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Taxonomic review of *Cratocerus* Dejean, 1829 (Coleoptera, Carabidae) with the description of six new species

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Abstract

A diagnosis of the South and Central American genus *Cratocerus* Dejean (Coleoptera: Carabidae) and a key to all species is provided. Eight species are recognized including six species that are newly described: *Cratocerus sinesetosus* sp. n. from French Guiana and Peru; *Cratocerus multisetosus* sp. n. from Costa Rica and Panama; *Cratocerus tanyae* sp. n. from Costa Rica, Guatemala, and Mexico; *Cratocerus indupalmensis* sp. n. a species widely distributed throughout Central and South America; *Cratocerus kavanaughi* sp. n. from French Guiana and Peru; and *Cratocerus culpepperi* sp. n. from Peru. A lectotype for *Cratocerus sulcatus* Chaudoir is designated. Habitus images are provided along with illustrations and images of male genitalia, female genitalia, and diagnostic morphological characters.

Keywords

Pterostichinae, Harpalinae, Cratocerini, Cratocerina, revision, key

Introduction

The genus *Cratocerus* (Coleoptera: Carabidae) was originally described by Dejean (1829) based on two specimens collected from Brazil. Dejean described these as *Cratocerus monilicornis* and placed the genus within his first division of the Carabidae characterized by moniliform antennae. This first division included two additional genera, *Somoplatus* Dejean and *Daptus* Fischer von Waldheim, *Cratocerus* was separated from these based...
on the oval shape of the second labial palpomere. Chaudoir (1852) described an additional species of the genus, *Cratocerus sulcatus* from specimens collected in Mexico. Lacordaire (1854) placed *Cratocerus* in his group Cratocérides, which included the genera of Dejean’s, first division along with *Cyclosomus* Latreille, *Pachytrachelus* Chaudoir, *Microderes* Faldermann, *Geopinus* LeConte, *Batoscelis* Dejean, *Agonoderus* Dejean, *Brachidius* Chaudoir, *Macracanthus* Chaudoir, *Euryderus* LeConte (as *Notiopus* LeConte), *Amblygnathus* Dejean, and *Polpolchila* Solier (as *Melandotus* Dejean). Murray (1858) placed this grouping at the rank of family, Cratoceridae, and included the newly erected African genus *Diatypus* Murray (currently considered a subgenus within *Notiobia* Perty). Chaudoir (1872) later dismantled this grouping and kept only *Cratocerus*, *Brachidius*, and *Catapiesis* Solier (as *Basoleia* Westwood) within the Cratocérides. Though this restricted Cratocérides was ignored by Chapuis (1876), Bertkau (1873) and Horn (1881) agreed with Chaudoir’s, restructuring and recognized the same grouping as Tribe XXX-VIII, the Cratocerini.

Bates (1882) separated out *Catapiesis* along with *Homalomorpha* Brulle as their own subfamily, the Catapiesinae, based on the truncate elytra of the species, which left *Cratocerus* and *Brachidius* to be grouped together as their own subfamily, the Cratocerinae. Sloane (1923) did not adopt the classification proposed by Bates, but he was not able to examine specimens of *Cratocerus* during his studies and instead based the tribal characters on *Catapiesis* exemplars. Csiki (1929) and Blackwelder (1944) kept the constitution of Bates’ subfamilies the same, but regarded these as subtribes within Pterostichini–Catapiesi and Cratoceri. Reichardt (1973) removed the Catapiesi from the Pterostichini, placing *Catapiesis* and *Homalomorpha* as their own tribe, the Catapiesini. *Cratocerus* therefore became a monogeneric subtribe, the Cratocerina, within the Pterostichini (Whitehead and Ball 1974, Reichardt 1977, Straneo 1979). In the checklist of Lorenz (2005), the tribe Cratocerini is considered to be within the subfamily Pterostichinae and is composed of the two subtribes Catapiesina (*Catapiesis* and *Homalomorpha*) and Cratocerina s. str. (*Cratocerus*, *Brachidius*, and *Oxyglychus* Straneo). Bouchard et al. (2011) alternatively placed the tribes Cratocerini and Catapiesini within the subfamily Harpalinae.

Very little is known regarding the natural history of either the larval or adult stages of any *Cratocerus* species. Emden (1942) described a larva of *Cratocerus*, which was found in a rotting stump of a banana tree in Costa Rica, and allied this larva with those he had seen of the African genus *Caelostomus* MacLeay. Label data of adult specimens indicate that they are often collected underneath decaying tree bark.

### Materials and methods

A Leica MZ12.5 stereomicroscope was used to examine 185 adult specimens during this study. Length and ratio measurements were obtained using a calibrated ocular micrometer. When available, ten specimens were measured with at least one from each locality for each measurement to encompass the range of variability. When less than
Ten were available, measurements for all specimens were taken. Measurements listed include apparent body length (ABL), which was measured from the apex of the labrum to the apex of the elytra; total width (TW), which was measured across the widest point of the elytra; head width (HW) measured across the supraorbital ridges; head length (HL) measured from apex of labrum to base of the head; pronotal width (PW) taken across the widest point of the pronotum, usually anterad to center; pronotal length (PL), measured at pronotal midline from apex to base; and elytral length (EL) measured from humeri to elytral apex.

