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PROCLUS, GIANT LATIN-AMERICAN PASSALIDS: REVISION, PHYLOGENY AND BIOGEOGRAPHY

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RESUMEN

El género *Proculus* y sus cinco especies conocidas son redescritas, además se describe *Proculus jicaquei* sp. nov. Son sinonimizados: *P. beckeri* Zang, 1905 (syn. nov.) y *P. densipennis* Casey, 1914 (syn. nov.) con *P. opacipennis* (Thompson, 1857); *P. mandibularis* Casey, 1914 (syn. nov.) con *P. burmeisteri* Kuwert, 1891; y *P. kraatzi* Kuwert, 1898 (syn. nov.) y *P. magister* Casey, 1897 (syn. nov.) con *P. mniszechi* Kaup, 1868. Se incluyen claves de los adultos y las larvas, e información biogeográfica sobre cada especie. El género se distribuye desde México hasta Colombia. *Proculus mniszechi* es parapátrica con *P. burmeisteri*, aunque son parcialmente simpátricas, en la Sierra de las Minas, Sierra de Santa Cruz y Sierra de los Cuchumatanes de Guatemala, *P. mniszechi* se encuentra en un tipo de bosque mesófilo por arriba de los 1500 m y *P. opacipennis* se encuentra en otro tipo de bosque mesófilo por abajo de los 1500 m. *Proculus opacipennis* tiene una relación similar con *P. opacus* en la Sierra de los Cuchumatanes, donde *P. opacus* aparentemente reemplaza a *P. mniszechi*. *Proculus goryi* (Melly, 1833) se encuentra en la cadena de volcanes de la costa pacífica de Guatemala y Chiapas, México. *Proculus jicaquei* sp. nov. únicamente es conocida de una localidad de las montañas al noroeste de Yoro, Honduras. La hipótesis filogenética muestra que *P. jicaquei* está más relacionada con *P. goryi*, estas dos especies forman el clado hermano de todas las otras especies de *Proculus*. En tanto que *P. mniszechi* y *P. burmeisteri* son taxa hermanos, como por su parte lo son *P. opacus* y *P. opacipennis*.

Palabras clave: Taxonomía, Passalidae, *Proculus*, análisis filogenético.

ABSTRACT

The genus and its five known species are redescribed and *P. jicaquei* sp. nov. is described. Synonymies include *P. beckeri* Zang, 1905 with *P. opacipennis* (Thompson, 1857) (new synonymy), *P. mandibularis* Casey, 1914 with *P. burmeisteri* Kuwert, 1891 (new synonymy), *P. magister* Casey, 1897 with *P. mniszechi* Kaup, 1868 (new synonymy), *P. densipennis* Casey, 1914 with *P. opacipennis* (Thompson, 1857) (new synonymy), and *P. kraatzi* Kuwert, 1898 with *P. mniszechi* Kaup, 1868 (new synonymy). We include a phylogenetic analysis, keys for larvae and adults, and biogeographic information for each species. The genus occurs from Mexico to Colombia. *Proculus mniszechi* is parapatric with *P. burmeisteri* and partially sympatric with *P. opacipennis* in Sierra de las Minas, Sierra de Santa Cruz and Cuchumatán Mountains; *P. mniszechi* occurs in a type of cloud forest above 1500 m altitude, whereas *P. opacipennis* occurs in another cloud forest type below 1500 m. *Proculus opacipennis* has a similar relation with *P. opacus* Kuwert 1891 in the Cuchumatán Mountains, where *P. opacus* apparently replaces *P. mniszechi*. *Proculus goryi* (Melly, 1833) occurs in the volcanic chain of the Pacific coast of Guatemala and Chiapas, Mexico. *Proculus jicaquei* sp. nov. is known only from the mountains northwest of Yoro, Honduras. Phylogenetic hypothesis shows that *P. jicaquei* is most closely to *P. goryi*, these two taxa form a sister clade to all other *Proculus* species. *Proculus mniszechi* and *P. burmeisteri* are sister taxa, as are *P. opacus* and *P. opacipennis*.

Key words: Taxonomy, Passalidae, *Proculus*, phylogenetic analysis.

INTRODUCTION

Proculus Kaup, 1868, is a distinctive genus of Passalidae (Fig. 1). Its large size (31-80 mm length), wide antennal lamellae, ovate elytra and reduced eyes readily make distinguish it from all other passalids. It has been cited from Mexico (Veracruz) to northern South America (Colombia). Considering several synonymies and a new species, described herein, we include six species in the genus. We present a comparative description of each of these species, a key to their identification (adults and larvae), and discuss their phylogeny and biogeography.

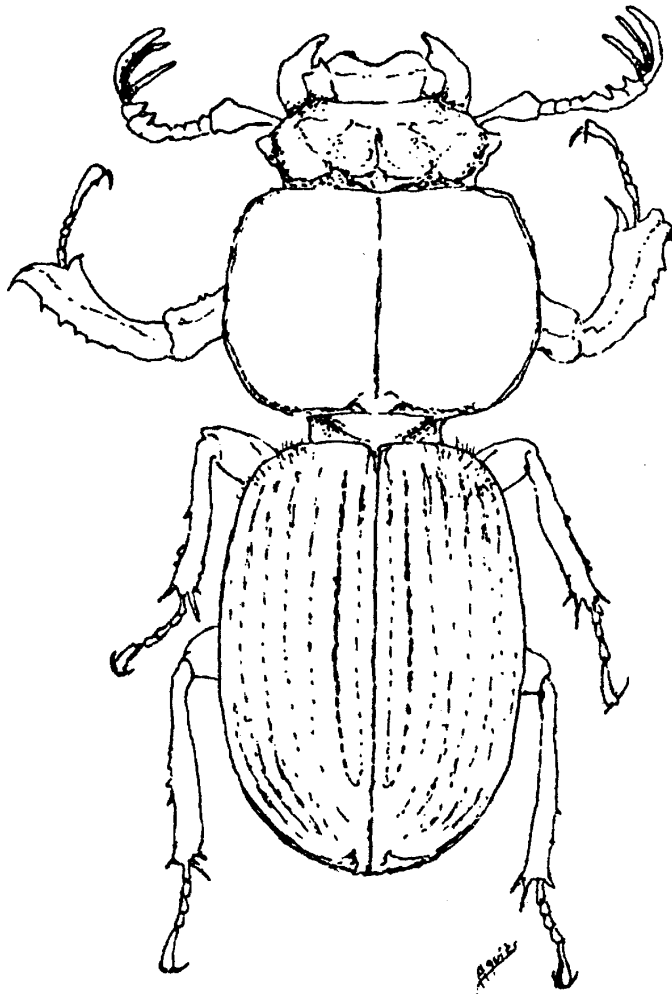


Figure 1
Dorsal habitus of *Proculus mniszewski* Kaup, 1868.

METHODS

We examined 584 adult specimens deposited in the Arthropod Collection at the Universidad del Valle de Guatemala (UVGC) and the Colección Entomológica at the Instituto de Ecología (IEXA) as well as from: Colecciones Zoológicas de Referencia, Universidad de San Carlos de Guatemala (USCG); Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México (CNIN); Museo de Historia Natural de la Ciudad de México (MHNM); private collections of Jorge J. Hendrichs (JHSC), Benigno Gómez (BGGC) and Miguel Agel Morón (MAM), Mexico; Museu de Zoologia, Universidade de São Paulo, Brazil (MZSP); Museum National d'Histoire Naturelle (MNHN), Paris, France; Muséum d'Histoire Naturelle Genève, Switzerland (MHNG); National Museum of Natural History, Leiden, Netherlands (NMNH); Deutsches Entomologisches Institut (DEI) of Eberswalde, Germany; and at the U.S.A: the Los Angeles County Museum of Natural History (LACM); United States National Museum (USNM), Washington, D.C., Carnegie Museum (ICCM), Pittsburg, and the American Museum of Natural History (AMNH), New York. Most of the specimens were collected by us or our students. Concerning the material examined for each species, we indicate in parentheses the number of individuals and the abbreviation for the collection to which it belongs (following those of Arnett and Samuelson [1969] where possible) except for those from UVGC.

Types associated with all names described under *Proculus* and *Cyphoproculus* were examined. Measurements were taken with a vernier. Measurements of the mandibular angle of *Proculus opacus* and *P. opacipennis* were taken with a protractor, aligning the vertical axis with the line of the mandible base to measure the curvature (Figs. 4c, d), in ventral side. Boxplot was obtained using SPSS 9.0 (1999).

Phylogenetic relationships among the six species of *Proculus* were analyzed using PAUP version 4.0b10 (Swofford 2002). Adult and larval external characters formed the basis of this analysis (Tables 1 and 2). In the absence of revisionary works, for character polarization we chose *Veturius platyrhinus* (Westwood) as the outgroup. We consider this species to be representative of primitive *Veturius* and to be a member of a genus closely related to *Proculus*. We obtained a single most parsimonious tree using heuristic search methods. Both ACCTRAN and DELTRAN optimizations were used. Characters 19 and 20 are multistate and linearly ordered (012), all others are unordered. Most characters we select are stable under examination of large series of specimens, nevertheless characters 2 and 3, present some variation in a few specimens.

PROCVLUS KAUP, 1868

Proculus Kaup 1868: 8-9. Type species *Passalus goryi* Melly 1833 (designated by Gravely 1918). Kaup 1871: 5, 9, 65, 118. Bates 1886: 3. Kuwert 1890: 1; 1891: 192; 1896: 210, 224, pl. 5 fig. 29; 1898: 177-178 (key to species). Arrow 1904: 733, 750 (stridulation). Sharp 1904: 274 (stridulation). Casey 1914: 374. Gravely 1918: 9, 10, 32, 33, 42, 125 (synonymy). Hincks: 1933: 10, 11 (flightlessness). Luederwaldt 1934: 4, 6. Hincks & Dibb 1935: 30-31.

Blackwelder 1944: 191. Hincks & Dibb 1958: 12. Johnston 1959: 124. Reyes-Castillo 1970: 10, 19, 26, 52, 55, 57, 87, 98, 154-158, 222. Virkki & Reyes-Castillo 1972: 62 (phylogeny). Reyes-Castillo & Halffter 1978: 225-226 (biogeography). Schuster & Summers 1978: 299 (mites). Schuster & Reyes-Castillo 1981: 88, 108 (larvae). Reyes-Castillo 1982: 1389, 1390, 1396 (biogeography). Quintero & Reyes-Castillo 1983: 6 (larvae). Reyes-Castillo 1985: 295, 296, 300 (biogeography). Reyes-Castillo, Fonseca & Castillo 1987: 65 (biogeography). Schuster & Reyes-Castillo 1990: 6 (taxonomic affinities). Schuster 1992b: 361, 365, 367, 368 (larvae); 1993a: 119; 1993b: 55, 58-59. Padilla & Schuster 1994: 2, 4-5. Serrano, Galián & Reyes-Castillo 1998: 163 (karyotype). Delgado, Pérez & Blackaller 2000: 72.

Cyphoproculus Kuwert 1896: 224, pl. 5 fig. 30. Type species *Proculus mniszewski* Kaup, 1868. Kuwert 1898: 178-179 (key to species).

