato, Guerrero, Michoacán, Morelos, Oaxaca, Puebla and Veracruz (Champion, 1911; Muñiz-Vélez et al., 2015; Ordóñez-Reséndiz et al., 2008). It was described by Schoenherr (1840) in his monumental work *Genera et species curculionidum, cum synonymia hujus familiae, specie novae aut hactenus minus cognitae* based on the type species *M. sturmi* Boheman, 1840 and has been traditionally characterized by the presence of a short antennal scape comparatively stouter at apex than in other genera (Champion, 1911; Figs. 1-3). The most complete treatment of *Megalostylus* was conducted by Champion (1911), who recognized 9 species and assigned this genus to "Otiorhynchinae alatae", group "Cyphina". He also provided a taxonomic key based on 32 morphological characters of adults and the complete distribution records of the species until then.

The classification of *Megalostylus* proposed by Champion (1911) more than a century ago needs a revision of the status of the species, the infraspecific varieties, and a phylogenetic analysis, to test the monophyly, species relationships, and synapomorphies that support the genus.

Materials and methods

We examined 347 adult specimens obtained from the following entomological collections: IBUNAM, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico; INECOL, Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico; USNM, National Museum of Natural History, Washington DC, USA; NHRS, Swedish Museum of Natural History, Stockholm, Sweden; and BMNH, Natural History Museum, London, England. Moreover, we included material collected by the working team at the Laboratorio de Sistemática y Evolución de Insectos (LabSei) of the ESSJicarero, UAEM.

Taxon sampling. The outgroup comprises 3 species: *Megalostylodes hirsutus* Champion, 1911, *Naupactus cervinus* (Boheman, 1840), and *Pantomorus albosignatus* Boheman, 1840, the former representing the most closely related genus. The ingroup includes 9 species (Figs. 1-3): *M. sturmi* Boheman,1840, *M. rhodopus* Boheman, 1840, *M. albicans* (Lacordaire, 1876), *M. splendidus* Chevrolat, 1878, *M. brevipilis* Champion, 1911, *M. dilaticollis* Champion, 1911, *M. fusiformis* Champion, 1911, *M. macrophthalmus* Champion, 1911, and *M. tomentosus* Champion, 1911 (Table 1). Additionally, 4 described varieties and 5 specimens of doubtful identification at species-level were included as morphospecies 1-5.

A list of 37 discrete characters (29 binary and 8 multistate) was recorded from adults, including 33 characters from the external morphology, 2 of the female genitalia, and 2 of the male genitalia (Table 2). The selection of characters was based on previous analyses of the tribe Naupactini (del Río, 2009; Lanteri & del Río, 2017; Rosas et al., 2011).

For the preparation of genital structures, we followed the methodology described in Rosas et al. (2011) and Lanteri and del Río (2017). A Carl Zeiss Stemi 2000 stereomicroscope, equipped with a reticle eyepiece was used for observations and measurements of the external and internal morphology. Photographs were taken with a Nikon D750 camera equipped with a SIGMA 150 mm 1:2.8 (macro) lens, and drawings were made with Corel Draw (2020 version 22.0.0412). Most characters were illustrated by photographs and drawings, to facilitate the recognition of character states (Figs. 4, 5). They were

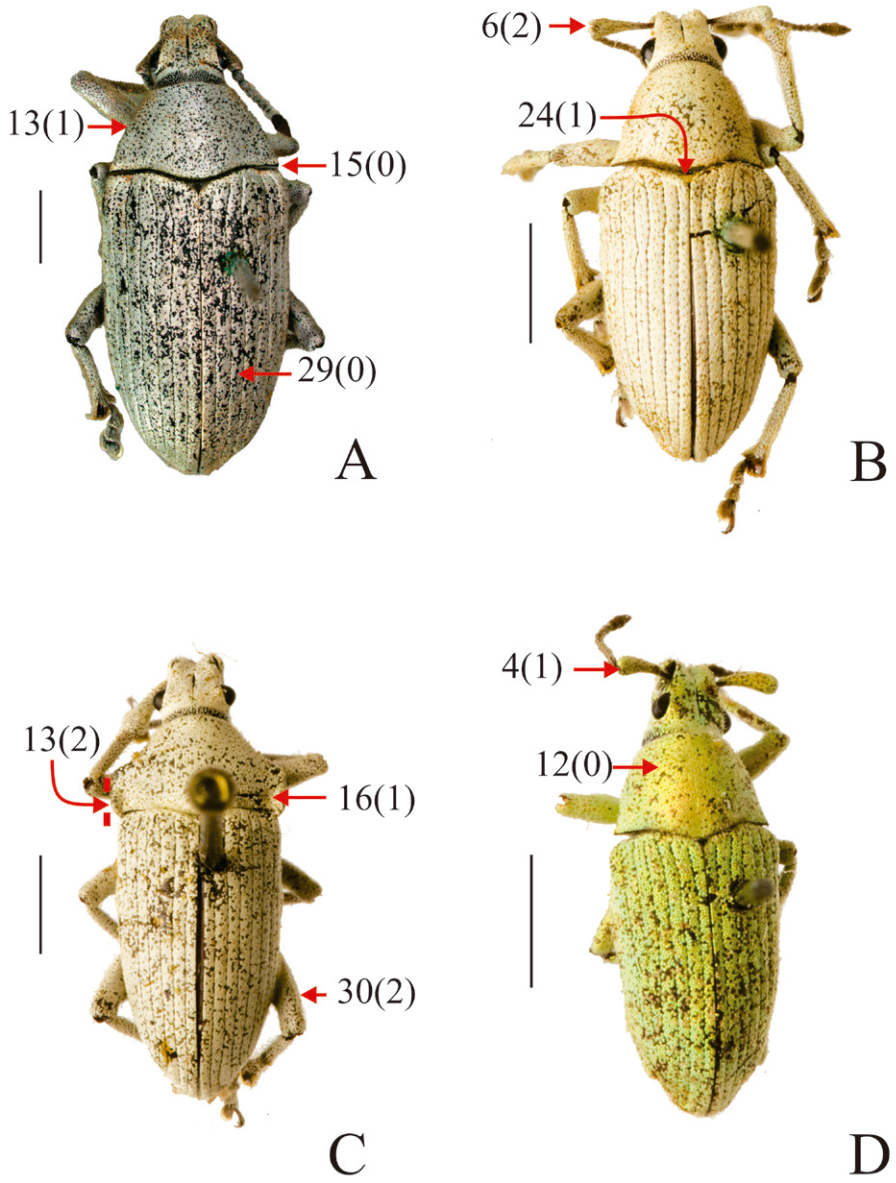

Figure 1. Habitus photographs of *Megalostylus* species, dorsal view. A) *Megalostylus albicans*, female; B) *M. brevipilis*, male; C) *M. dilaticollis*, male; D) *M. fusiformis* male. Arrows and numbers indicate character codification, and the character state is indicated between parentheses. Scale bars = 2 mm.