Habitus images were taken with a BK Lab Imaging system (Visionary Digital) and montaged in Helicon Focus 5.3. At least one male and one female specimen were dissected from each collection locality. Male dissections were performed by first using a hooked insect pin to extract the terminalia, which were then placed into a warm 10% KOH solution for 15–20 minutes to clear surrounding tissue. Dissections were then neutralized in 10% acetic acid and washed in water. For female specimens, the entire abdomen was removed, softened, and subsequently cleared in warm 10% KOH for 20–25 minutes. The genitalia were then removed and placed in chlorazol black for 5–10 minutes in order to stain membranous structures. Line drawings were made using a camera lucida and then digitally inked in Adobe Illustrator. Scanning electron micrographs were obtained at the California Academy of Sciences using a Leo 1450VP. Specimens were air dried and coated with gold/palladium using a Denton Vacuum Desk-II prior to imaging. Maps were created using the Cartographer package version 1.31 in Mesquite version 2.75 (build 566) (D. R. Maddison and Maddison 2011; W. P. Maddison and Maddison 2011) using portions of the World, shaded relief and colored height base image from NASA (NASA/JPL/NGA 2004), which was modified for color contrast and cropped to fit.

Verbatim label data for primary type material are listed for each species. A slash (/) indicates separation of lines within one label and a double slash (//) indicates different labels for the specimen. All specimens evaluated in this study were determined to species and bear an identification label. Specimens were borrowed from and will be deposited in the following institutions: American Museum of Natural History, New York, NY (AMNH); Natural History Museum, London, UK (BMNH); Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Canadian National Collections of Insects, Ottawa, Canada (CNCI); Cornell University Insect Collection, Cornell, NY (CUIC); Museum of Comparative Zoology, Essig Museum of Entomology, Berkeley, CA (EMEC); Harvard University, Cambridge, MA (MCZC); Museo Civico di Storia Naturale, Milan, Italy (MSNM); Muséum National d’Histoire Naturelle, Paris, France (MNHN); and the National Museum of Natural History, Washington, DC (NMNH). All specimen data have been entered into the Essig Museum of Entomology Collection (EMEC) database and records can be accessed online using the EMEC numbers listed for each specimen (http://essigdb.berkeley.edu/query_specimens.html).

The Phylogenetic Species concept sensu Wheeler and Platnick (2000) is used in this study where species are the smallest aggregation of specimens diagnosable by a unique set of character states.
Taxon treatments

**Cratocerus Dejean, 1829**


**Type species:** *Cratocerus monilicornis* Dejean 1829:14–15.

**Diagnosis.** Medium to small, rufopiceous to black beetles with a compact, convex body form. Head is relatively broad with prominent eyes and moniliform antennae. Elytral striae are distinctly sulcate. Tergite VIII is divided into hemitergites and those divided into epitergites. This combination of characters distinguishes members of *Cratocerus* from all other carabids within their range including similar genera, e.g. *Catapiesis* and *Moriosomus* Motschulsky.

**Description.** *Microsculpture.* Head dull in appearance with isodiametric microsculpture; pronotum shining with markedly transverse microsculpture; procoxa distinctly granulate isodiametric; abdominal sternites with transverse microsculpture. *Head.* Prominent supraorbital ridge, occasionally with slight rugosity; one or two pairs of supraorbital setae. Frons glabrous. Fronto-clypeal suture distinct. Clypeus with pair of setae present mediolaterally. Labrum with six anterior marginal setae, outer pair length 1/3 × middle pair, middle pair length 1/3 × inner pair; apex of labrum often slightly medially emarginate. Mentum with one pair of setae and prominent medial tooth, submentum with two pairs of setae; transverse suture between mentum and submentum complete. Scape glabrous except for one dorsal seta; pedicel length 1/3 × length of scape, constricted at base with slight apical expansion, with one ring of testaceous setae surrounding apex, antennomere 3 length 1 ½ × that of scape, longer than wide, with several rings of testaceous setae confined to apical 2/3; antennomeres 4–10 transverse and subequal to one another, covered with dense pubescence similarly colored to integument laterally, resulting in matte appearance, midline of antennomeres moderately pubescent; antennomere 11 slightly longer than 10 and broadly rounded apically; antennal length extended to pronotal base. *Thorax.* Pronotal disc 1.1–1.4 × wider than long. Median impression distinct, single basal fovea laterad or pair of fovea laterad with additional fovea overlaying medial impression. Pronotal hind angles sharply denticulate. Elytral length 2.3–2.9 × pronotal length and 1.3–1.6 × elytral width; striae moderately impressed, impunctate or crenulostriate, striae 1, 2, and 7 reaching elytral apex; striae 3 and 4 anastomozing anterad of elytral apex; striae 5 and 6 anastomozing anterad of elytral apex; intervals slightly convex or subsectiform; elytral humeri sharply denticulate; apex rounded, not truncate; plica absent. *Legs.* Protarsomeres 1–4 of males with paired rows of ventral setal pads formed from squamate setae; females with ventral mediolateral spines. Metatrochanter
with one basal seta. Metafemur anterior face with one seta basally located and one medially located. Abdomen. Abdominal sternites IV–VII glabrous except for a single pair of ambulatory setae; males without setiferous fovea; males and females with single pair of setae on sternite VII. Males with parameres glabrous, left paramere larger than right paramere, left paramere with simple to complex curvature (Fig. 11a–g). Females without medial sclerotized ramus at base of gonocoxa; gonocoxa IX clearly separated into basal and apical aspects, gonocoxite 1 and gonocoxite 2; gonocoxite 2 apex pointed and curved laterad, with short, single, broad lateral ensiform seta and short, single, broad dorsal ensiform seta, apical sensory furrow with two nematiform setae; spermathecal gland lacking.