Etymology. *Proculus*, a noble Roman surname.

Description. Head: anterior border of labrum almost straight, slightly concave, or slightly bisinuate. Clypeus declivous, anterior border thin with anterior angles rounded and little developed. External tubercles lacking. Frontoclypeal suture between internal tubercles lacking (except partially present in *P. jicaquei* and some specimens of *P. mniszewski* from eastern Sierra de los Cuchumatanes). Frontal fossae glabrous, frontal ridges lightly present or absent, internal tubercles present and rounded. Median frontal structure (MFS) of "marginatus" type (Reyes-Castillo 1970). Supraorbital ridges swollen, eyes reduced. Ligula unidentate, often eroded in old specimens. Mentum lobes with lateral depressions poorly marked. Hypostomal process wide, separated from labium. Apex of mandibles bidentate, internal teeth of equal size on each mandible, with the basal teeth larger and bidentate. In mature specimens, the basal teeth often worn, appearing as tubercles at the base of anterior tooth. Antennal lamellae wide, width of segment more than 4 times length (see figure 22 in Reyes-Castillo 1970). Thorax: Pronotum large quadrate, more than 1/2 the length of the elytra; anterior corners right-angled; marginal groove narrow, impunctate; lateral fossae marked with few to no setae. Scutellum with small punctate setae. Prosternal process rhomboidal. Mesosternum without lateral depressions. Mesepimera pubescent. Metasternal disk delimited partially or totally by setose punctation; marginal groove weak, narrow, almost linear. Elytra: Humeri pubescent, epipleura glabrous or pubescent extremely anteriorly. Striae notable with fine to moderate punctation. Interstriae always wider than striae. Elytra oval, strongly interlocked along interfacing edge. Wings: Reduced and coriaceous. Legs: Tarsi short. Ventral face of profemur with marginal groove anteriorly. Apical spur of protibia with sharp point slightly directed down. Longitudinal dorsal ridge of mesotibia low and hair brush not dense. Mesotibiae and metatibiae with small spine or spines on external border. Abdomen: Marginal groove of last sternite complete.

Diagnosis Larvae. The larvae are easily separated from other passalid by their great size (head width of third instars: 8.0-11.6 mm) and the lack of tergal setae on, at least, tergites 1-6. Anal ring setae and raster setae are similar, but there are at least 19 and perhaps as many as 33. The raster has many stout setae 0.4-0.7 mm long. Sternite AV9 has 3-4 pair of setae. The abdominal sternites are covered with short (0.05-0.1 mm) stout setae (Schuster & Reyes-Castillo 1981).

Affinities. *Proculus*, together with *Verres*, *Veturius* and *Publius* is thought to represent a single phyletic lineage (Virkki & Reyes-Castillo 1972). On the basis of the aedeagus, *Proculus* appears most closely related to the *Publius-Veturius* complex (basal piece not fused to lateral lobes).

Species. We consider *Proculus* to include the next six species: *Proculus mniszewski* Kaup, 1868; *P. burmeisteri* Kuwert, 1891; *P. opacipennis* (Thompson, 1857); *P. opacus* Kuwert, 1891; *P. goryi* (Melly, 1833), and *P. jicaquei* Schuster, Cano y Reyes-Castillo, sp. nov.

The synonymies of *P. densipennis* with *P. opacipennis* and *P. magister* with *P. mniszewski* were formerly proposed by Johnston (1959, see article 15.1 ICZN 1999); nevertheless, they were

conditionally proposed, pending review of the holotypes. We reviewed Thompson's and Kaup's holotypes and are in agreement with Johnston.

KEY TO ADULTS OF SPECIES OF *PROCLUSUS*

- 1 Dorsal mandibular tooth large (Fig. 2a) 2
 1' Dorsal mandibular tooth small (Fig. 2b, 2c) or indistinct (Fig. 2d) 4
 2(1) Elytron matte, elytral hairs present from humeral angle to more than 1/2 distance to elytral apex; lateral lobe of mentum flat; anterior border of labrum slightly bisinuate or nearly straight 3
 2' Elytron shiny, elytral hairs present only on humeral angle; lateral lobe of mentum protruding ventrally forming a longitudinal ridge; anterior border of labrum slightly concave (East Guatemala; El Portillo, Santa Bárbara, Celaque, Honduras) *P. burmeisteri* Kuwert, 1891
 3(2) Elytral hairs present slightly past midelytron; external edge of mandible angular (Fig. 3a, 4d); pronotum matte (Sierra del Norte de Chiapas, Mexico; Cuchumatan Mtns., Huehuetenango, Guatemala; Antioquia, Colombia) *P. opacus* Kuwert, 1891
 3' Elytral hairs extend almost to elytral apex; external edge of mandible rounded (Fig. 3b, 4c); pronotum shiny (Sierra del Norte de Chiapas, Mexico; Sierra Santa Cruz, Sierra de las Minas, Cerro San Gil, Guatemala; apparently Costa Rica) . *P. opacipennis* (Thompson, 1857)
 4(1') Elytral hairs present only on humeral angle; lateral lobe of aedeagus 1/2 as long as basal piece; horn of median frontal structure small with tip not obviously free 5
 4' Elytral hairs present almost to elytral apex; lateral lobe of aedeagus expanded, same length as basal piece; horn of median frontal structure larger with tip obviously free [Veracruz (?), Sierra Madre de Chiapas (Soconusco), Mexico; coastal volcanic range, Guatemala]
 *P. goryi* (Melly, 1833)
 5(4) Lateral lobe of mentum flat; aedeagus small; internal frontal tubercles small, located 1/4 of distance from anterior clypeal border to horn of median frontal structure; dorsal mandibular tooth not distinct (Fig. 2d); lateral pronotal fossae with setae (mountains NW of Yoro, Honduras) *P. jicaquei* nov. sp.
 5' Lateral lobe of mentum protruding ventrally forming a longitudinal ridge; aedeagus large; internal frontal tubercles large, located 1/3 or more of distance from anterior clypeal border to horn of median frontal structure; dorsal mandibular tooth distinct (Fig. 2c); lateral pronotal fossae glabrous (Belize; Sierra Santa Cruz, Sierra de las Minas, Sierra de Merendón, eastern Sierra de los Cuchumatanes, Guatemala; San Pedro Sula, Honduras)
 *P. mniszehi* Kaup, 1868

KEY TO SPECIES OF KNOWN THIRD INSTAR LARVAE OF *PROCLUSUS*

- 1 Tergite 8 without many long setae, at most very short setae 2
 1' Tergite 8 with many long setae *P. opacipennis* & *P. opacus*
 2(1) Area below spiracle line bare or with short setae, no long setae present; center frons with any setae more than 0.6 mm long 3
 2' Area below spiracle line with many long setae; center frons with 3-5 setae 0.4-0.8 mm long
 *P. goryi*
 3(2) Tergite 9 with many long setae; metathoracic leg with 4-5 subapical teeth . *P. mniszehi*
 3' Tergite 9 bare or with very short setae; metathoracic leg with 6 subapical teeth
 *P. burmeisteri*

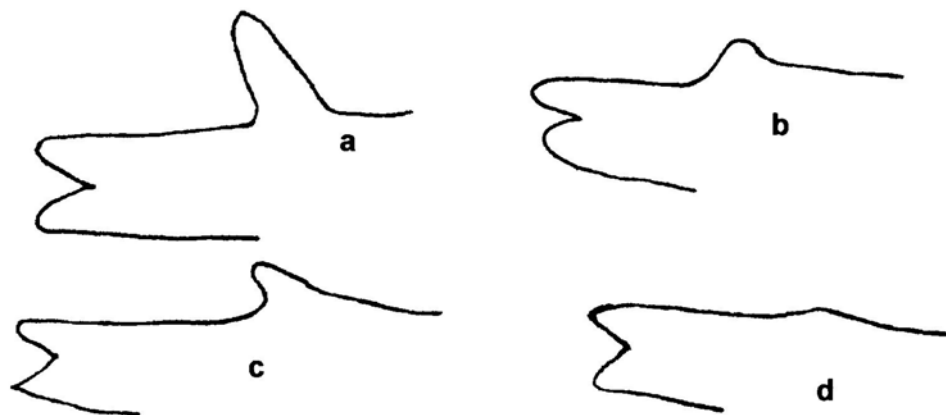


Figure 2

Lateral view of dorsal tooth of mandible of: **a)** *Proculus opacus* Kuwert, 1891; *P. opacipennis* (Thompson, 1857); and *P. burmeisteri* Kuwert, 1891; **b)** *Proculus goryi* (Melly, 1833); **c)** *Proculus mniszechi* Kaup, 1868; **d)** *Proculus jicaquei* n.sp.

***Proculus mniszechi* Kaup, 1868**

Figures 1, 2c, 4a, 5a, 6, 7

Proculus mniszechi Kaup 1868: 11-12. Holotype at MNHN, Paris. Type locality: Guatemala. Kaup 1871: 67-69, 118; Bates 1886: 3-4; Kuwert 1891: 192; Arrow 1907: 450; Heyne & Taschenberg 1908: 58; Sharp & Muir 1912 (aedeagus); Casey 1914: 374 (*mneszechi*, typographical error). Gravelly 1918: 10, 43 (mislabelled specimen from Ecuador); Hincks & Dibb 1935: 31; Van Doesburg 1942: 330; Blackwelder 1944: 191; Johnston 1959: 124-126; Reyes-Castillo 1970: 156, 158; Schuster & Summers 1978: 301, 381, 384 (mites); Morón 1984: 46-47; Schuster 1985: 166; Rosario & Hunter 1988: 131 (mites); Schuster 1992a: 288, 289, 291; 1992b: 361; Cano 1994: 33 (aedeagus); Padilla & Schuster 1994: 1-5 (mites); Schuster & Schuster 1997: 264, 265; Schuster, Cano & Cardona 2000: 200.

Cyphoproculus mniszechi: Kuwert 1898: 179.

Cyphoproculus kraatzi Kuwert 1898: 178. Type at MNHN, Paris. Type locality: Colombia. (**New synonymy**).

Proculus kraatzi: Hincks & Dibb 1935: 31; Blackwelder 1944: 191; Reyes-Castillo 1970: 156; Van Doesburg 1942:330.

Proculus magister Casey 1897: 641-642. Holotype at USNM. Type locality: San Pedro Sula, Honduras; Casey 1914: 374; Hincks & Dibb 1935: 31; Blackwelder 1944: 191; Johnston 1959: 124-125 (conditionally proposed synonymy). (**New synonymy**).

Passalus goryi Melly *sensu* Thompson 1857: 421, clarified by Kaup 1868:11-12.