highlighted with arrows, with indication of character numbers and character states between parentheses.

A data matrix of 21 terminal groups and 37 morphological characters was compiled (Table 3). Character states that could not be examined (due to insufficient material) were scored with a "?" and character states with inapplicable entries on various terminals were scored with a "–". Species or varieties showing 2 or more characters were coded as polymorphic characters. To facilitate the coding, Mesquite software version 3.70 was used (Maddison & Maddison, 2021). An implicit enumeration search was performed in the program TNT version 1.5 (Goloboff & Catalano, 2016). The characters were treated as unordered or non-additive, and under equal weights. The species *Pantomorus albosignatus* was used to root the trees. To evaluate branch support

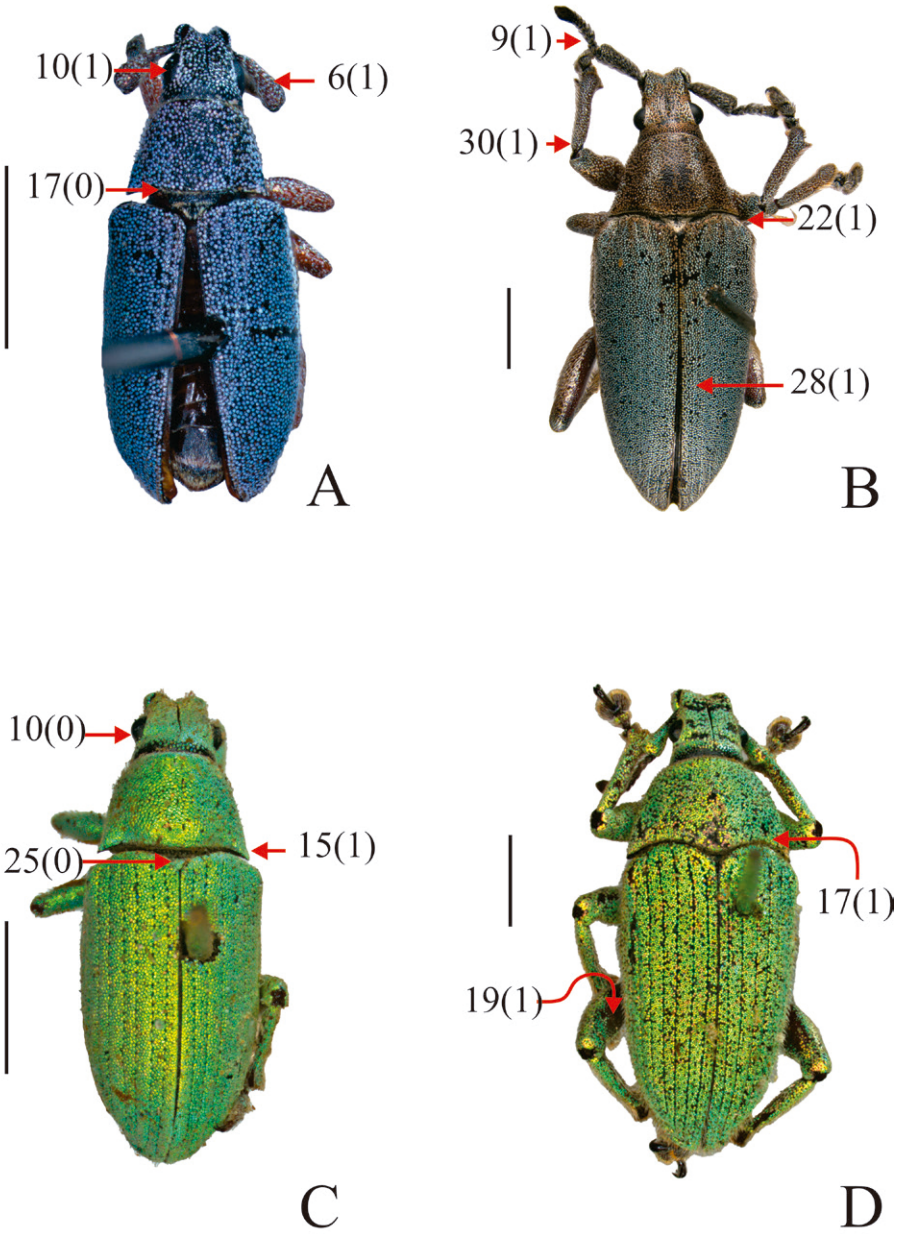

Figure 2. Habitus photographs of *Megalostylus* species, dorsal view. A) *Megalostylus macrophthalmus*, male; B) *M. rhodopus*, male; C) *M. splendidus*, male; D) *M. sturmi*, male. Arrows and numbers indicate character codification, the character state is indicated between parentheses. Scale bars = 2 mm.

(BS), a standard Bootstrap with 1000 replicates was calculated in TNT. Branch support values greater than 50 were mapped in the cladogram. The resulting cladogram and character state transformations were examined in WINCLADA under fast optimization. All records were georeferenced, and maps created in ArcMap version 10. 4.1 (ESRI, 2015).

Results

The search for the most parsimonious trees under equal weights yielded one most parsimonious tree (Fig. 6) (L = 63, IC = 0.73, IR = 0.83), showing the following phylogenetic sequence: (*Pantomorus albosignatus* (*Naupactus cervinus* (*Megalostylodes hirsutus* (*Megalostylus*)))).