**Distribution.** The genus is distributed (Fig. 13) from southern Mexico throughout Central America, and into the South American countries of Colombia, Ecuador, Peru, French Guiana, Brazil, and Argentina.

**Ecology.** Adults are often collected under the bark of fallen tree branches.


**Cratocerus monilicornis** Dejean, 1829
Figs 1, 9a, 11c


**Diagnosis.** This species is easily distinguished from all other congeners by its relatively large overall body size (9.5–12.0 mm), two pairs of supraorbital setae, and rounded lateral lobes of the mentum.

**Description.** Size large for the genus, ABL 9.5–12.0 mm, TW 4.0–5.0 mm. Color. Head, clypeus, mandibles, pronotum, elytra, and venter rufo-piceous; labrum, antennae, remaining mouthparts, and legs fusco-ferrugineous. Head. HL 1.6–1.9 mm, HW 1.4–1.7 mm. Two supraorbital setae present over each eye. Apices of mandibles slightly curved,
Figure 1. Dorsal habitus image of *Cratocerus monilicornis* Dejean. Scale bar = 1.0mm.
apices at less than 45 degree angle to mandibular midline. Apical maxillary palpmere length 5 x width at base. Mentum with rounded lateral lobes. **Thorax.** Pronotum (Fig. 9a) with distinct median impression, one distinct basal fovea laterad; one lateral setae located on apicolateral pronotal bead; one posterior setae present on posterior bead; pronotal anterior margin convex, greatest width at center; pronotal width 1.3–1.4 x pronotal length. Elytral length 1.4–1.5 x combined elytral width. **Legs.** Protibia with five distinct, stout spines confined to distal half on lateral margin. **Genitalia, male.** Median lobe curved sharply, between forty-five and ninety degrees, with respect to basal 1/3, remaining 2/3 with continuing curvature; not expanded apically; length average for genus. Left paramere complexly curved (Figure 11c). **Genitalia, female.** Spermatheca not examined for this species.

**Distribution.** This species is geographically distributed in Brazil and northeastern Argentina (Fig. 13). According to Csiki 1929 and Blackwelder 1944, *C. monilicornis* has also been recorded from Venezuela, but specimens from this locality were not examined during this study.

**Additional literature.** Dejean and Boisduval 1832: fig. 3; Ragusa 1887: 210.

**Cratocerus sulcatus** Chaudoir, 1852

*Cratocerus sulcatus* Chaudoir 1852: 77-78; Schaum 1853: 190-191; Gemminger and Harold 1868: 250; Chaudoir 1872: 18; Bates 1882: 91, tab. IV, fig. 18; Csiki 1929: 493; Blackwelder 1944: 34; Reichardt 1977: 407; Lorenz 2005: 248.


**Other material.** 1 male, labeled: “PERU: San Martin:Hera, 15 km S.E. Moya-bamba 860m, VII-1947 F. Woytkowski Coll. Donor Wm. Procter” (EMEC207958) borrowed from AMNH; 1 male, labeled: “Ega Bates coll” (EMEC207859) borrowed from MNHN.

**Diagnosis.** This species is most easily confused with *Cratocerus sinesetosus* and *Cratocerus multisetosus*, but is distinguished by the one pair of pronotal apicolateral setae whereas *C. sinesetosus* has no setae at this location and *C. multisetosus* has two or three pairs of setae at this location.

**Description.** Size average for the genus, ABL 5.9–6.1 mm, TW 2.6–2.7 mm. **Color.** Head and prothorax brunneopiceous, elytra and abdominal sternites brunneous, legs, antennae, and mouthparts rufotestaceous. **Head.** HL 0.8 mm, HW 0.8–0.9 mm. One supraorbital setae present over each eye. Apices of mandibles slightly curved, apices at less than 45 degree angle to mandibular midline. Apical maxillary palpmere length 5 x width at base. Mentum with triangular lateral lobes. **Thorax.** Pronotum (Fig. 9b) with distinct median impression, one distinct basal fovea laterad; one lateral setae located on apicolateral pronotal bead; one posterior setae present on posterior bead near
Figure 2. Dorsal habitus image of *Cratocerus sulcatus* Chaudoir, lectotype. Scale bar = 1.0mm.
hind angle; pronotal anterior margin convex; pronotal width 1.3x pronotal length. Elytral length 1.4–1.5x combined elytral width. Elytral intervals prominent, subtriform. Legs. Protibia with three distinct, stout spines confined to distal half of lateral margin; distance between spines 1 and 2 slightly less than distance between spines 2 and 3. Genitalia, male. Median lobe curved sharply, between forty-five and ninety degrees, with respect to basal 1/3, remaining 2/3 with continuing curvature; not expanded apically; length average for genus. Left paramere complexly curved into an “S” shape with basal projection, indistinguishable from Cratocerus multisetosus (Fig. 11b). Genitalia, female. Not examined for this species.