Description. Head: anterior border of labrum concave, anterior angles rounded. Frontoclypeal suture generally lacking between internal tubercles but superficially completely marked in some specimens from the Sierra de los Cuchumatanes. Frontal ridges absent or present, internal tubercles present and distinct. Median frontal structure (MFS) with short center horn, apex not free; lacking setae on each side of horn. Ligula between insertions of labial palpi, wide, concave or flat, lacking medial setae, anteriorly triangular; surface shiny. Lateral lobes of mentum with longitudinal central tumosity or ridge; center of mentum anteriorly triangular and unilobate (some specimens with indentation). Last segment of labial palpus large, 1/2 or slightly more than 1/2 length of second segment. Dorsal mandibular tooth small to medium, with acute angle in lateral view (Fig 2c), aspect of mandibles in ventral view rounded, external part of mandible with ventral keel. Thorax: Pronotum shiny and smooth, lateral fossae lacking setae and punctation. Scutellum with small punctate setae. Mesosternum with setae on posterior sides, mesosternellum moderately setose posteriorly. Metasternal disk delimited partially or totally by setose punctation, marginal groove narrow. Elytra: Shiny and smooth; elytral striae marked with superficial and weak punctation. Setae presents only on humeri and anterior margin. Legs: Mesotibiae with two (sometimes three) spines on external border (one in some old specimens). Dimensions: (mm) (n = 18). Total length 53.95-79.30, O = 66.44; elytral length 28.75-39.20, O = 34.07; pronotal length 13.00-22.35, O = 17.71; pronotal width 19.00-29.10, O = 23.83; elytral width 18.95-28.65, O = 23.89; head width 16.00-23.00, O = 19.54.

Material Examined. 146 specimens and 3 in pieces.

Holotype: *mniszewi* Kaup, *Passalus goryi* Th. nec Melly, Guatemala (sic), Ex Musaeo J. Thompson (MNHN). Holotype: *kraatzi* Kuw., Colombie, Ex Musaeo A. Kuwert 1894 (MNHN). Holotype: *Proculus magister* Casey 1897 (USNM).

GUATEMALA: Izabal, Sierra de Caral, 18 VI 1991, E. Smith & J. Monzón, >1300 m (1). Izabal, Los Amates, Cerro Nylon, above San Antonio, 8-11 IV 1990, J.C. Schuster, # Wlp-2, 1200 m (1). Alta Verapaz, Tucurú, Chelemhá, 25 III 1989, J. Monzón (7). Same data but 18 V 1994, J. Quiñonez, 2100 m (1). Same data but VI 1989, F. Herrera. Same data but Montaña Yalijux, 20 IV 1994, J. Quiñonez (1). Same data but Mt. Yalijux, 23 III 1989 G. Ibarra, 2000-2300 m (1). Alta Verapaz, Rocja-Nao Tactic, 15 II 1975, 1525 m (1). Alta Verapaz, Rocja, VI 1976, 1525 m, E. Welling, col. (4, MAM). Tactic, Alta Verapaz, IV 1976, >1400 m, E.C. Welling, leg. (2, IEXA). Rocja, IV 1976, E. Welling, leg., *Proculus mniszewi* Kaup, Reyes-Castillo, det. 1984 (16, IEXA). Baja Verapaz, Purulhá, Biotopo del Quetzal, 28 VI 1993, M. Caal (1). Same data but 11 IV 1990, collector unknown (1). Same data but 29 IV 2001, S. Hidalgo (1). Baja Verapaz, Purulhá, 17 VI 1992, crossing the highway, R. Pérez (1). Baja Verapaz, S. of Purulhá, 9 V 1976, Km. 152 rd, J.C. Schuster, # DT 1,2, 1640 m (2). Baja Verapaz, nr. Purulhá, walking, # DZ-59, 27 IV 1986, E. Klanderud (1). Baja Verapaz, nr. Purulhá, 6 VIII 1984, # FSI-4, J.C.S. (4). Baja Verapaz, nr. Purulhá, km 150, 23-24 VI 1980, # MEa, J.C.S., 1570 m (1). Baja Verapaz, Purulhá, 23 V 1981, S. Durán (1). Baja Verapaz, 3 Km E. of Chilascó, 13 IX 1981, J.C. Schuster, # OKG-12, 1930 m (4). Baja Verapaz, La Unión Barrios, Cerro Verde, IX 2000, A. Higueros (1). Baja Verapaz, Purulhá, 28 III 1993, H. Castañeda, 1500 m (6). Purulhá, Baja Verapaz, V 1976, 1500 m, E.C. Welling, leg. (2, IEXA). Purulhá, 30 VIII 1956, R. Adlington, *Proculus mniszewi* Kaup, Reyes-Castillo, det. 1972 (1, IEXA). Baja Verapaz, Fca. Luisiana, 22 VI 1993, walking, J. Skinner, 2300 m (1). Baja Verapaz, Senahú, 25 VI 1985, P. Pérez, walking on ground 11:00 hrs. (1). Baja Verapaz, 8 VIII 1991, C. Mayorga, col. (1, CNIN). Baleu, Prov. Verapaz, 28 VI 1966, E. Welling, col. (2, IEXA). Same data but, 19 VIII 1966 (1, IEXA). Zacapa, above Jones, 16-18 IV 1992, J.C. Schuster, # WOo, 1910 m (1). Zacapa, above La Unión, 14 VIII 1993, J. Monzón (6). Zacapa, La Unión, 10 V 1992, H. Castañeda, 1500 m (1). Zacapa, La Unión, 26 VI 1992, H. Castañeda (1). Same data but 26 VI 1993 (3). Same data but 22-23 VIII 1992, J. MacVean (1). Zacapa, La Unión, 28 III 1988, J.C.Schuster, # UX-7, 1475 m (1). Same data but # UZ-1,2, 1570 m (2).

Same data but # UX-5,6 (3). Quiché, Uspantán, montaña al norte de Laj Chimel, VII 1998, 2000 m, bosque nuboso, R. Pinula (3). Same data but, 2100 m, VII 1998, E. Cano & J. Monzón (3). Same data but 8-16 VIII 1996, J. Monzón (2). Same data but VII 1996 (1 in pieces). Same data but 1600-2100 m, 20 VII 1997, bosque nuboso, E.Cano & A. Villegas (2). Same data but Cuatro Chorros, 1500 m, VIII 1998, J. Monzón (1). Quiché, Uspantán, Macalajau 14 XI 1996, 1530 m. M. Acevedo (1). Quiché, Uspantán, aldea Laguna Danta, 31 V 1998, ex bosque nuboso, E. Cano (2 elytra). Paris Museum, Guatemala, Dept. de Chiquimula, 600 a 1000 m alt., R. Guérin, 1900 (1, MNHN). *Passalus mniszechi* Kaup, Guatemala, *Passalus goryi* Melly, ile de Carmen (1, MNHN). Guatemala, Sammlung G. Schneider, Museumsverein, *Proculus mniszechi* Kaup, Reyes-Castillo, det. 1974, compare au type par Reyes-Castillo, I 1975 (1, IEXA). Museum Paris, Guatemala, env. Guatemala, R. Guérin 1908, *Proculus mniszechi* Kaup, Reyes-Castillo, det. 1972 (1, IEXA). Coll. R.I.Sc.N.B. Guatemala, LeMoult vendit (1, IEXA). Guatemala Sallé, col. *Proculus mniszechi* Kaup, apud Sallé, H.W. Bates, Biol. Cent Amer. (1) (MNHN). *mniszechi*, Guatemala, *Proculus mniszechi* Kaup, apud Sallé, H.W. Bates, Biol. Cent Amer. (1, MNHN). Guatemala (1, MNHN). *Proculus mniszechi* K., Guatemala, Guatemala, *Proculus mniszechi* Kaup (1) (MNHN). *Proculus mniszechi*, Guatemala, Ex Musaeo Felder (3, MNHN). Paris Museum, Guatemala, R. Guérin, 1900 (2, MNHN). Guatemala (1). Guatemala, Collection d'Bonvouloir (1, MNHN). *mniszechi*, Guatemala (1, MNHN). HONDURAS: San Pedro Sula, El Merendón Park, 1500 m, 8 VIII 1980, R. Lehman (1). "Nonfried Coll. Sammlung G. Schneider Museumsverein" (1). "Honduras, Coll. Nonfried" (1, IEXA). "Honduras", 1579 (1). "*Proculus mniszechi* Kaup, Honduras" (1, MNHN). OTHERS: "Sr. Bocourt, 1865, Exp. Fr. Scient. de Mex." (2, MNHN). "Mexico", Chevrolat Coll. Bought may (1, NMNH) "*Proculus mniszechi* Kaup, Nicaragua, 64/7661" (1, MNHN). "Central America" (1, MNHN). "Venezuela" (6, MNHN). Unknown locality: "Ex Musaeo J. Thompson" (2, MNHN). "*kraatzi* Kuw., Ex Musaeo A. Kuwert 1894" (1, MNHN). 190, 2412/65 (1, MNHN). Collection Mniszech (2, MNHN). Collection Mniszech, Ex Musaeo van Lansberge (7, MNHN). Ex Musaeo A. Kuwert 1894 (3, MNHN). (1, IEXA). Coll. Carl Schuchardt, Seckenberg Museum, *Proculus mniszechi* Kaup, P. Pereira det. 1964 (1, MZSP).

Biogeography. This species occurs commonly in cloud forests between 1500 and 2300 m altitude from west of the Río Chixoy near Macalajau in Guatemala through the Sierra de Chamá and the Sierra de las Minas to the Sierra del Merendón (Espíritu Santo) in Guatemala and the Sierra del Gallinero of Honduras (Fig. 7). Isolated records cite the species from Belize (Bates 1888, cited as British Honduras), Costa Rica (Alfaro 1935, cited from "las montañas húmedas de Carrillo"), Colombia (Kuwert 1891), and Ecuador (Gravely 1918). The record of Colombia includes the type for *P. kraatzi* (Kuwert 1898). Kuwert (1891: 192) cites this species from Colombia and Guatemala; in Kuwert (1898: 179) he cites only Guatemala and describes the Colombian specimen as *kraatzi* 1898: 178. Ecuador is cited originally by Gravely (1918); and van Doesburg apparently copied this without reference to specimens, as did subsequent authors that we have mentioned. Specimens labeled "Nicaragua" and "Venezuela" in the Paris museum are probably errors in labeling (pers. comm., S. Boucher 1994). Interestingly, there are no *Proculus* among the thousands of passalid specimens in the collection of the Instituto Nacional de Biodiversidad in Costa Rica. Data of specimens labeled "Mexico" in the Leiden Museum and Exp. Fr. Scient. de Mex. in Paris Museum, must be confirmed.

Casey (1897: 640) claims that the specimens he studied were collected "in the vicinity of San Pedro Sula, Honduras, on the Atlantic slope", surely the place from which he described *Proculus magister* as confirmed by Johnston (1959: 125).

An interesting genetic study utilizing RAPD-PCR showed three populations of *P. mniszechi* in the Sierra de las Minas to be essentially identical, but differing from a disjunct population near La Union, Zacapa (Villatoro 1997). These differences may reflect recent isolation events as result of the dry and hot Motagua Valley, that has existed since the end of the Pleistocene.

Proculus burmeisteri Kuwert, 1891

Figures 2a, 4b, 5b, 6, 7

Proculus burmeisteri Kuwert 1891: 192. Holotype at MNHN, Paris. Type locality: Guatemala?. Casey 1914: 374; Hincks & Dibb 1935: 31; Blackwelder 1944: 191; Reyes-Castillo 1970: 156; Schuster 1985: 165, 166; 1992a: 288, 289; Schuster 1992b: 361; Padilla & Schuster 1994: 1-5 (mites); Schuster & Schuster 1997: 264.