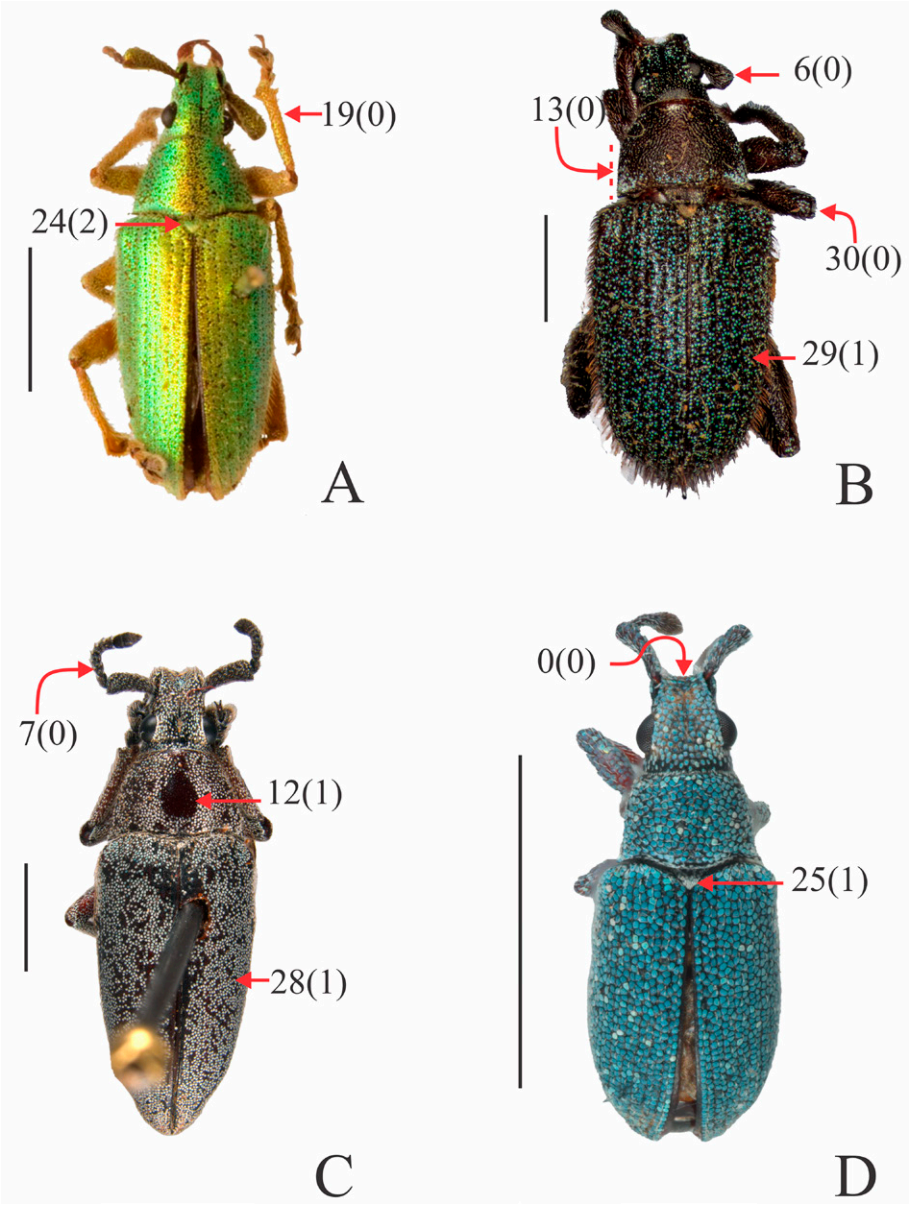

Figure 3. Habitus photographs of *Megalostylus* species, dorsal view. A) *Megalostylus tomentosus*, male; B) *Megalostylodes hirsutus*, male; C) morphospecies 1, male; D) morphospecies 2, male. Arrows and numbers indicate character codification, the character state is indicated between parentheses. Scale bars = 2 mm.

Megalostylodes was found to be sister to the genus *Megalostylus* based on 12 synapomorphies: epistome scales similar in size, density, and color to those on the rest of the rostrum (0:0), dorsal surface of rostrum slightly to strongly depressed (1:1), absence of pair of dorsolateral carinae (2:0), scape very wide in males and thin in females (3:1), width of scape at apex greater than club width in males (4:1), shape of scape strongly clavate (5:1), color brown to black of the verticillate setae of funicle (9:1), slight lateral projection of pronotum (14:1), absence of a row of denticles on inner margin of protibia (20:0), vestiture of scutellum present, consisting of white scales or seta-like scales (25:1), presence of medial longitudinal depression of ventrites 1 and 2 on males

Table 1

List of species included in the cladistic analysis of the genus *Megalostylus* and their geographic distributions (countries and states).

Species names	Geographic distributions
Pantomorus albosignatus Boheman	Mexico (Aguascalientes, Chihuahua, Coahuila, Mexico City, Durango, Guanajuato, Guerrero, Hidalgo, Monterrey, Oaxaca, Puebla Querétaro, San Luis Potosí, Veracruz, Zacatecas)
Naupactus cervinus (Boheman)	Argentina (Buenos Aires, Catamarca, Córdoba, Corrientes, Entre Ríos, Jujuy, Mendoza, Misiones, Salta, Santa Fe, Tucumán), Brasil (Paraná, Río Grande do Sul, Santa Catarina, São Paulo), México (Distrito federal), Uruguay (Artigas, Canelones, Colina, Durazno, Maldonado, Montevideo, Rio Negro, Treinta y Tres)
Megalostylodes hirsutus Champion	Mexico (Oaxaca)
Megalostylus albicans (Lacordaire)	Mexico (Colima, Estado de México, Guanajuato, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla)
Megalostylus brevipilis Champion	Mexico (Colima, Guerrero, Oaxaca)
Megalostylus dilaticollis Champion	Mexico (Guerrero, Michoacán, Morelos, Jalisco)
Megalostylus fusiformis Champion	Mexico (Morelos, Guerrero)
Megalostylus macrophthalmus Champion	Mexico (Oaxaca)
Megalostylus rhodopus Boheman	Mexico (Oaxaca)
Megalostylus splendidus Chevrolat	Mexico (Durango, Guerrero, Morelos, Puebla)
Megalostylus sturmi Boheman	Mexico (Guerrero, Michoacán)
Megalostylus tomentosus Champion	Mexico (Oaxaca)

Table 2

List of 37 morphological characters, character states and codes.