**Distribution.** Figure 13. The lectotype specimen (here designated) for this species is from Mexico, with the type locality having no further restriction at this time. Only two additional specimens were identified as this species -- one from Peru and one from Brazil. These deviate from the type in having slightly less prominent elytral intervals and in the Brazilian specimen, which was smaller, a broader ninth interval near the bases. However, no decisive differences were found and male genitalia were identical. Without additional specimens to examine from across the range, we have tentatively included all three specimens in *C. sulcatus*.

**Additional literature.** Emden 1942: 65.

*Cratocerus sinesetosus* Grzymala & Will, sp. n.  
http://zoobank.org/89EB4B99-B0B5-4B1D-8E23-52AC96847732  
Figs 3, 9c, 10a, 11a, 12a

**Type locality.** French Guiana, Region de Saul, Commune de Saul, coordinates 3.6223°N, 53.2159°W.


Figure 3. Dorsal habitus image of *Cratocerus sinesetosus* Grzymala & Will, sp. n. Scale bar = 1.0 mm.
specimens EMEC207948, EMEC207950 deposited in EMEC, and specimen EMEC207957 deposited in Museo de Historia Natural, Lima, Peru (UNMSM). When the Natural History Museum in French Guiana has completed construction several specimens currently held in NMNH will be transferred there.

**Diagnosis.** This species is distinguished from other members of *Cratocerus* by the absence of setae on the apicolateral bead of the pronotum. This species most closely resembles *Cratocerus sulcatus* and *Cratocerus multisetosus* in overall body shape and coloration, but is easily separated by the absence of apicolateral pronotal setae, whereas there is one pair of apicolateral setae present in *C. sulcatus* and two or three pairs present on the pronota of *C. multisetosus*.

**Description.** Size average for the genus, ABL 5.4–6.1 mm, TW 2.3–2.7 mm. *Color.* Head, prothorax, and elytra piceous. Labrum, mandibles, mentum, and submentum brunneopiceous. Antennae, legs, and remaining mouthparts testaceous. *Head.* HL 0.7–0.9 mm, HW 0.8–1.0 mm. One supraorbital seta present over each eye. Apices of mandibles slightly curved, at less than 45 degree angle to mandibular midline. Apical maxillary palpomere length 5 × width at base. Mentum with triangular lateral lobes. *Thorax.* Pronotum (Fig. 9c) with distinct median impression, one distinct basal fovea laterad; no seta located on apicolateral pronotal bead; one posterior seta present on posterior bead near posterior angle; pronotal anterior margin convex; pronotal width 1.1–1.3 × pronotal length. Elytral length 1.3–1.5 × combined elytral width. *Legs.* Protibia with three distinct, stout spines confined to distal half of lateral margin; distance between spines 1 and 2 slightly less than distance between spines 2 and 3 (Fig. 10a). *Genitalia, male.* Median lobe curved sharply, between forty-five and ninety degrees, with respect to basal 1/3, remaining 2/3 with continuing curvature; not expanded apically. Left paramere complexly curved into an “S” shape with basal projection (Figure 11a). *Genitalia, female.* Spermatheca with 2/3 length thin, gradually expanding approximately 1/3 below apex, ended with broad bulb (Fig. 12a).

**Etymology.** The specific epithet refers to the absence of any anterior marginal setae on the pronotum of this species. The name is formed by combining the Latin *sine* (without) and *setosus* (setose); adjective.

**Distribution.** This species is distributed (Fig. 13) throughout French Guiana, Peru, and Ecuador.

**Ecology.** Specimens have been collected from underneath the bark of rotting trees during the month of February and from flight intercept traps throughout the year.

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**Cratocerus multisetosus** Grzymala & Will, sp. n.
Figs 4, 9d, 10b, 11b

**Type locality.** Costa Rica, Heredia Province, La Selva, 3 km S Puerto Viejo, coordinates 10.42 N 84.00 W.
Type material. HOLOTYPE [male, deposited in INBio] labeled: “COSTA RICA: Heredia, La Selva (3 km S Puerto Viejo, 10°25’N, 84°0’W); 80m; 14 June 1996; R.S. Hanley / fogged from downed logs- Arboretum; #RSHCR052// Cratocerus / sp. 2 // ADP / 105074 // U.C. Berkeley / EMEC 207,970”


Diagnosis. Distinguishable from similar looking species such as C. sulcatus and C. sinesetosus, by the additional setae on the pronotal margin (Fig. 9d) and moderately convex elytral intervals.
Figure 4. Dorsal habitus image of *Cratocerus multisetosus* Grzymala & Will, sp. n. Scale bar = 1.0 mm.
**Description.** Size average for the genus, ABL 5.2–5.8 mm, TW 2.5–2.7 mm. *Color.* Head and prothorax bruneopiceous, elytra and abdominal sternites bruneous, legs, antennae, and mouthparts rufotestaceous. *Head.* HL 0.7–0.9 mm, HW 0.7–0.9 mm. One supraorbital seta present over each eye. Apices of mandibles slightly curved, at less than 45 degree angle to mandibular midline. Apical maxillary palpmere length 5 × width at base. Mentum with triangular lateral lobes. *Thorax.* Pronotum (Fig. 9d) with distinct median impression, one distinct basal fovea laterad; two to three lateral setae located on apicolateral pronotal bead; one posterior seta present on posterior bead near posterior angle; pronotal anterior margin convex; pronotal width 1.2–1.3 × pronotal length. Elytral length 1.4–1.5 × combined elytral width. *Legs.* Protibia with three distinct, stout spines confined to distal half of lateral margin; distance between spines 1 and 2 slightly less than distance between spines 2 and 3 (Fig. 10b). *Genitalia, male.* Median lobe curved sharply, between forty-five and ninety degrees, with respect to basal 1/3, remaining 2/3 with continuing curvature; not expanded apically; length average for genus. Left paramere complexly curved into an “S” shape with basal projection (Figure 11b). *Genitalia, female.* Spermatheca with 2/3 length thin, gradually expanding approximately 1/3 below apex, ended with broad bulb, similar to *Cratocerus sinesetosus* (Fig. 12a).