Cyphoproculus burmeisteri: Kuwert, 1898: 178.

Proculus mandibularis Casey 1914: 374. Holotype at USNM. Type locality: San Pedro Sula, Honduras. Hincks & Dibb 1935: 31; Blackwelder 1944: 191; Johnston 1959: 124-126; Reyes-Castillo 1970: 156. (**New synonymy**)

Proculus mniszewski Kaup *sensu* Casey 1897: 641, 642.

Description. Head: anterior border of labrum concave, anterior angles rounded. Frontoclypeal suture lacking between internal tubercles. Frontal ridges absent, internal tubercles small, distinct. Median frontal structure (MFS) with short center horn with apex not free, lacking setae on each side of horn. Ligula between insertions of labial palpi, wide and concave, flat or divided by a keel or a moderately deeply longitudinal sulcus, with punctured setae at center; surface shiny, anteriorly trapezoidal, apex acute. Lateral lobe of mentum with longitudinal central tumosity or ridge, center of mentum anteriorly triangular with unilobate apex but with a little indentation. Last segment of labial palpi large, less than 1/2 of length of second segment. Dorsal mandibular tooth large, with acute angle in lateral view (Fig. 2a), external aspect of mandibles in ventral view rounded, external part of mandible with ventral keel. Thorax: Pronotum shiny and smooth, lateral fossae without setae and punctuation. Scutellum with abundant small punctate setae. Mesosternum with setae on posterior sides and mesosternellum. Metasternal disk delimited partially or totally by setose punctuation, marginal groove narrow. Elytra: Shiny and smooth; elytral striae marked with superficial and weakly punctuation. Setae present only on humeri and anterior margin. Legs: Mesotibiae with two (sometimes one) spines on external border.

Dimensions (mm) (n = 5). Total length 63.35-73.20, O = 67.61; elytral length 31.45-38.00, O = 34.58; pronotal length 15.80-20.90, O = 17.88; pronotal width 22.00-27.50, O = 24.03; elytral width 22.55-27.40, O = 24.48; head width 18.20-21.65, O = 19.52.

Material Examined. 24 specimens.

Holotype: *burmeisteri* Kuw. Guatem. Ex Musaeo A. Kuwert, 1894 (MNHN). Holotype: *Proculus mandibularis* Casey 1914 (US).

HONDURAS: Ocotepeque Dept., El Portillo Mtn., 14 IV 1981, J.C.Schuster, 1900 m. (7, one specimen lived five years in captivity). Same data but 31 III 1980, # LQ-1, J.C.S., 1810 m. (1). Same data but 2VII 1985, # TK-15, 1900 m. (1). Same data but 13-14 IV 1981, # NJ3, J.C. Schuster (1). Ocotepeque, montaña El Portillo, 13 IV 1981, 1900 m, cloud forest, J.C. Schuster, col. (2%, IEXA). Ocotepeque, El Portillo, 13 IV 1981, 1800 m, bosque nebuloso, J.C. Schuster, col., XXII₂ (3, IEXA). Santa Bárbara, 1750 m, VIII 1995, Th. Porion (4). Lempira, Corquin, Cerros de Celaque, 1800, 17 VII 1999, J. Monzón (2). GUATEMALA: Chiquimula, Esquipulas, mountain east of El Pedregal and Chanmagua, near Honduran border on the Sierra del Gallinero, XII-1999, 1800 m, coffee plantations mixed with cloud forest, J. Monzón (2).

Biogeography. This species is definitely known from north of Nuevo Ocotepeque, between 1810 and 1900 m altitude, and from Santa Barbara Mtn. west of Lake Yojoa (Fig. 7). Although the type cites Guatemala with a question mark, we have seen two specimens collected near the Honduras border, from Chiquimula Dept. in Guatemala (Fig. 7). The type locality in the original description (Casey 1914) of *P. mandibularis*, though cited from San Pedro Sula, seems illogical to us, far to the north of other known specimens and in the range of *P. mniszewski*.

Proculus opacipennis (Thompson), 1857

Figures 2a, 3, 4d, 5d, 6, 7

Passalus opacipennis Thompson 1857: 420-421. Holotype at MNHN, Paris. Type locality: Guatemala.

Proculus opacipennis: Kaup 1868: 13; 1871: 68-69, 118; Bates 1886: 3-4; Kuwert 1891: 192; 1898: 177; Heyne & Taschenberg 1908: 58; Sharp & Muir 1912: 579; Casey 1914: 375; Gravely 1918: 43 (mislabelled specimen from Ecuador); Hincks & Dibb 1935: 31; Van Doesburg 1942:330; Blackwelder 1944: 191; Johnston 1959: 124; Reyes-Castillo 1970: 156-158; Schuster & Summers 1978: 341, 382, 384; Reyes-Castillo & Jarman 1980: 265; Schuster & Reyes-Castillo 1981: 108-109; Schuster 1985: 165, 166; 1992a: 288, 289, 290; Padilla & Schuster 1994: 1-5 (mites); Cano 1994: 33 (aedeagus); Schuster & Schuster 1997: 265; Schuster, Cano & Cardona 2000: 200.

Proculus beckeri Zang 1905: 315. Holotype with seven labels: Syntypus/ Mex/ Beckeri Zg, D.E.Z. 1905. p.315, Typus!! (hand written)/Mex/Zang det/Coll. Kraatz/Coll. DEI Eberswalde. This is the holotype and we have labeled it as such. Type locality: Mexico: Chiapas: Salto de Agua (locality data from Zang 1905, not on the holotype). Casey 1914: 375; Hincks & Dibb 1935: 31; Blackwelder 1944: 191; Johnston 1959: 124; Reyes-Castillo 1970: 156-158; Schuster 1985: 166; 1992a: 289; Padilla & Schuster 1994: 4. (**New synonymy**).

Proculus densipennis Casey 1914: 374-375. Holotype at USNM. Type locality: Chiquimutilla (*sic*), Guatemala. Hincks & Dibb 1935: 31; Blackwelder 1944: 191. Johnston 1959: 124 (conditionally proposed synonymy). (**New synonymy**).

Proculus opacus Kuwert *sensu* Schuster, 1992a: 288, 289.

Proculus opacipennis (in part): Schuster, 1992a: 287.

Description. Head: anterior border of labrum thin, slightly bisinuate to nearly straight, anterior angles rounded. Frontoclypeal suture between internal tubercles lacking. Frontal ridges poorly marked to almost absent, internal tubercles small to very small, distinct. Median frontal structure (MFS) with central horn, short, apically rounded and not free; lacking setae on each side of horn. Ligula between insertions of labial palpi narrow and deeply divided by longitudinal sulcus, anteriorly triangular, apex acute; surface shiny. Lateral lobes of mentum flat; center of mentum anteriorly bilobate with or without punctured setae. Last segment of labial palpus large, 1/2 or more than 1/2 length of length second segment. Dorsal mandibular tooth large, with acute angle in lateral view (Fig. 2a); aspect of mandibles in ventral view rounded (Fig. 3b); external part of mandible lacking ventral keel. Thorax: Pronotum opalescent and smooth (some specimens with bluish cast), lateral fossae lacking setae and punctation. Scutellum with small punctate setae. Mesosternum with setae on posterior sides and mesosternellum. Metasternal disk delimited partially or totally by setose punctation, marginal groove narrow. Elytra: Opaque and strongly grooved; elytral striae marked with fine punctation; interstriae covered with annular closed (to reticulated) micropunctation, only visible at great magnification. Setae present in anterior margin of all interstriae, and abundant on humeri. Interstria VIII with setae from the humerus to the first 1/6 of the elytron to slightly past the middle; interstria IX with setae at or slightly past middle; interstria X with setae from humerus to posterior apex. Legs: Mesotibiae with two (occasionally one, three or four) spines on external border.

Dimensions (mm) (n = 18). Total length 52.25-68.95, O = 60.86; elytral length 29.00-33.50, O = 31.67; pronotal length 14.60-19.95, O = 17.13; pronotal width 20.00-25.80, O = 22.26; elytral width 19.50-25.70, O = 22.63; head width 16.20-19.00, O = 17.20.

**Mandibular curvature for "opaque"
group of *Proculus***

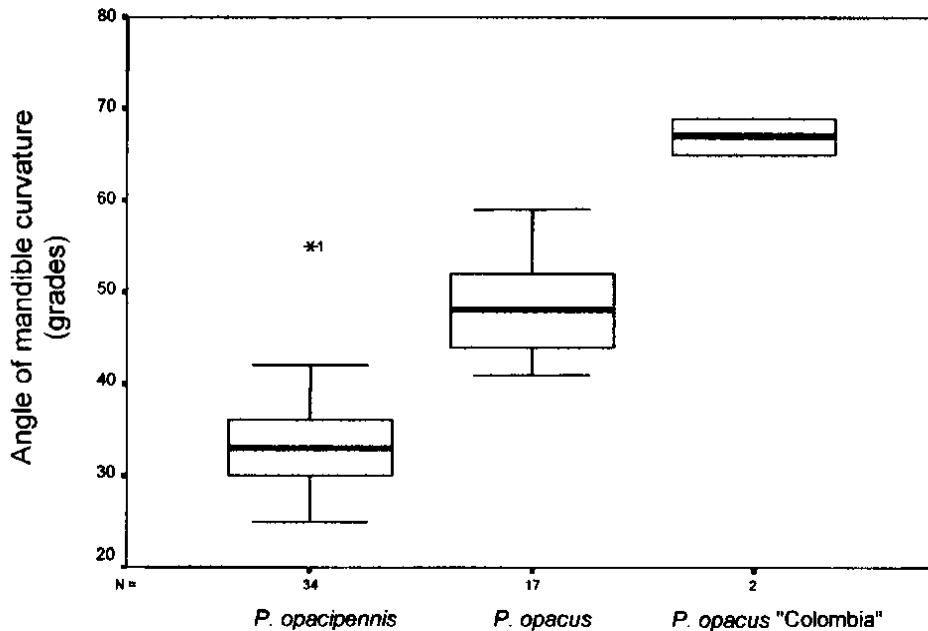


Figure 3
Boxplot of mandibular curvature of "opaque" group of *Proculus*.

Material Examined. 100 specimens.

Holotype: *P. opacipennis* Thomps, type, Guatemala, Ex Musaeo J. Thompson (MNHN). Holotype: *Proculus beckeri*, Zang (Syntypus), Typus!!, Mex, Zang det., Coll. Kraatz. Coll. DEI in Eberswalde, Germany. Holotype: *Proculus densipennis* Casey 1914 (USNM).