Character	Character states
0. Shape, size, density and color of epistome scales compared to those on the rest of the rostrum	Similar in size, density and color (0); smaller, scarcer and generally different in color (1)
1. Dorsal surface of rostrum	Flat (0); slightly to strongly depressed (1)
2. Pair of dorsolateral carinae	Absent (0); present (1)
3. Sexual dimorphism in antennae	Scape width subequal in males and females (0); scape very wide in males and thin in females (1)
4. Width of scape at apex with respect to width of club, in males	Less than club width (0); greater than club width (1)
5. Shape of scape	Capitate (0); strongly clavate (1)
6. Vestiture of scape	Absent to almost absent (0); scales dispersed leaving integument exposed (1); dense, space between scales reduced or absent, not leaving integument exposed (2)
7. Length of funicular antennomeres 1 and 2	Antennomere 2 slightly shorter than 1 or both sub-equal (0); antennomere 2 longer than 1 (1)
8. Antennae, scales on funicular antennomere 2	Absent (0); present (1)
9. Color of verticillate setae of funicle	Whitish or golden (0); brown to black (1)
10. Convexity of eyes	Convex, pronounced curvature, hemispherical shape (0); slightly convex, less pronounced curvature, small elevations (1)

Table 2. Continued

11. Shape of pronotum	Subcylindrical, curved sides and maximum width about half (0); subconical, with sides moderately to strongly curved and strongly divergent from apex to base (1); subconical, with sides slightly curved to straight and strongly divergent from apex to base (2); bell-shaped (3); subtrapezoidal, with sides slightly concave at anterior half and progressively expanding towards lateral sides at posterior half (4)
12. Glabrous areas at midline of pronotum	Absent (0); present (1)
13. Width of pronotum with respect to elytral base	Narrower (0); subequal (1); wider (2)
14. Lateral projection of pronotum	Absent or indistinct (0); slightly projected (1); strongly projected (2)
15. Shape of lateral projections of posterior margin of pronotum	Extended towards sides (0); strongly extended backwards, towards elytral base (1)
16. Sides at basal third of pronotum	Not depressed (0); strongly depressed (1)
17. Shape of posterior margin of pronotum	Straight to slightly bisinuate (0); strongly bisinuate (1)
18. Bulging surface beneath intercoxal granule, at anterior margin of prothorax	Indistinct or absent (0); present (1)
19. Color of legs integument	Light tones, reddish or orange (0); dark tones, black or brown (1)
20. Row of denticles on inner margin of protibia	Absent (0); present (1)
21. Prominence opposite to mucro in protibia	Absent (0); present (1)
22. Elytral anterior margin	Straight (0); bisinuate (1)
23. Shape of elytra in lateral view	Moderately convex (0); almost flat (1)
24. Width of base of scutellum with respect to width of interstria 2	Reduced to indistinct (0); subequal to width of interstria 2 (1); wider than interstria 2 (2)
25. Scutellum vestiture	Scales similar in color to those covering whole surface of elytra (0); Scales similar, consisted of white scales or seta-like scales (1)
26. Disposition of elytral setae	Recumbent to suberect (0); erect (1)
27. Size of elytral setae	Short (0); long, almost as long as width of interstria 2 at middle (1); very long, longer than width of elytral interestriae 2 at middle (2)
28. Arrangement of elytral setae	Uniform throughout elytral disc (0); only on lateral edges of elytral disc, dorsally without setae (1)
29. Convexity of interstriae	Flat (0); slightly convex (1)
30. Vestiture on legs	Absent or almost absent (0); inconspicuous, scales are scattered leaving integument exposed (1); conspicuous, space between scales is reduced or absent, and covered the integument (2)
31. Deep excavation on metafemur, near apex	Absent (0); present (1)
32. Medial longitudinal depression of ventrites 1 and 2, on males	Indistinct or absent (0); present (1)
33. Spermatheca, body shape	Subcylindrical, slender (almost as wide as base of cornu) (0); subspherical (1)
34. Shape of plate of sternite VIII	Subrhomboidal very elongated, with basal part much longer than apical part (0); subrhomboidal slightly elongated, with basal part as long as apical part (1)
35. Aedeagus, sculpture of median lobe	Granulose (0); smooth (1)
36. Aedeagus, shape of apex of median lobe	Acute to slightly acute (0); truncated (1); arrow shape (2)

Table 3

Data matrix of 21 taxa and 37 morphological characters of *Megalostylus* and outgroups used for the cladistic analysis. Inapplicable characters are indicated with a dash (-), and missing characters with a question mark (?).

Taxa	Characters						
	0-4	5-9	10-14	15-19	20-24	25-29	30-36
Pantomorus albosignatus	101?0	00000	00010	00000	10000	-0100	00?01??
Naupactus cervinus	10100	00100	00010	00000	10100	00000	00001?2
Megalostylodes hirsutus	01011	10001	01101	00000	00102	11201	0111100
Megalostylus albicans	01011	12010	02012	00101	01111	00000	1011010
Megalostylus albicans var. *expansus*	01011	12010	02022	00101	01111	00000	101??10
Megalostylus albicans var. *farinosus*	01011	120?0	02012	00101	01111	00000	101????
Megalostylus brevipilis	010?1	120?0	03011	10101	01111	00000	101??10
Megalostylus dilaticollis	01011	12000	04022	01001	01111	00000	10110??
Megalostylus fusiformis	010?1	120?0	03011	10101	01111	00000	10?????
Megalostylus macrophthalmus	01011	100?	12011	00000	01112	10000	00?10??
Megalostylus splendidus	01011	12010	01011	10101	01112	00000	1011010
Megalostylus splendidus var.	01011	12010	01011	10101	01112	00000	1011010
Megalostylus sturmi	01011	12010	0100&11	10111	01112	01100	1011?11
Megalostylus sturmi var. *villosus*	01011	12010	0100&11	10111	01112	01100	1011011
Megalostylus rhodopus	01011	12001	01111	00000	01112	10010	0011010
Megalostylus tomentosus	01011	110?0	02011	00000	01112	01100	00110??
Morphospecies 1	010?1	12001	01111	10000	0111?	10010	001??10
Morphospecies 2	010?1	11000	01011	10100	01112	10000	001??10
Morphospecies 3	010?1	10001	02011	00000	01112	10011	001??10
Morphospecies 4	010??	11000	02011	00000	01112	01100	00?10??
Morphospecies 5	010?1	12000	04011	00001	01111	00000	101??10