**Etymology.** The specific epithet refers to the two or three anterior marginal setae on each side of the pronotum found in this species. The name is formed by combining the Latin *multi* (many) and *setosus* (setose); adjective.

**Distribution.** This species is distributed (Fig. 13) throughout Costa Rica and has also been collected in Panama.

*Cratocerus tanyae* Grzymala & Will, sp. n.
http://zoobank.org/D830BA01-460D-4E9B-8848-0FF697B94BD4
Figs 5, 9d, 10c, 11d

**Type locality.** Costa Rica, Limon Province, Reserva Biológica Hitoy-Cerere, Sendero Bobocara. Estimated coordinates 9.67 N 83.03 W.


L N 194500_469850 #2202” (EMEC207991); 1 male and 1 female, labeled: “Est. Queb. Bonita, 50m, Res. Biol. Carara, Prov. Puntarenas, Costa Rica Dic 1992, R. Guzman L_N 194500, 469850” (EMEC207992, EMEC207993); 1 male, labeled: “COS-

Diagnosis. This species most closely resembles *Cratocerus indupalmensis* and can be distinguished by the smaller size, differently shaped pronotum (Fig. 9e, f), and the differently sized and shaped median lobe of the male genitalia (Fig. 11d, e).

Description. Size small for the genus, ABL 4.1–4.7 mm, TW 1.8–2.1 mm. Color. Head and prothorax brunneopiceous; elytra, abdominal sternites, and mandibles brunneous; legs, antennae, and remaining mouthparts rufotestaceous. Head. HL 0.5–0.7 mm, HW 0.6–0.8 mm. One supraorbital seta present over each eye. Apices of mandibles slightly curved, at less than 45 degree angle to mandibular midline. Apical maxillary palpmere length 6 × width at base. Mentum with triangular lateral lobes. Thorax. Pronotum (Fig. 9d) with distinct median impression, one distinct basal fovea laterad; one lateral seta located on apicolateral pronotal bead; one posterior seta present on posterior bead and projecting over posterior angle; pronotal anterior margin convex, greatest width just anterad of center; pronotal width 1.3–1.4 × pronotal length. Elytral length 1.3–1.5 × combined elytral width. Legs. Protibia with three distinct, stout spines confined to distal half of lateral margin; distance between spines 1 and 2 approximately half of distance between spines 2 and 3 (Fig. 10c). Genitalia, male. Median lobe curved sharply, between forty-five and ninety degrees, with respect to basal 1/3, remaining 2/3 with continuing curvature; not expanded apically; length short for genus. Left paramere simply curved (Figure 11d). Genitalia, female. Spermatheca with entire length thin, not gradually expanding towards apex, form similar to spermatheca of *C. kavanaughi* (Fig. 12c), but much longer (2x length) and relatively narrower (1/2x width).
Etymology. This species is named in recognition of Tanya Shahjanian. As an undergraduate student at the University of California, Berkeley, Tanya participated in an insect art and culture project competition and was selected by the panel of judges as the winner with a sculpture piece called “It’s an insect world”. As a prize this fine species of beetle is named for her.

Distribution. This species is distributed (Fig. 13) from Mexico through the Central American countries of Guatemala and Costa Rica.

Ecology. Specimens have been collected from underneath decaying wood and at ultraviolet light traps from July to November.

Cratocerus indupalmensis Grzymala & Will, sp. n.
http://zoobank.org/BFD57836-FE56-474C-9A96-C47A6075D3E3
Figs 6, 9f, 10d, 11e

Type locality. Costa Rica, Puntarenas Province, Canton de Osa, Peninsula de Osa, Rancho Quemado. Estimated coordinates 8.70N, 83.55W.