GUATEMALA: Alta Verapaz, Sierra de Santa Cruz, Sexán, V 1989, J. Monzón (6). Alta Verapaz, 1976, G. Kramer (1 specimen lived 4 years in captivity). Alta Verapaz, Finca Seacté, Coban, II 1976, G. Kramer, col. (1%, IEXA). Same data but Carchá, II 1976, Kramer (1%, IEXA). Senahu, Vera Paz, Champion, H.W. Bates, Biol. Cent. Amer. (1, MNHN). Izabal, Cerro San Gil, VII 1993, J. Monzón (1%, IEXA). Izabal, Puerto Barrios, Cerro San Gil, VII 1993, J. Monzón (11). Same data but 17 VII 1989, J. Bucklin, 600-700 m snm (1). Same data but 9 VII 1990, S. Marshall, 950 m. (1). Same data but H. Castañeda, no date, 990 m. (1). Same data but VI 1993, J. Monzón (2). Same data but 16 V 1993 (4). Sto. Tomas de Castilla, Cerro San Gil, 18 V 1993, H. Castañeda, col., 950 m (1%, IEXA). Same data but XI 1993, *Proculus opacus*, det. J. Schuster (1%, IEXA). Izabal, nr. Río Zarco Grande, above El Arenal, # EER-C, 11-20 V 1993, E. Cano, 1000-1500 m snm (18). Same data but #EER-C, 11-20 IV 1993, Col. Enio Cano (1%, 1%, IEXA). Izabal, El Estor, Fca. Semuc, II 1989, J. Monzón, 900 m. (1). Izabal, Cemococh, Semuc, 17 VI 1987, J. Monzón (1). Izabal, Las Escobas, 10 I 1991, J. Monzón (2). Zacapa, Gualán, above El

Arenal, Fca. La Providencia, 9-10 V 1993, 1495 m. (5). Zacapa, N. of Gualán, Fca. Valle Verde, 7 VI 1985, # TE 1,2, 920 m J.C.Schuster (2). Same date but, #TE-1, broad leaf wet forest (1, IEXA). ¿FGT, 4822 (1). Quiché, Uspantán, vertiente norte de la montaña al norte de Laj Chimel, 8-16 VIII 1996, J. Monzón, near 1500 m (2). "opacipennis Thoms Guatem., Ex Musaeo A. Kuwert", no other data (1, MNHN). "Guatemala, *Proculus opacipennis* Thoms. H.W. Bates, Biol. Cent. Amer." (1, MNHN). "Guatemala, Ex Musaeo Thorey" (1, MNHN). "Guatemala, *Proculus opacipennis*, Guatemala" (1, MNHN). "Guatemala, *Passalus opacipennis*" (1, IEXA). "*Proculus opacipennis*, Guatemala, Ex. Musaeo Felder" (1, MNHN). Same data but *Proculus opacipennis* (Thompson), Reyes-Castillo. Det. 1971 (1, IEXA). "Guatemala" (3, MNHN). Same data but *Proculus opacipennis* (Thompson), Reyes-Castillo, det. 1981 (1). Same data but *Proculus opacipennis* (Thompson), Reyes-Castillo, det. 1972 (1, IEXA). "Guatemala" (1, MNHN). "171, *Proculus opacipennis* Thoms., Guatemala" (1, MNHN). "Guatemala, Le Moutt vendit, Coll. R.I.Sc.N.B., *Proculus opacipennis* Thoms" (1, IEXA). MEXICO: Chiapas, Tumbalá, 1700 m, VII 1946, M. del Toro, *P. beckeri*, det. P. Reyes-Castillo (2, IEXA). Same data but *P. opacipennis* Thoms., P. Pereira det. (2, MZSP). Chiapas, Tumbalá, 3 IV 1985, P. Reyes-Castillo, *P. beckeri*, det. P. Reyes-Castillo (1 adult with larvae). "Mexico" (1, MNHN). OTHERS: "Costa Rica, Carn. Mus. Acc. 2275" (1, ICCM). "Venezuela" (5, MNHN). "Sudamerica" (1, IEXA). Unknown locality: Ex Musaeo J. Thompson (1, MNHN). "*Proculus opacipennis*" (1, MNHN): "Collection Mniszech, Ex Musaeo van Lansberge" (4, MNHN). "122/72, *Proculus opacipennis*, 2 a 8 Frumen" (1, MNHN). "122/72" (1, MNHN).

Biogeography. This species occurs from Salto de Agua and Tumbalá, Chiapas, México 1700 m, to Guatemala in what appears to be disjunct populations between 600 and 1500 m in the Cuchumatán Mountains, Sierra de Santa Cruz, Sierra de las Minas, and Cerro San Gil (Fig. 7). The type of *P. densipennis* Casey is cited from Chiquimutilla (sic), which, if the same Chiquimulilla (Santa Rosa Dept.), is probably in the volcanic chain of the Guatemalan south coast, an unlikely site. One specimen was seen with a label of Costa Rica. In the Paris Museum there are five specimens from Venezuela, probably errors in labeling.

Commentary. Zang (1905: 315) based his description of *Proculus beckeri* on a single specimen in his collection, now deposited in the Deutsches Entomologisches Institut (DEI) in Eberswalde, Germany, and mentioned a specimen that he had seen from Tumbala in the collection of Mr R. Becker. The first label on the Zang's original specimen, written in Zang's handwriting, on the upper surface says "Beckeri Zg. D.E.Z. 1905.p.315" and, on the lower surface, says "Typus!!". This specimen is the holotype according to article 73.1.2 of the International Code of Zoological Nomenclature (1999).

Proculus opacus Kuwert, 1891

Figures 2a, 3, 4c, 5c, 6, 7

Proculus opacipennis Thompson var. *opacus* Kuwert 1891: 192. Holotype at MNHN, Paris. Type locality: Guatemala.

Proculus opacus Kuwert 1898: 177-178; Hincks & Dibb 1935: 31; Blackwelder 1944: 191; Reyes-Castillo 1970: 156; Schuster 1985: 165, 166; Schuster, Cano & Cardona 2000: 200 (ecological notes).

Proculus beckeri Zang *sensu*: Jarman & Reyes-Castillo 1985: 17 (mandibular force); Jarman 1985:28; Schuster 1985: 166; Reyes-Castillo, Fonseca & Castillo 1987: (nota); Castillo & Morón 1992:37, 39, 41-43; Serrano, Galián & Reyes-Castillo 1998: 160, 163-166 (karyotype). *Proculus opacipennis* (in part) Schuster 1992a: 287.

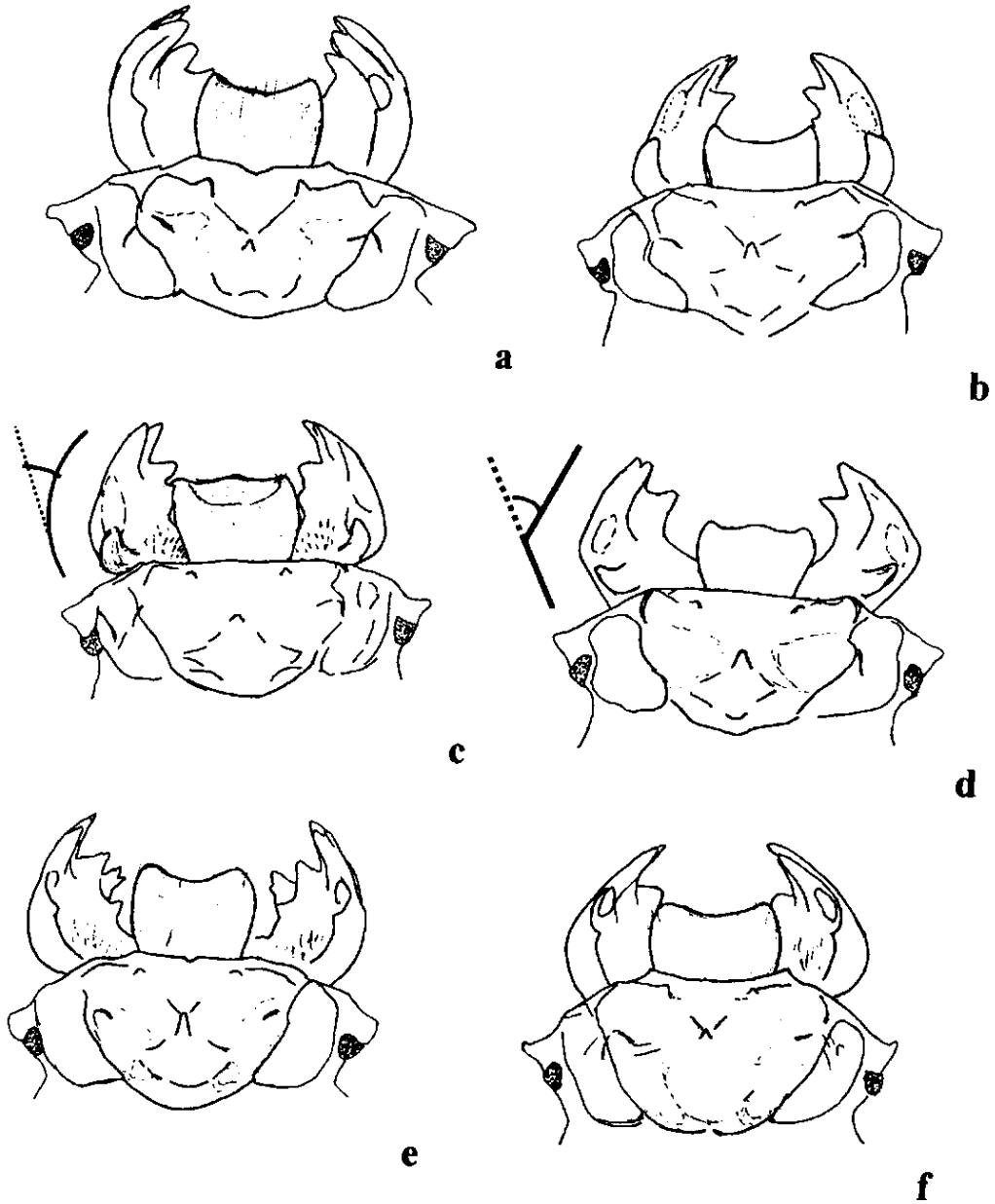


Figure 4

Heads of *Proculus* a) *Proculus mniszewski* Kaup, 1868; b) *Proculus burmeisteri* Kuwert, 1891; c) *Proculus opacus* Kuwert, 1891; d) *Proculus opacipennis* (Thompson, 1857); e) *Proculus goryi* (Melly, 1833); f) *Proculus jicaquei* n. sp.

Redescription. Head: anterior border of labrum bisinuate, thin; anterior angles rounded. Frontoclypeal suture between internal tubercles lacking, deeply marked on outer side of internal tubercles. Frontal ridges poorly marked, internal tubercles small to very small, distinct. Median frontal structure (MFS) with central horn short (size similar to inner tubercles), with apex rounded and not free; lacking setae on each side of horn. Ligula between insertions of labial palpi, narrow, and deeply divided by a longitudinal sulcus, with or without punctured setae at center, anteriorly triangular (acute); ligula matte. Lateral lobes of mentum flat; anterior border of mentum at center bidentate (rounded in old specimens). Last segment of labial palpus large, 1/2 or slightly greater than 1/2 length of second segment. Dorsal mandibular tooth large, with acute angle in lateral view (Fig. 2a); aspect of mandibles in ventral view angular (Figs. 3, 4d); external part of mandible without ventral keel. Two specimens from Colombia have extremely angular mandibles (Fig. 3). Thorax: Pronotum matte and somewhat smooth, lateral fossae lacking setae and punctation. Scutellum with small setigerous punctation. Mesosternum with many setae on posterior sides and mesosternellum. Metasternal disk delimited partially or totally by setose punctation, marginal groove narrow. Elytra: Matte and strongly grooved; elytral striae marked with fine punctations. Setae present on anterior margin of all interstriae, apical margin glabrose. Interstriae VIII with setae on only anterior 1/6, interstriae IX with setae only in apical 1/3; interstriae X with setae covering 1/2 of anterior apex or extending slightly past middle, but never reaching the apex. Legs: Mesotibiae with two or three spines on external border. Dimensions (mm) (n = 4). Total length 50.55-53.45, O = 52.29; elytral length 27.15-28.60, O = 28.07; pronotal length 14.50-14.85, O = 14.62; pronotal width 18.90-19.90, O = 19.56; elytral width 19.60-20.30, O = 19.91; head width 15.45-16.10, O = 15.76.