(32:1), and subspherical body shape of spermatheca (33:1). There are also 2 homoplastic characters that support this relationship: pronotum subconical, with sides curved and strongly divergent from apex to base (11:1) and width of base of scutellum wider than interestria 2 (24:2).

Megalostylus was recovered as monophyletic based on 4 synapomorphies: presence of prominence opposite to mucro in protibia (21:1), elytra in lateral view almost flat (23:1), plate of sternite VIII, subrhomboidal very elongated (34:0), and sculpture of aedeagus smooth (35:1).

The sister genus *Megalostylodes* is characterized by 3 autapomorphies: pronotum narrower with respect to elytral base (13:0), very long elytral setae, longer than width of elytral interstriae 2 at middle (27:2), and presence of deeply excavated metafemur near apex (31:1), and 3 non-exclusive synapomorphies: presence of glabrous areas in midline of pronotum (12:1), erect disposition of elytral setae (26:1), and slightly convex interestriae (29:1).

Two main clades were found within *Megalostylus*: clade I, including *Megalostylus rhodopus* and morphospecies 1 and 3 (considered belonging to *M. rhodopus*), is supported by 1 exclusive synapomorphy: elytral setae only present on the lateral edges of elytral disc (28:1). Clade II is supported by 1 exclusive synapomorphy and 1 non-exclusive synapomorphy: scales of scape separate, leaving integument exposed (6:1) and whitish or golden color of the verticillate setae of funicle (9:0), respectively. Within clade II, morphospecies 2 is sister to the remaining species, which form a clade supported by 1 non-exclusive synapomorphy: pronotum subconical, sides slightly curved to straight and strongly divergent from apex to base (11:2). *Megalostylus macrophthalmus* is the sister

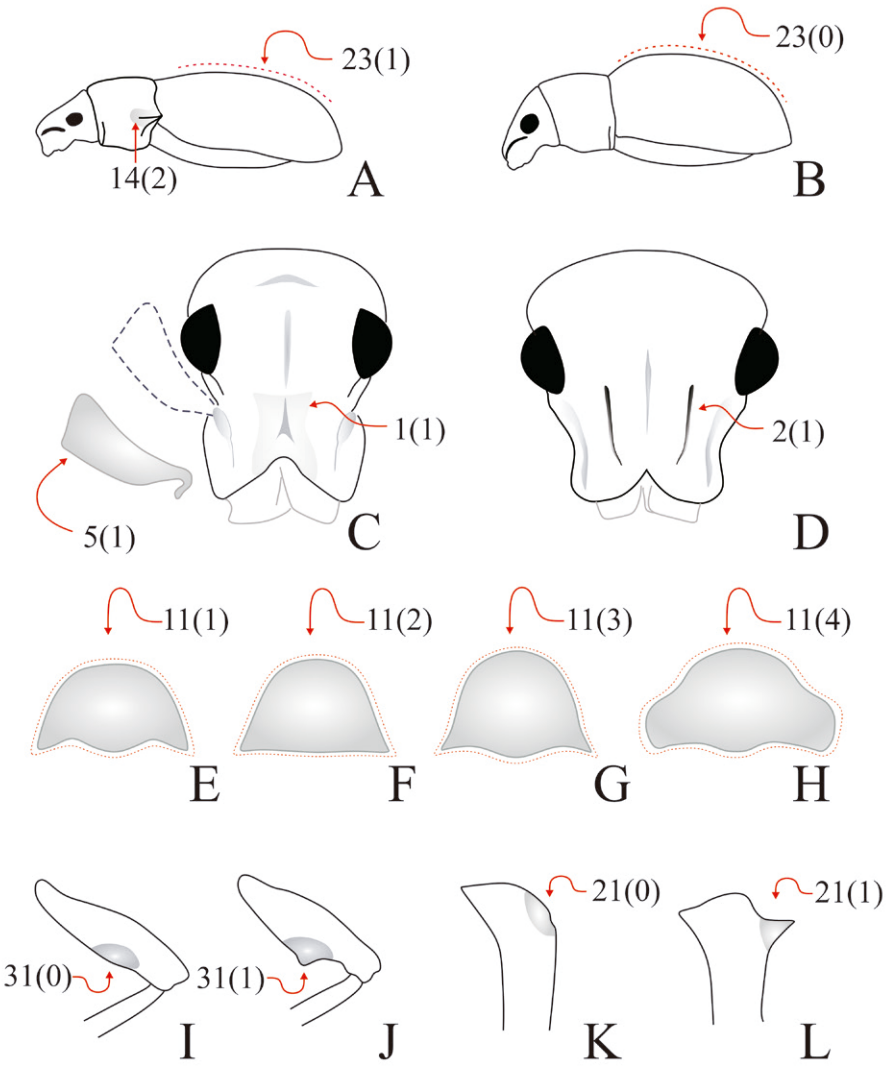

Figure 4. Diagrammatic illustrations with arrows and numbers indicating character codification of head, pronotum, legs, and elytra in *Megalostylus* and outgroup species. A) *Megalostylus dilaticollis*, lateral view; B) *Pantomorus albosignatus*, lateral view; C) *M. rhodopus*, head; D) *Naupactus cervinus*, head; E) *M. sturmi*, pronotum; F) *M. tomentosus*, pronotum; G) *M. brevipilis*, pronotum; H) *M. dilaticollis*, pronotum; I) *M. albicans*, metafemora; J) *Megalostylodes hirsutus*, metafemora; K) *M. hirsutus*, protibiae; L) *M. albicans*, protibiae.