Figure 6. Dorsal habitus image of *Cratocerus indupalmensis* Grzymała & Will, sp. n. Scale bar = 1.0 mm.
lectors 1991” (EMEC207852); 1 female, labeled: “PERU: LORETO, Cocha Shinguito 27 May 90, 74°45’W, 05°08’S, Erwin et al colls TSShs/1; under bark of rotten branch” (EMEC207853); 1 female, labeled: “PERU LORETO 1 km SW Boca del Rio Samiria Vigilante Post No. 1 130m 15 Aug 1991 04°40.5’S 74°18.9’W, Under bark and on logs in restringa forest off Tr. Norte Lot 12 T.L. Erwin” (EMEC654889); 1 female, labeled: “FRENCH GUYANA: Region de Saül, Commune de Saül, Belvedere de Saül 3.6223 N 53.2159 W, 283-325 meters 24 Jan. 2011, flight intercept trap, VPV S. Brule, P.H. Dalens & E. Poirier” (EMEC654892); 2 males, labeled: “Brasilien Nova Teutonia 27°11 B 52°23 L Fritz Plaumann IX 1948 19” (EMEC207855, EMEC207856); 1 female, labeled: “S. Paulo d’Olivenca Amazones M de Mathan Cratocerus vois bronilinni Chd” (EMEC207857); 1 female, labeled: “Rio Jan. Sulcatus Chaud Bates coll” (EMEC207858); 9 males and 6 females, labeled: “Colombia / San Alberto / Indupalma / Dro Cesar / IX-XI-1968” (EMEC207864, EMEC207861, EMEC207863, EMEC207866, EMEC207867, EMEC207870, EMEC207871, EMEC207872, EMEC207874, EMEC207869, EMEC207860, EMEC207862, EMEC207865, EMEC207868, EMEC207873). Specimens with unique identifier label EMEC207855, EMEC207856, EMEC207857, EMEC207858, EMEC207864, EMEC207861, EMEC207863, EMEC207866, EMEC207867, EMEC207869, EMEC207860, EMEC207862, EMEC207865, EMEC207868, EMEC207873 deposited in MNHN. All remaining specimens deposited in NMNH except EMEC207847 deposited in UNMSM, EMEC207852 deposited in University of Alberta Entomology Collection (UASM), and EMEC207848, EMEC207853 deposited in EMEC.

**Diagnosis.** This species is most easily confused with *Cratocerus tanyae* and can generally be separated by its slightly larger overall body size and the differently shaped pronotum (Fig. 9e, f). The size and shape of the median lobe of the male genitalia distinctly diagnose these two species (Fig. 11d, e).

**Description.** Size average for the genus, ABL 4.8–5.5 mm, TW 1.8–2.4 mm. Color. Head and prothorax brunneopiceous; elytra and abdominal sternites bruneous; legs, antennae, and mouthparts rufotestaceous. Head. HL 0.7–0.9 mm, HW 0.7–0.8 mm. One supraorbital seta present over each eye. Apices of mandibles slightly curved, at less than 45 degree angle to mandibular midline. Apical maxillary palpomere length 6 × width at base. Mentum with triangular lateral lobes. Thorax. Pronotum (Fig. 9f) with distinct median impression, one distinct basal fovea laterad; one lateral seta located on apicolateral pronotal bead; one posterior seta present on posterior bead and projecting over posterior angle; pronotal anterior margin convex, greatest width anterad of center; pronotal width 1.2–1.3 × pronotal length. Elytral length 1.5–1.7 × combined elytral width. Legs. Protibia with three distinct, stout spines confined to distal half of lateral margin; distance between spines 1 and 2 equidistant to distance between spines 2 and 3; one additional smaller spine laterad to spine 1 and one additional smaller spine anterad to spine 1, both only slightly visible with magnification of 125×, clearly visualized with scanning electron microscopy (Fig. 10d). Genitalia, male. Median lobe curved sharply, between forty-
five and ninety degrees with respect to basal 1/3, remaining 2/3 with continuing curvature; very slight apical expansion; length average for the genus. Left paramere simply curved (Figure 11e). Genitalia, female. Spermatheca extremely thin, filamentous, form similar to spermatheca of C. kavanaughi (Fig. 12c), but much longer (2× length) and relatively narrower (1/2× width).

**Etymology.** The specific epithet refers to a series of specimens bearing locality labels specifying “Indupalma”. This series represent the specimens that were first recognized as constituting part of this quite variable new species of *Cratocerus. Indupalma* is treated as an adjective.

**Distribution.** This widespread species (Fig. 13) has been collected in Belize, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Mexico, Panama, and Peru.

**Ecology.** This species has been collected under the bark of rotting, fallen trees.

*Cratocerus kavanaughi* Grzymala & Will, sp. n.
http://zoobank.org/DD97E235-56AB-46C3-9003-9956C66D1A96
Figs 7, 9g, 10e, 11f, 12c

**Type locality.** French Guiana, Nouragues Scientific Station, Pararé site, coordinates 4.02 N 52.41 W.


Figure 7. Dorsal habitus image of *Cratocerus kavanaughi* Grzymala & Will, sp. n. Scale bar = 1.0 mm.

**Diagnosis.** This species is distinguished from other members of *Cratocerus* by the strongly curved mandibles, 45 degrees in relation to the mandibular midline and the two basal pronotal fovea. This species is most easily confused with *Cratocerus culpepperi* as both have the distinctively curved mandibles, a character which does not occur in any other species within *Cratocerus*. *Cratocerus kavanaughi* is easily identified by the larger overall body size and the two pronotal basal fovea as opposed to the five found with *Cratocerus culpepperi* specimens (Fig. 9g, h).