Material Examined. 40 specimens and three elytra.

Holotype: Guatemala, var. *opacus* Kuw., Ex Musaeo A. Kuwert 1894.

GUATEMALA: Huehuetenango, 14 mi. N. W. of Barillas, Fca. Chiblac, Buena Vista, 19-23 VII 1990, Brody & Campbell, 1150 m. (1). Same data but 10 VII 1997, M. Jolón (2). Same data but 27 V 1998, E. Cano, bosque nuboso (2). Huehuetenango, Fca. Chiblac, VIII-IX 1974, 1000 m (1). Huehuetenango, Barillas, camino entre Nuevo San Mateo y San Juan las Milpas, cerca de la Laguna Maxbal, 28-30 V 1998. E. Cano, bosque nuboso (4). Huehuetenango, Barillas, aldea Malpais, near Buena Vista Chiblac, aprox. 1200 m, VI-1998, E. Cano, C. Bailey & J. Monzón (6 whole specimens and 2 elytra). Huehuetenango, Barillas, Malpais, 1200 m, VI 1998 E. B. Cano, C. Bailey, J. Monzón, *Proculus opacus* det J.C.S., 1988 (1, IEXA). Same data but 27 V 1998 (2). Huehuetenango, Fca. San Luis, 8 km N.E. de Santa Eulalia, VII 1994, J.C. Schuster, 2030 m (1); same data but, 2100 m (1 elytron). MEXICO: Chiapas: 8 mi N of Pueblo Nuevo de Solistahuacán, 31 VII 1956, Bell & Van Horn (1). La Yerbabuena, Pueblo Nuevo, 25 VII 1976, D. Ely, col., 1200 m, bajo tronco podrido, bosque niebla (1, IEXA). Selva Negra, 15 III 1989, 1800 m, J. de la Maza, col., bosque mesófilo (1, IEXA). Mpio. El Bosque, Fca. La Trinidad, 29 IV 1983, P. Reyes-Castillo, 1340 m. (1). km 1 desv. La Trinidad, El Bosque, 22 V 1983, 1300 m, M.A. Morón, col. (3, IEXA). Same data but, M.A. Morón, R. Terrón y J. Valenzuela, col., bosque mesófilo, tocón volteado con dos galerías, pupas y tenerales, *Proculus beckeri*, M.A. Morón, det. (2, MAM). Same data but, alt. 1300 m, ex pupa, 22 V 82, adulto 30 V 82, muere 4 VII 82 (1, MAM). Same data but, 18 VI 1983, M.A. Morón and J. Valenzuela, col. (2, IEXA); Finca La Trinidad, Mpio. El Bosque, 4 IX 1981, 1450 m, P. Reyes, col. (2, IEXA). Same data but, 29 IV 1983, 1340 m, P. Reyes-Castillo, col. (4, IEXA); Mpio. Jitotol, 1 IV 94, A. Horwáth (1, BGG). COLOMBIA: Columbia, 1968, Silverstone (2, LACM). Unknown locality: Carl F. Krueger Colln. Via Dr. John E.S. Dockweiler Collection, Acc. LACMNH Fdn., 1980 (1, LACM).

Biogeography. *Proculus opacus* is known between 1000 and 2100 m altitude from the Cuchumatán Mtns. of Guatemala and west into the northern range of Chiapas (Fig. 7). Two

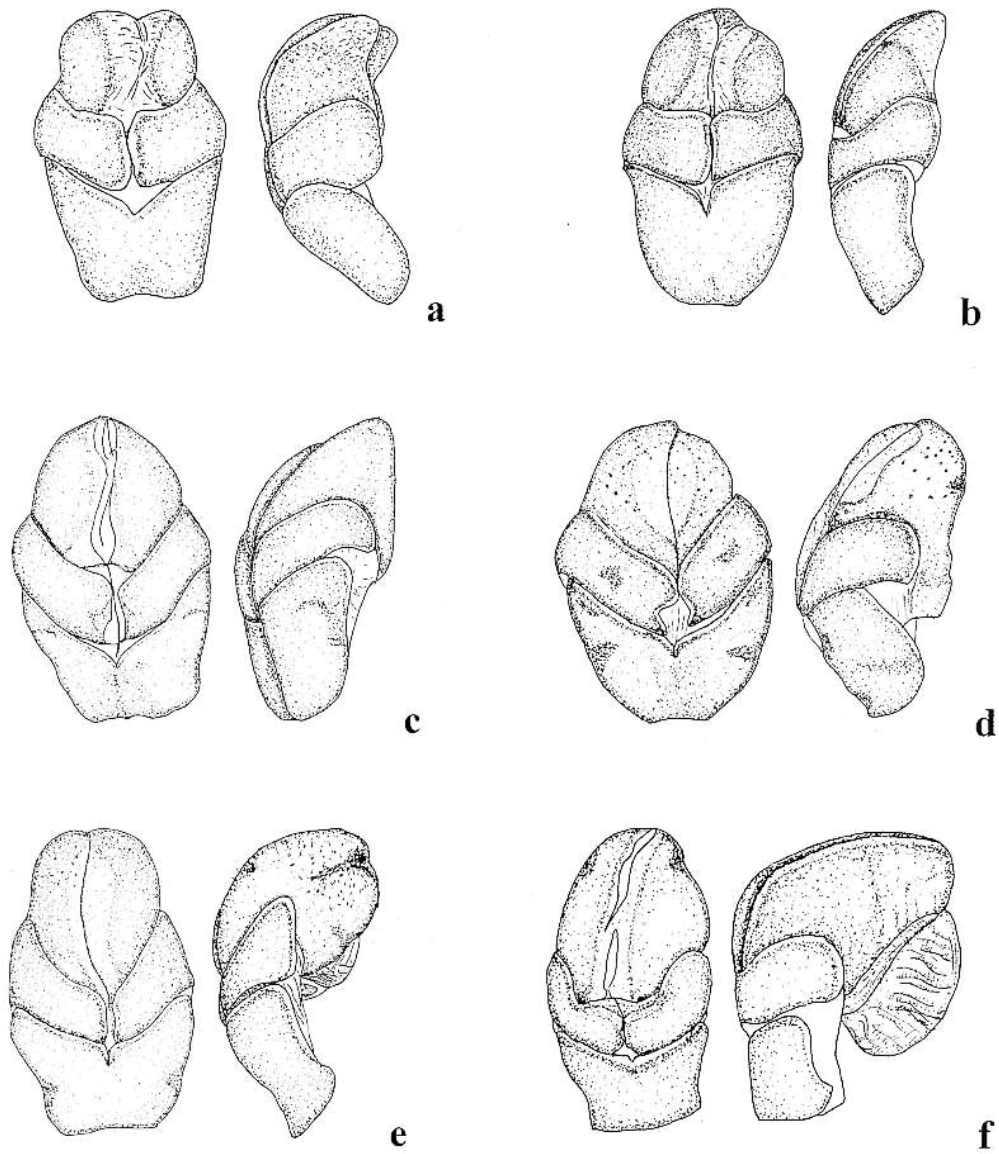


Figure 5

Ventral and lateral view of *Proculus* aedeagi a) *Proculus mniszewi* Kaup, 1868; b) *Proculus burmeisteri* Kuwert, 1891; c) *Proculus opacus* Kuwert, 1891; d) *Proculus opacipennis* (Thompson, 1857); e) *Proculus goryi* (Melly, 1833); f) *Proculus jicaquei* n. sp.

specimens that are apparently *P. opacus* (Fig. 3), deposited in the Los Angeles County Museum, were collected in Antioquia Dept., Colombia on the western slopes of the Cordillera Occidental between 100 and 200 m altitude (Schuster 1994). This record seems highly unlikely considering the flightlessness and lack of intermediate populations between Guatemala and Colombia. except those reported in Costa Rica. Nevertheless, one of us (Schuster) visited the collector in Colombia (now a botany professor at the Universidad del Valle in Cali) and presented various specimens of passalid genera to him. He recognized the *Proculus* specimen as similar to those he had collected many years before in Antioquia.

Proculus goryi (Melly, 1833)

Figures 2b, 4e, 5e, 6, 7

Passalus goryi Melly, 1833: 56 (*gorgyii*, typographic error). Holotype at Muséum d'Historie Naturelle Genève, Switzerland (MHNG). Type locality: "Guatemala". Percheron, 1841: 47; Burmeister, 1847: 480.

Proculus goryi: Kaup, 1868: 9-11; Kaup, 1871: 5, 9, 66-67, 118; Bates, 1886-1890: 3, 383; Kuwert, 1891: 192; 1898: 178; Heyne & Taschenberg, 1908: 58; Schulze, 1912: 209-213; Gravely, 1918: 43; Hincks & Dibb, 1935: 31; Blackwelder, 1944: 191; Trägårdh, 1946:384 (mites); Barrera 1969: 6-7; Reyes-Castillo, 1970: 35, 54, 156-158; Schuster & Lavoipierre, 1970: 3 (associated mites); Schuster & Summers, 1978: 301 (mites); Hammond, 1979:113-180; Reyes-Castillo & Jarman, 1980: 265; Schuster & Reyes-Castillo, 1981: 108 (larvae); Reyes-Castillo, 1985: 299; Schuster 1985: 165, 166; 1992a: 287, 289; 1992b: 361; Padilla & Schuster, 1994: 4; Castillo & Reyes-Castillo 1997: 298; Schuster & Schuster 1997: 261; Schuster, Cano & Cardona 2000: 200; Reyes-Castillo 2000: 176; Reyes-Castillo 2002: 479.