species of *M. tomentosus*-*M. sturmi* var. *villosus* based on 1 non-exclusive synapomorphy: vestiture of scutellum present, scales similar in color to those covering the whole surface of elytra (25:0). *Megalostylus tomentosus* (along with morphospecies 4) is the sister of a supported clade (BT 58) *M. dilaticollis*-*M. sturmi* var. *villosus* clade, which is supported by 3 exclusive synapomorphies and 1 non-exclusive synapomorphy: integument of legs with dark tones, black or brown (19:1), and width of base of scutellum reduced to indistinct (24:1), vestiture on legs inconspicuous, scales are scattered leaving integument exposed (30:1), and scales separated leaving integument of scape exposed (6:2). Within this clade *M. dilaticollis* (along with morphospecies 5) is sister to a subclade supported by 1 exclusive synapomorphy and 1 non-exclusive synapomorphy: presence of scales on the second funicular antennomere (8:1) and posterior margin of pronotum strongly bisinuate (17:1) that includes *M. albicans* and its varieties, *M. albicans* var. *expansus*, and var. *farinosus* sister to *M. brevipilis* to *M. sturmi* var.

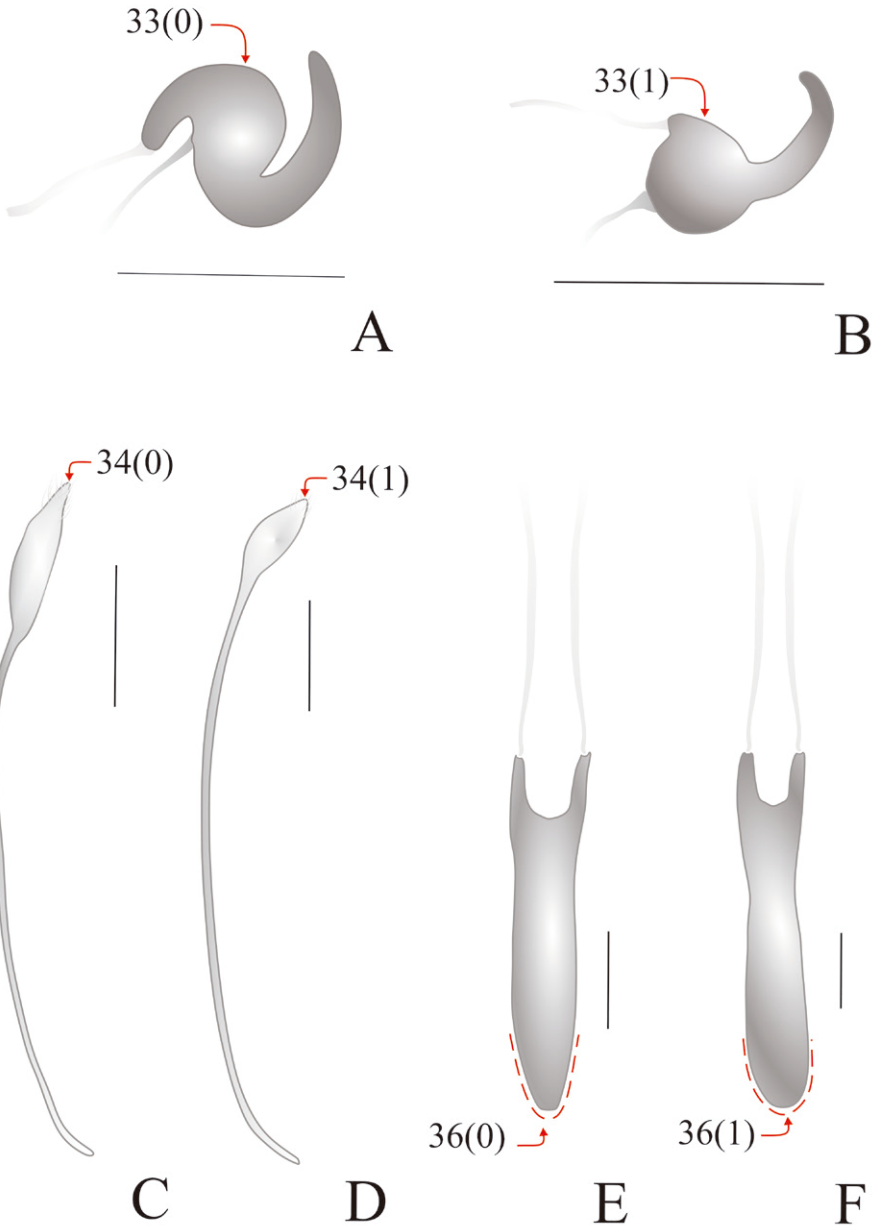

Figure 5. Diagrammatic illustrations with arrows and numbers indicating character codification of female and male genitalia in *Megalostylus* and outgroup species. A) *Pantomorus albosignatus*, spermatheca; B) *M. albicans*, spermatheca; C) *M. splendidus*, sternite VIII; D) *Megalostylodes hirsutus*, sternite VIII; E) *M. rhodopus*, aedeagus; F) *M. sturmi*, aedeagus. Scale bars = 0.5 mm.

villosus clade supported by 1 exclusive synapomorphy and 1 non-exclusive synapomorphy: pronotum flared or bell-shaped (11:3) and lateral projections of posterior margin of pronotum strongly extended backward, towards elytral base (15:1). Within this clade, *M. brevipilis* and *M. fusiformis* are sisters to the *M. splendidus*-*M. sturmi* var. *villosus* clade which is supported by 2 non-exclusive synapomorphies: pronotum subconical, sides curved and strongly divergent from apex to base (11:1), and width of base of scutellum wider than interestria 2 (24:2). The clade