**Description.** Size average for the genus, ABL 4.8–5.6 mm, TW 1.9–2.4 mm. **Color.** Head and prothorax brunneopiceous; elytra, abdominal sternites, and mandibles brunneous; legs, antennae, and remaining mouthparts rufotestaceous. **Head.** HL 0.7–1.0 mm, HW 0.8–0.9 mm. One supraorbital seta present over each eye. Apices of mandibles strongly curved, apices at more than 45 degree angle to mandibular midline. Apical maxillary palpi length 4 × width at base. Mentum with triangulate lateral lobes. **Thorax.** Pronotum (Fig. 9g) with distinct median impression, one distinct basal fovea laterad; one lateral seta located on apicolateral pronotal bead; one seta present on posterior bead and projected over posterior angle; pronotal anterior margin convex, greatest width anterad of center; pronotal width 1.3–1.4 × pronotal length. Elytral length 1.4–1.6 × elytral width. **Legs.** Protibia with three small, stout spines confined to distal half of lateral margin, only visible with extreme magnification (Fig. 10e). **Genitalia, male.** Median lobe curved sharply, between forty-five and ninety degrees with respect to basal 1/3, remaining 2/3 without continuing curvature; narrowed apically; length average for species of the genus. Left paramere curved and simple (Figure 11f). **Genitalia, female.** Spermatheca with entire length equal and moderate, length average for genus; apex rounded, without broad bulb (Fig. 12c).

**Etymology.** The specific epithet, *kavanaughi*, is a Latinized version (genitive case) of the surname of Dr. David H. Kavanaugh, an entomology curator at the California Academy of Sciences. Dr. Kavanaugh provided numerous resources and support to TLG throughout the duration of this project. This species is named in gratitude of this support.

**Distribution.** This species is geographically distributed (Fig. 13) throughout French Guiana and Peru.

**Ecology.** Specimens have been collected in flight intercept traps during the months of November, December, January, February, April, and July and under tree bark in October.
Cratocerus culpepperi Grzymala & Will, sp. n.
http://zoobank.org/B4B00EFA-34CC-4DCC-83B3-40CF563F9303
Figs 8, 9h, 10f, 11g, 12b

Type locality. Peru, Loreto region, Rio Napo, Explomapo Camp, Rio Sucusari, coordinates 3.25S 72.92W.


Paratypes. 8 females with same data as the holotype (EMEC207960, EMEC207961, EMEC207962, EMEC207964, EMEC207965, EMEC207966, EMEC207968, EMEC207969), deposited in NMNH. 2 males, labeled: PERU: “LORETO Rio Napo Explomapo Camp, Rio Sucusari 100m, 15 June 1992 03°15’S, 072°55’W, T.L. Erwin, E. & F. Pfuno S. Insecticidal fog of 20m high canopy mixed with dry leaves (8m3)(14 sheets), with 1 sheet nearly pure Guadua (dry and green leaves) Lot 387” (EMEC207963, EMEC654858). All paratype specimens deposited in NMNH except EMEC207960 deposited in UNMSM.

Diagnosis. This species is distinguished from congeners by the small overall body size, light brunneous coloration, the five basal pronotal fovea, and the mandibles curved more than 45 degrees in relation to the mandibular midline. This species most closely resembles C. kavanaughi, but is easily distinguished by the smaller size and the five basal pronotal fovea as opposed to two.

Description. Size small for the genus, ABL 3.5–4.0 mm, TW 1.4–1.6 mm. Color. Head, labrum, mandibles, prothorax, elytra, and abdominal sternites castaneous; remaining mouthparts, antennae, and legs testaceous. Head. HL 0.4–0.6 mm, HW 0.5–0.7 mm. One supraorbital seta present over each eye. Apices of mandibles strongly curved, apices at more than 45 degree angle to mandibular midline. Apical maxillary palpmere length 3.5 × width at base. Mentum with triangular lateral lobes. Thorax. Pronotum (Fig. 9h) with distinct median impression, two distinct basal fovea laterad and one basal fovea centered on median impression; one lateral seta located on apicodorsal pronotum bead; one posterior seta present on posterior bead and projecting over posterior angle; pronotal anterior margin convex, greatest width anterad of center; pronotal width 1.1–1.2 × pronotal length. Elytral length 1.5–1.6 × combined elytral width. Legs. Protibia with one small, stout spine confined to distal half of lateral margin, only visible with extreme magnification (Fig. 10f). Genitalia, male. Median lobe curved sharply, between forty-five and ninety degrees with respect to basal 1/3, remaining 2/3 with continuing curvature; expanded apically; length average for genus. Left paramere curved and simple (Figure 11g). Genitalia, female. Spermatheca with 1/3 length moderately thin, following 1/3 length extreme-
Figure 8. Dorsal habitus image of *Cratocerus culpeperi* Grzymala & Will, sp. n. Scale bar = 1.0 mm.
Figure 9. Pronotal drawings for: a Cratocerus monilicornis b Cratocerus sulcatus c Cratocerus sinesetosus d Cratocerus multisetosus e Cratocerus tanyae f Cratocerus indupalmensis g Cratocerus kavanaughi and h Cratocerus culpepperi. Scale bars = 0.5 mm.
Figure 10. Scanning electron micrographs of left protibia for: a Cratocerus sinesetosus b Cratocerus multitetosus c Cratocerus tanyae d Cratocerus indupalmensis e Cratocerus kavanaughii f Cratocerus culpeperi. Arrows point to distinct, stout spines referred to in text. Scale bars = 100 µm.