Redescription. Head: anterior border of labrum concave, anterior angles rounded. Frontoclypeal suture lacking between internal tubercles. Frontal ridges absent, internal tubercles absent or very small. Median frontal structure (MFS) with a notable central horn, relatively short and with apex free and rounded; with 0-4 setae on each side or 0-2 small punctations. Ligula between insertions of labial palpi, wide, concave or flat, without setae at center, anteriorly triangular (almost pentagonal with the base); ligula matte. Lateral lobes of mentum flat; center of mentum anteriorly bilobate. Last segment of labial palpi large, 1/2 or more than 1/2 of second segment. Dorsal tooth of mandible small, with obtuse angle in lateral view (Fig. 2b); aspect of mandibles in ventral view rounded; external part of mandible without a ventral keel. Thorax: Pronotum shiny and smooth, lateral fossae without setae and punctation. Scutellum with small punctate setae. Mesosternum with many long setae on posterior sides and similar abundant setae on mesosternellum. Metasternal disk delimited partially or totally by setose punctation, marginal groove very narrow. Elytra: Shiny and smooth (in some cases slightly grooved); elytral striae marked with strong punctation. Setae present in all interestriae of anterior margin and all of posterior except I, II and III; interestriae VIII, IX and X totally covered with setae; IX more densely setose in apical 1/3. In old specimens these setae appear only as punctures. Legs: Mesotibiae with two or three spines on external border (one in some old specimens). Dimensions (mm) (n = 6). Total length 68.45-73.10, O = 70.12; elytral length 34.80-38.60, O = 36.54; pronotal length 18.35-20.50, O = 19.45; pronotal width 23.30-25.95, O = 24.81; elytral width 24.65-27.25, O = 25.93; head width 18.95-21.40, O = 20.17.

Material Examined. 65 specimens and two in pieces.

Holotype: *Passalus goryi* Melly, Guatemala (MHNG).

GUATEMALA: Quetzaltenango, El Palmar (Viejo), finca San Juan Patzulín, 1320 m, 21 III 1998, I. Chavez (1). Quetzaltenango, Colomba, Costa Cuca, 1987, O. Bonilla (2). Costa Cuca,

Guatemala, F. Sarg, H. W. Bates, Biol. Cent. Amer. (2, MNHN). Museum Paris, Guatemala, env. Du Quetzaltenango, 2000 m, R. Guérin 1905 (2, MNHN). Suchitepequez, Fca. La Pista, 23-25 IV 1991, S. Pérez (2). Suchitepequez, N. of Mazatenango, Fca. Asturias, collector unknown, 1400-1500 m. (3). San Marcos, La Fraternidad, I 1994, J. Monzón, 1900 m, cloud forest (7). Same data but, VIII 1997 (1). Same data but, VII 1998 (1). Same data but, VIII 1996, 1950 m (2). San Marcos, Esquipulas Palo Gordo, aldea Noche Buena, near La Fraternidad, 19 IX 1997, 5500 pies, A. Anzueto (8 whole, 2 in pieces). San Marcos, La Fraternidad, camino a El Bojonal, 1600 m, 28 VI 2000, J. Monzón (1). San Marcos, El Tumbador, finca Austria, 4 IV 1998, 1520 m, H. Liere (3). Cerro Zunil, 4-5000 ft, Champion, H.W. Bates, Biol. Cent. Amer. (4, MNHN). Cerro Zunil, 4-5000 ft, Champion, Museum Paris, Amerique Centrale Coll. Du Biol Central Amer., Godman 1906, *Proculus goryi* Gr. (1, MNHN). Cerro Zunil, 4-5000 ft. Champion (1, IEXA). "Guatemala", Coll. E. Witte, Senckenberg Museum, *P. goryi* Kaup, P. Pereira det, 1964 (1, MZSP). "Guatemala?", affazado Lc. Psencoh. Recibido do Dr. Bercal, 1931, Luederwaldt 1931, 06153 (1, MZSP). Guatim. *Proculus goryi* Melly, Ex. Musaeo J. Thompson (1, MNHN). *Goryi* Guér., Guatemala, Ex Musaeo A. Kuwert 1894 (1, MNHN). MEXICO: Chiapas, Finca las Nubes, 2 X 1946, 1200 m, C. Bolivar (1, MZSP). Same data but 1000 m (1, MZSP). Chiapas, volcán Tacaná, 1 X 1956, 1600 m C. Bolívar, col. (1, IEXA); Same data (2, CNIN). Chiapas, volcán Tacaná, V 1965, 1400 m, G. Halffter, col. (1, IEXA). Chiapas, Finca Guatimoc, 18 V, G. Halffter, col. (1, MHNM). Chiapas, Tapachula, Finca Irlanda, 18 IV 1950, J. Hendrichs, col. (1, JHSC). Chiapas, Mpio. Tapachula, Ejido Nueva Independencia, 15° 03' 34" N 92° 17' 06" W, 21 VI 1998, 1550 m J. Macías, col. (1, IEXA). Chiapas, San Luis Malacatán, IV 1958, on ground at light, G. Velásquez, col. (1, MAM). Chiapas, Mpio. Villa Corzo, Cerro Tres Picos, 28 V 1995, 1640 m, P. Hernández y D. Navarrete, col. (1, IEXA; 1, BGG). Chiapas, P. Pereira, det. 1962 (1, IEXA). Veracruz, San Andrés Tuxtla, XI 1942, P. Pereira, det. 1962 (1, IEXA). México (1, MNHN). OTHERS: Senckenberg Museum, Columb. 82, Lehmann 85, Veber Mujulya 19.6.82, *Pr. Goryi* Kaup, P. Pereira det 1964 (1, MZSP). Venezuela (1, MNHN). Collection Mnizech, Ex Musaeo van Lasberge (3, MNHN).

Biogeography. This species occurs between 800 m [though Bates (1886) mentions 350 m], and 1950 m altitude in the western portion of the chain of volcanoes of Guatemala and into Sierra Madre of Chiapas on Volcán Tacaná through Cerro Tres Picos (Fig. 7). One specimen is cited from San Andrés Tuxtla, Veracruz (Reyes-Castillo 1970), far from the known range.

Proculus jicaquei Schuster, Cano & Reyes-Castillo, new species

Figures 2d, 4f, 5f, 6, 7

Description. Head: anterior border of labrum slightly concave, anterior angles rounded. Frontoclypeal suture partially present between internal tubercles. Frontal ridges absent, internal tubercles very small, distinct. Median frontal structure (MFS) with short center horn with apex not free; lacking setae on each side of horn. Ligula between insertions of labial palpi, posteriorly longitudinally divided with both sides protuberant, lacking setae at center; surface matte, anteriorly triangular. Lateral lobes of mentum flat; center of mentum anteriorly trapezoidal and with unilobate apex. Last segment of labial palpus short, 1/2 or less than 1/2 length of second segment. Dorsal mandibular tooth small (Fig. 2d), with obtuse angle in lateral view (Fig. 2d); aspect of mandibles in ventral view rounded; external part of mandible without ventral keel. Thorax: Pronotum shiny and smooth, lateral fossae with various setae and punctation. Scutellum with small abundant punctured setae. Mesosternum with many short setae on posterior sides and mesosternellum. Metasternal disk delimited partially or totally by setose punctation, marginal groove narrow. Elytra: Shiny and smooth, elytral striae marked with visible punctation. Setae

present only on humerus and anterior margin, interstriae X with setae extending 1/3 elytral length. Legs: Mesotibiae with one spine on external border.

Dimensions (mm): Total length 59.5 (%), 67.0 (&); elytral length 31.5 (%), 33.35 (&); pronotal length 17.05 (%), 19.35 (&); pronotal width 21.70 (%), 24.0 (&); elytral width 22.80 (%), 25.75 (&); head width 17.0 (%), 18.75 (&).

Material Examined. Two specimens.

Type Material: Holotype ♀: HONDURAS, Yoro, 10 km. NW of Morazán, 24 III 1991, J.C. Schuster & A. Pineda, # WJG. Paratype ♂: same location and collection data as holotype. Types deposited at the Universidad del Valle de Guatemala collection.

Etymology. Named in honor of the Jicaque, a tribe of people who lives in the area where the specimens were found.

Distribution and Ecology. Known only from the type locality at 575 m on the north side of the Valley of Yoro (Fig. 7). Rotten logs with evidence of this *Proculus*, in the form of characteristic tunnels and feces, were also seen at 800 m.

DISCUSSION

PHYLOGENY: The phylogenetic matrix includes 27 morphological characters, 21 of which are informative and six are autapomorphies. Phylogenetic analysis under assumptions of maximum parsimony results in only one most parsimonious tree (Fig. 6), with a consistency index of 0.72, a retention index of 0.67 and a longitude of 38 steps, excluding autapomorphic states of characters 2, 4, 5, 6, 14 and 23. Under DELTRAN optimization, character 10 (ligula) evolved independently from shiny to matte in the common ancestor of *P. goryi* and *P. jicaquei* and *P. opacus*. Character 13 (center of mentum) evolved independently from unidentate to bidentate in *P. goryi* and *P. opacipennis*. DELTRAN also assumes that the common ancestor of all *Proculus* had minimal setation on 10th elytral interval (state 0 of character 21), that increased in length (state 1) on elytral interval 10 independently in *P. goryi* and the ancestor of *P. opacus* and *P. opacipennis*. Under ACCTAN optimization, tergite 9 of larvae (character 25) presents long setae in the common ancestor of all *Proculus*, but represents a reversal (short setae) in *P. burmeisteri* (larvae of *P. jicaquei* is unknown). Also, character 26 (hairs below spiracle line in tergites 1-2 of larvae) represents a reversal (short hairs) in the ancestor of *P. burmeisteri* and *P. mniszechi* (larvae of *P. jicaquei* is unknown). Under ACCTAN optimization, the mandibular tooth was gained in the ancestor of *P. opacus*, *P. opacipennis*, *P. burmeisteri* and *P. mniszechi* and subsequently lost by *P. mniszechi* as indicated by a reversal in character 7. Under DELTRAN optimization the mandibular tooth represents a parallelism between *P. burmeisteri* and the ancestor of *P. opacus* and *P. opacipennis*. A better understanding of the adaptative significance of the dorsal mandibular tooth could help to differentiate between these two different evolutionary scenarios.

Another interesting character is the elytral setation. There are two equally parsimonious optimizations for this character. The first would assume the common ancestor of all *Proculus* had moderate setation (state 1). Under this assumption, the common ancestor of *P. burmeisteri* and *P. mniszechi* underwent a subsequent reduction

in setation (to state 0) as did *P. jicaquei*; and *P. goryi* underwent an opposite trajectory, increasing the amount of elytral setation (state 2). Under another equally parsimonious optimization, the common ancestor of all *Proculus* had minimal elytral setation (state 0), which was increased once in the lineage leading to *P. opacus* and *P. opacipennis* (state 1) and once independently in *P. goryi* to a highly setose condition (state 2). Again, understanding of adaptive significance of elytral setation might allow one of these two scenarios to be favored.

Table 1
Phylogenetic characters and character states for the species of *Proculus*.