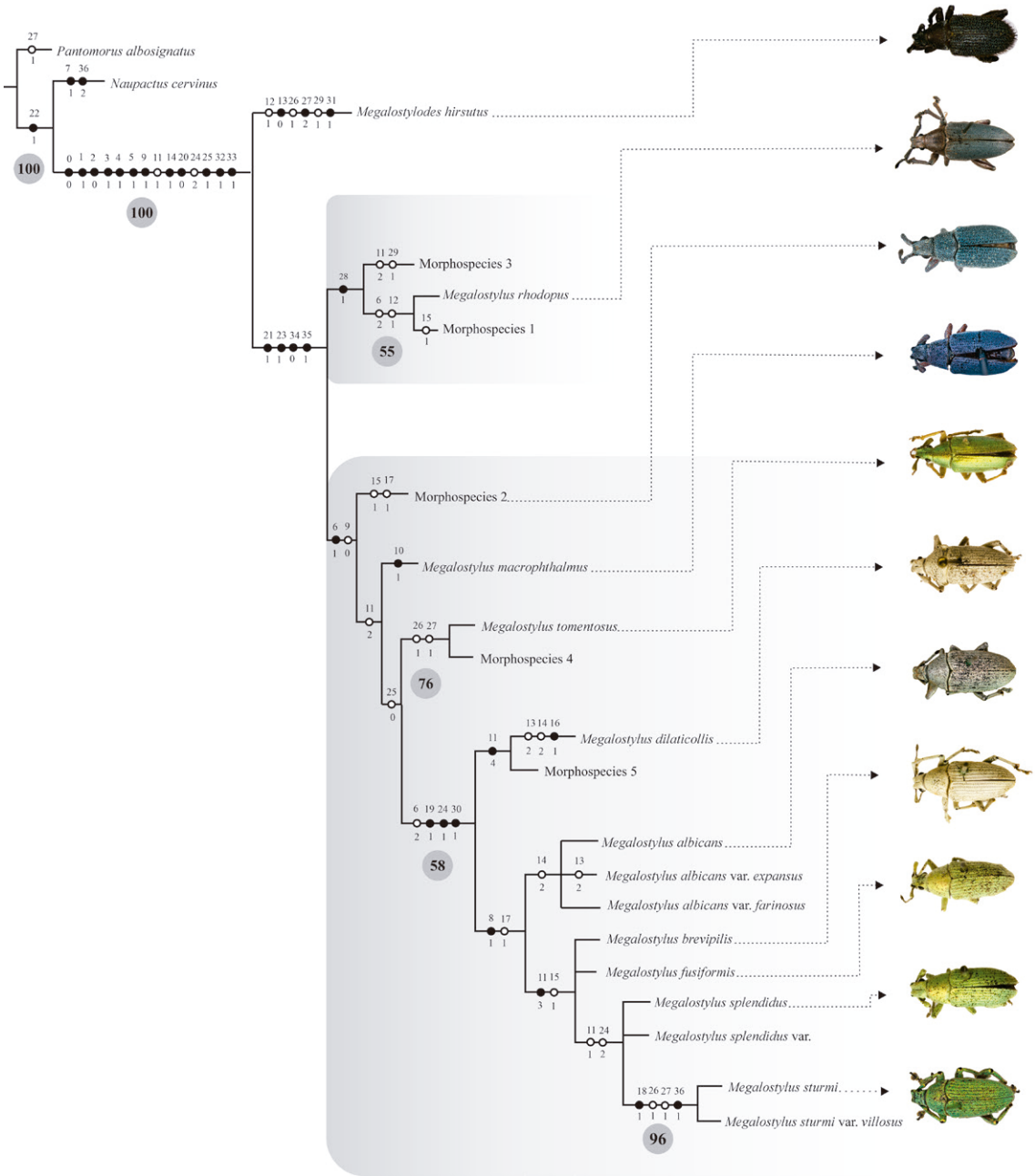

Figure 6. Most parsimonious cladogram of *Megalostylus* plus 3 outgroups under equal weights, showing character fast optimization. Black circles indicate synapomorphies, whereas white circles indicate non-exclusive synapomorphies. Numbers on and below each circle correspond to character and state codes, respectively. Bootstrap values are indicated below the branches.

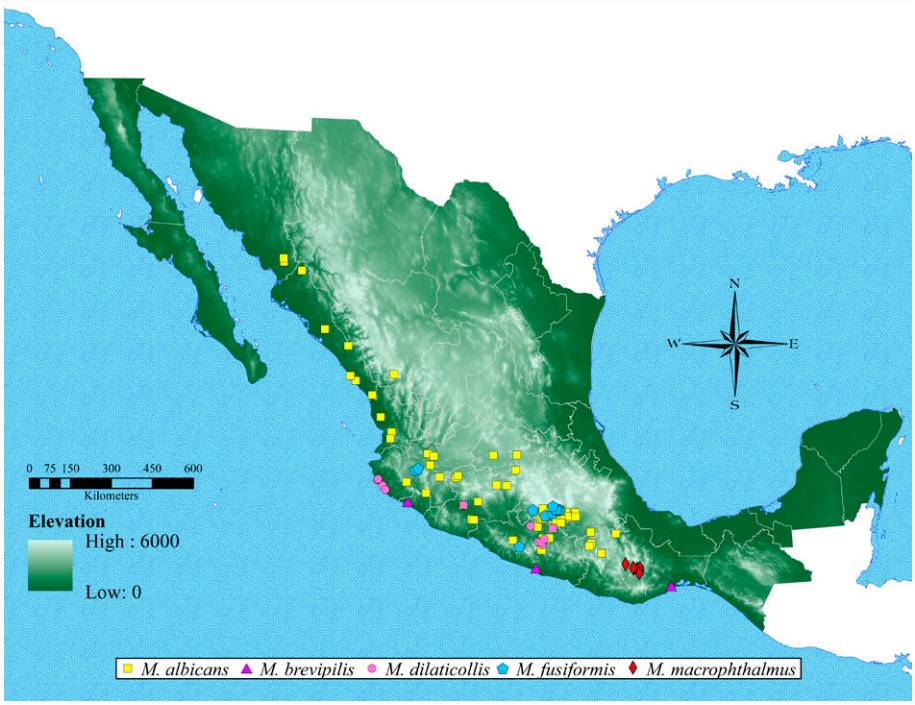

Figure 7. Occurrence map of 5 *Megalostylus* species, ordered alphabetically. *Megalostylus albicans* (yellow square); *M. brevipilis* (purple triangle); *M. dilaticollis* (pink circle); *M. fusiformis* (blue pentagon) and *M. macrophthalmus* (red diamond). Map by A. Lizama-Hernández.