Etymology. This species is named in recognition of Meghan Culpepper, currently a PhD student of carabid phylogenetics and biogeography who provided endless amounts of support throughout the duration of this project. Though this species is one of the smallest within the genus Cratocerus, the red hue of the integument and
Figure 11. Male genitalia, left lateral view of the median lobe and left paramere for: a Cratocerus sinisetosus b Cratocerus multisetosus c Cratocerus monilicornis; d Cratocerus tanyae e Cratocerus indupalmensis f Cratocerus kavanaughii g Cratocerus culpepperi. Scale bar = 0.5mm.

Figure 12. Ventral view of anterior portion of female reproductive tract. a Cratocerus sinisetosus b Cratocerus culpepperi and c Cratocerus kavanaughii. Abbreviations: bc, bursa copulatrix; co, common oviduct; sp, spermatheca. Scale bar = 0.25 mm.
morphological characters mentioned above make it one of the most distinctive. Miss Culpepper is equally unique and we name this species for her.

**Distribution.** This species is currently only known from Peru (Fig. 13).

**Ecology.** Specimens examined in this study were all collected from insecticidal fogging of suspended dry leaves in the canopy and a tree during the month of June.

**Figure 13.** Map showing location of material examined for species of *Cratocerus*. 
Key to the species of *Cratocerus* Dejean

1 Two pairs of supraorbital setae; pronotum widest at midpoint; larger species, ABL 9.5–12.0 mm; habitus as in Figure 1; Venezuela, Brazil–northeast Argentina.......................................................... *Cratocerus monilicornis*
   – One pair of supraorbital setae; pronotum widest anterad of middle; smaller species, ABL 3.5–6.5 mm .................................................................

2 Pronotum with two, occasionally three, pairs of anterior marginal setae (Fig. 9d); habitus as in Figure 4; Costa Rica–Panama ........... *Cratocerus multisetosus* sp. n.
   – Pronotum with one or no pairs of anterior marginal setae (Fig. 9b, c, e–h). . . . .

3 Apices of mandibles strongly curved, forming an approximately right angle with the mandibular midline ......................................................
   – Apices of mandibles slightly curved, forming less than 45 degree angle to the mandibular midline .................................................................

4 Outer and inner pair of pronotal basal fovea present (Fig. 9h); small in size, ABL 3.5–4.0 mm; habitus as in Figure 8; Peru .. *Cratocerus culpepperi* sp. n.
   – Outer pair of pronotal basal fovea present, inner pair absent (Fig. 9g); mid-sized, ABL 4.8–5.6 mm; habitus as in Figure 7; French Guiana and Peru...

5 Pronotum without anterior marginal setae (Fig. 9c); habitus as in Figure 3; French Guiana, Peru, and Ecuador ............... *Cratocerus sinesetosus* sp. n.
   – Pronotum with one pair of anterior marginal setae (Fig. 9b, e, f) ................

6 Pronotum wider than long (Fig. 9b); larger specimens, ABL 5.7–6.1 mm, maximum elytral width 2.7 mm; habitus as in Figure 2; males with aedeagus as in Fig. 11b; Mexico, Brazil, Peru .......................... *Cratocerus sulcatus*
   – Pronotum approximately as wide as long (Fig. 9e and f); smaller specimens, ABL 4.1–5.5 mm, maximum elytral width 2.4 mm...........................

7 Smaller in size, ABL 4.1–4.7 mm; pronotum widest just anterad of center (Fig. 9e); males with aedeagus as in Fig. 11d; habitus as in Figure 5; Mexico–Costa Rica ................................................................. *Cratocerus tanyae* sp. n.
   – Larger size, ABL 4.9–5.5 mm; pronotum widest near anterior apices (Fig. 9f); males with aedeagus as in Fig. 11e; habitus as in Figure 6; Mexico–Brazil.... ................................ *Cratocerus indupalmensis* sp. n.

Discussion

No detailed study of the characteristics of *Cratocerus* relative to their possible placement in a tribal scheme has been done. They are clearly placed in Harpalinae based on the shared harpalidian abdominal configuration (Liebherr and Will 1998, Deuve 1993). An association with *Catapiesis, Brachidius* and *Oxyglychus* was suggested by Will et al. (2000) given similarities of tergite VIII, whereby the tergite is divided into hemitergites and those further divided into epitergites in a manner unlike lebiomorphs and
orthogonines. The tergal configuration in *Cratocerus, Catapiesis, Brachidius* and *Oxyglychus* is not equivalent to “tergite turrets” of lebiomorphs and orthogonines (contra Erwin 1984, Erwin 1985, Bousquet 2012, Ober and Maddison 2008).

Decyl acetate is an uncommonly produced compound in carabids that was found in the defensive chemicals of the pygidal glands in *Catapiesis* species (Will et al. 2000) and has also been found in *Brachidius* (Will and Attygalle unpublished data). Pygidal gland compounds are not known for *Cratocerus* and *Oxyglychus*. Preliminary analyses of three independent molecular loci consistently group *Cratocerus, Catapiesis*, and *Brachidius* (Will, Kanda and Maddison unpublished data), but no sequence data are available for *Oxyglychus*. Though preliminary and incomplete, these new findings are consistent with recognition of Cratocerini sensu Lorenz (2005), and the placement of the tribe in Harpalinae remains *sedis mutabilis*.

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