	Character	Plesiomorphic (0)	Apomorphic (1, 2)
	HEAD		
1	Anterior border of labrum	concave	bisinate
2	Frontoclypeal suture	absent	slightly present
3	Frontal ridges	present	absent
4	Inner tubercles	distinct, present	indistinct, absent
5	Median Frontal Structure	apex of horn not free	apex of horn free
6	Setae each side of central horn	absent	present
7	Dorsal tooth of mandible	small	large
8	Dorsal mandibular tooth angle	acute	obtuse
9	Mandible in ventral view	plain	with a keel
10	Ligula	shiny	matte
11	Anterior part of ligula	acute	trapezoidal
12	Lateral lobes of mentum	flat, without ridge	with a ridge
13	Center of mentum	unidentate	bidentate
14	Ventral view of mandibles	rounded	angulate
	THORAX		
15	Pronotum	shiny	matte
16	Lateral fossae of pronotum	without setae and punctation	with setae and punctation
17	Elytral surface	shiny	matte
18	Elytra	smooth	grooved
19	Setae on 8th elytral interval	<1/2	1/2 (=1), >1/2 (=2)
20	Setae on 9th elytral interval	<1/2	1/2 (=1), >1/2 (=2)
21	Setae on 10th elytral interval	<1/2	>1/2
22	Elytral striae	punctation distinct	punctation non distinct
	LARVAE*		
23	Tergite 7 setation	absent	3 TM (median tergal) setae
24	Tergite 8 setation	absent	present
25	Tergite 9 setation	short setae	long setae
26	Hairs below spiracle line in tergites 1-2	absent	many long hairs
27	Many long hairs on center frons	3-5 hairs	10 to many hairs

*For details of larval morphology, see Schuster & Reyes-Castillo (1981)

Table 2

Scoring of character states of *Proculus* and *Veturius platyrhinus* (character state ? = unknown).

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
<i>V. platyrhinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. opacus</i>	1	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	1	1	0	0	1	1	0	1	1	1	1	1
<i>P. opacipennis</i>	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>P. burmeisteri</i>	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	
<i>P. mniszzechi</i>	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
<i>P. jicaquei</i>	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	
<i>P. goryi</i>	0	0	1	1	1	1	0	0	0	1	1	0	1	0	0	1	0	0	2	2	1	0	0	0	1	1	0	

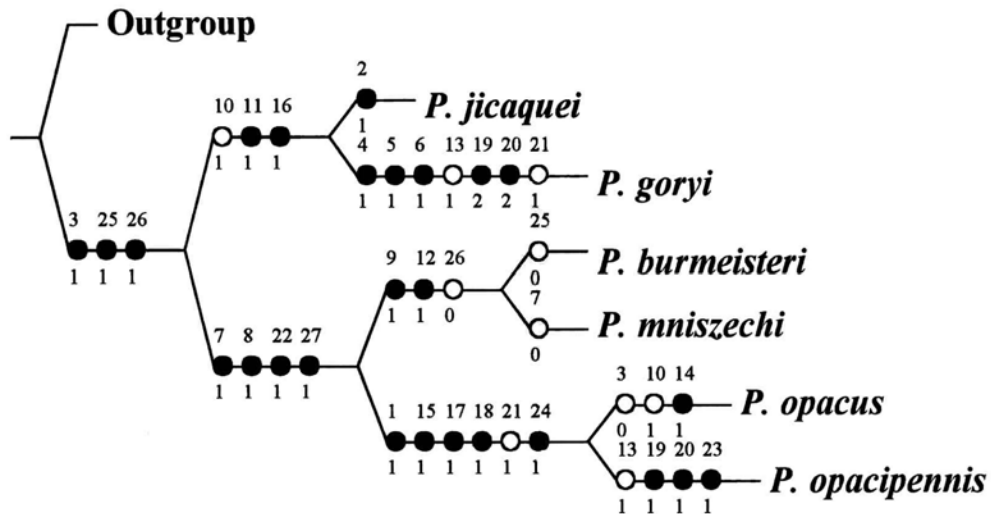


Figure 6
Phylogenetic hypothesis of *Proculus*.

Phylogenetic hypothesis shows that *P. jicaquei* is most closely related to *P. goryi*, these two taxa form a sister clade to all other *Proculus* species. *Proculus mniszzechi* and *P. burmeisteri* are sister taxa, as are *P. opacus* and *P. opacipennis*. Due to the use of larval characters in the analysis, we presume that a better resolution of the relationship between *P. goryi* and *P. jicaquei* will result when larvae of *P. jicaquei* are discovered. Also, more state changes in *P. goryi* since separation from *P. jicaquei* suggest most rapid evolution, especially because *P. goryi* is distributed in more geologically recent terrain (Pliocene-Pleistocene).

BIOGEOGRAPHY: Considering the distribution of *Proculus* species in relation to the phylogenetic hypothesis, two groups of species become evident to the north and south of the line in figure 7 corresponding to the first branching of the cladogram. This correlates with the subhumid corridor described by Stuart (1954) that runs from Chiapas Central Depression to Motagua and Comayagua valleys in Guatemala and Honduras. A more detailed analysis of passalid ensemble distribution in Mesoamerica (see Schuster and Cano in press) also correlates with this north-south separation, suggesting that the origin of this corridor represents a vicariance event. A second possible vicariance event may have separated *P. mniszzechi* from *P. burmeisteri*, as well as *P. goryi* from *P. jicaquei* in the area of the border between Honduras and Guatemala. A similar (same time?) event may have separated *P. opacus* from *P. opacipennis*. These events may be related to the formation of dry valleys separating montane wet regions as occur today in these areas. In glacial times they were probably connected. The cladogram suggests at least two wet-dry cycles, perhaps two glaciations.

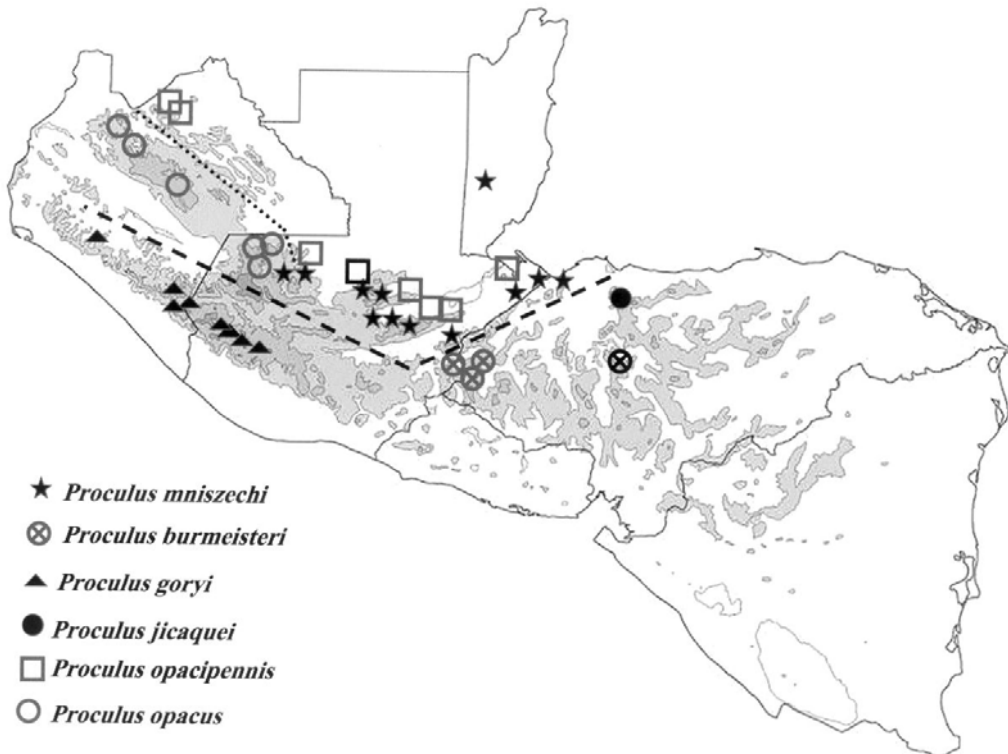


Figure 7
 Map: distribution of *Proculus* in Mesoamerica. Area below 900 m in white.

Though *Proculus opacipennis* and *P. mniszewski* both occur in the Sierra de las Minas and the western Cuchumatán Mountains, they occur in different forest types at different elevations. The latter occurs in cloud forest above 1500 m, whereas the former occurs in a forest that is a mixture of cloud forest and lowland rain forest between 600 and 1500 m. A similar relationship occurs between *P. opacipennis* and *P. opacus* in the western Cuchumatán Mountains and, probably, in the northern mountain ranges of Chiapas. All of the Chiapas *P. opacipennis* were collected between Tumbalá and Salto de Agua in the northernmost mountains (Fig. 7). The *P. opacus* of Chiapas were all collected between La Yerbabuena, municipio El Bosque and Nuevo Solistahuacán in the higher range further south. The ranges of the species of *Proculus* in northern Mesoamerica are shown in figure 7. The drier altiplano to the north of the volcanic chain of Guatemala and Chiapas separates *P. goryi* from all others, a distribution that it shares with *Ogyges laevissimus* (Kaup). The dry Chiquimula Valley separates *P. burmeisteri* from *P. mniszewski* and *P. goryi*. The Copán Valley and the valley north of Santa Barbara Mountain separate *P. burmeisteri* from the other species.

One would expect a high degree of endemism in large, flightless beetles such as *Proculus*; nevertheless, being mid-elevation species (600-2300 m), some were able to disperse relatively widely during glacial periods when mid-elevation forests moved down the mountains and filled the valleys (MacVean & Schuster 1981). This probably explains the presence of *P. mniszewski* on both sides of the deep, dry Motagua Valley, as well as perhaps some of the isolated citations from countries to the south of Honduras (e.g., Costa Rica, in Alfaro 1935). Interestingly, the mite *Klinckowstroemia multisetilosa* Rosario and Hunter, known only from *Proculus*, is found on *P. burmeisteri*, *P. mniszewski* and *P. opacipennis* in the Sierra de las Minas, Sierra del Merendón and El Portillo (Padilla & Schuster 1994), evidence of a possible union of these forests at one time.

Though sometimes aridness in the lowlands of Central America is associated with late Pleistocene glaciations (e.g., Leyden 1984), Bush *et al.* (1992) mention lowland (650 m) of Panama with abundant montane forest elements (*Quercus* and *Magnolia*) at this time. Hooghiemstra *et al.* (1992) mention a drop of ca. 1400 m in the upper forest line in Costa Rica at the Pleistocene-Holocene transition. At any rate, the presence of flightless *Proculus* from Chiapas to at least Colombia implies the presence of contiguous wet subtropical or cloud forest, or at least overlapping forests through time, connecting these areas.

In general *Proculus*, as well as other montane species of passalids, is probably in danger of extinction throughout its range due to the elimination of most of the forest where it occurs.

ACKNOWLEDGMENTS

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Los Angeles County Museum of Natural History for the Colombian specimens and Philip A. Silverstone of the Universidad del Valle, Cali, Colombia, for providing data on the Colombian specimens; the Carnegie Museum of Natural History and Ross Bell of the University of Vermont for the loan of a Costa Rican specimen; Also we thank Gonzalo Halffter, Miguel Angel Morón, Jorge Valenzuela, María Luisa Castillo, Jorge Macías Sámano, Benigno Gómez y Gómez, José Monzón, Abel Anzueto, Erick Smith, Cristina Bailey, Catherine Cardona, Karla Villatoro, J.P. Beraud, Sergio Pérez, Mario Jolón and Armando Higueros for contributed and loaned specimens. John W. Grimes of Lafayette, Louisiana, who kindly donated camping equipment for use in our combined studies of biodiversity and ecotourism. Drawing of figure 1 was made by Claudio Aquiles Méndez. Christopher J. Marshall, Juan J. Morrone, Alan Gillogly and Claudio R. Vasconcelos da Fonseca provided cogent comments that allowed us to improve the manuscript.

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