M. splendidus-*M. sturmi* var. *villosus* also has unresolved relationships between *M. splendidus* and his variety, both sister to the *M. sturmi* + *M. sturmi* var. *villosus* clade.

Geographic distribution. The maps (Figs. 7, 8) indicate that the species of *Megalostylus* are mostly distributed along the Pacific coast, with the greatest richness in the central and southern parts of the country. *Megalostylus albicans* shows the largest distribution, ranging from Oaxaca to Sinaloa. Six species are distributed in the central states of the country (Guanajuato, Guerrero, Michoacán, Morelos, and Puebla): *M. albicans*, *M. brevipilis*, *M. dilaticollis*, *M. fusiformis*, *M. splendidus*, and *M. sturmi*. The species *M. rhodopus*, *M. macrophthalmus*, and *M. tomentosus* are restricted to Oaxaca, and *M. rhodopus* reaches the southernmost distribution extending to the Isthmus of Tehuantepec.

Discussion

The sister group relationship between *Megalostylodes* and *Megalostylus* is well supported by 12 exclusive synapomorphies, and the monophyly of *Megalostylus* is supported by a combination of 4 exclusive synapomorphies of the protibiae, elytra, and female and male genitalia. Champion (1911) distinguished *Megalostylus* based on the presence of a prominence opposite to mucro (or toothed tibiae at the external apical angle), and Lanteri and del Río (2017) recovered this character state (car 69[1]) as an apomorphy of *Megalostylus*.

Within *Megalostylus* most of the relationships are not well supported nevertheless, it is clear the position of *M. rhodopus* (including morphospecies 1 and 3) as sister species of the remaining, and it was recovered a well-supported group including *M. dilaticollis* (= morphospecies 5), *M. albicans*, *M. brevipilis*, *M. fusiformis*, *M. splendidus*, and *M. sturmi*. *Megalostylus macrophthalmus* and *M. tomentosus* (= morphospecies 4) would be basal regarding this clade. Morphospecies 2 is considered a probable new species, however, this status needs further studies.

The species of *Megalostylus* are very variable in scale color, size and pronotum shape, and due to that intraspecific variation, some nominal species have been synonymized: *M. farinosus* Chevrolat, 1878 [junior synonym of *M. albicans* (Lacordaire, 1876)], *M. expansus* Pascoe, 1881 [junior synonym of *M. albicans* (Lacordaire, 1876)] and

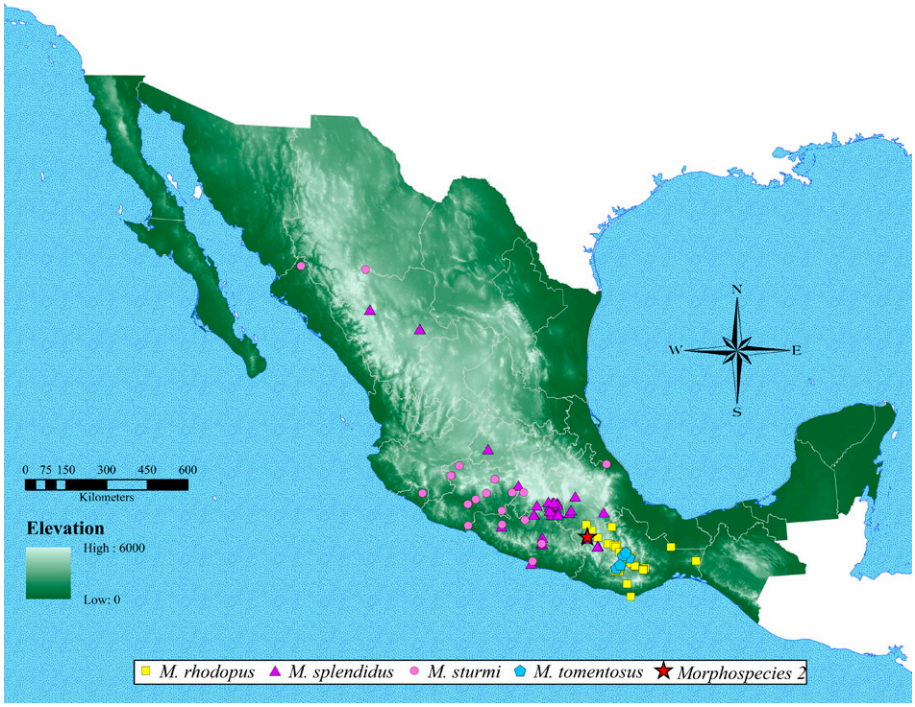

Figure 8. Occurrence map of remaining 4 *Megalostylus* species, ordered alphabetically plus a new *Megalostylus* species (indicated here as morphospecies 2). *Megalostylus rhodopus* (yellow square); *M. splendidus* (purple triangle); *M. sturmi* (pink circle); *M. tomentosus* (blue pentagon) and morphospecies 2 sp. nov. (red star). Map by A. Lizama-Hernández.

M. villosus Chevrolat, 1878 [junior synonym of *M. sturmi* Boheman, 1840]. Our analysis explored the relationships among intraspecific varieties of the genus *Megalostylus*, and the results support the previously established synonymies. In the case of *M. albicans* with its varieties (*M. albicans* var. *expansus* and *M. albicans* var. *farinosus)* there is no reason to consider them as different species. Characters with the greatest contribution to the species relationships are those referring mainly to the vestiture of antennae, legs, elytra, shape, and characteristics of the pronotum, scutellum, and apex of aedeagus.

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