INSECTA MUNDI

A Journal of World Insect Systematics

0050

Taxonomic review of the Neotropical *Tetragonoderus* quadriguttatus assemblage (Coleoptera: Carabidae: Cyclosomini) with description of *T. deuvei*, new species, and new West Indian and Nearctic locality records

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Date of Issue: October 10, 2008

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Insecta Mundi 0050: 1-16

Published in 2008 by

Center for Systematic Entomology, Inc. P. O. Box 141874 Gainesville, FL 32614-1874 U. S. A. http://www.centerforsystematicentomology.org/

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Printed Copy On-Line ISSN 0749-6737 ISSN 1942-1354 CD-ROM ISSN 1942-1362

Taxonomic review of the Neotropical *Tetragonoderus* quadriguttatus assemblage (Coleoptera: Carabidae: Cyclosomini) with description of *T. deuvei*, new species, and new West Indian and Nearctic locality records

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Abstract. The *Tetragonoderus* (*Peronoscelis*) quadriguttatus assemblage is a postulated monophyletic part of the intersectus complex. This assemblage is characterized against a background that includes review of a classification of the genus and comparison, in the form of a key, to other unrelated Western Hemisphere genera that share elongate tibial spurs with *Tetragonoderus* Dejean. The principal, easily observed feature that unites the three members (*T. laevigatus* Chaudoir, 1876; *T. deuvei*, new species (type locality: Cuijaba, Mato Grosso, Brazil), and *T. quadriguttatus* Dejean) of the quadriguttatus assemblage is the four-spotted elytra (two spots per elytron). These species are treated in detail, including key, synonymy (as required), comparisons, description (external and male genitalic features), habitat (if known), locality data, and geographical range map. Also, *T. subfasciatus* Putzeys, 1846, the elytral color pattern of whose members may be confused with the spotted pattern of the quadriguttatus assemblage, is treated similarly. The following new synonymies were established: *T. quadriguttatus* Dejean 1829 = *T. columbicus* Steinheil 1875 = *T. lacordairei* Chaudoir 1876 = *T. tetragrammus* Chaudoir 1876; and *T. laevigatus* Chaudoir 1876 = *T. chaudoiri* Liebke 1928 (replacement name for the junior homonym, *T. unicolor* Chaudoir, 1876).

Lectotypes are designated for *T. unicolor* Chaudoir, *T. lacordairei* Chaudoir, and *T. subfasciatus* Putzeys. A neotype is designated for *T. quadriguttatus* Dejean.

New distribution records in the West Indies for *T. quadriguttatus* are recorded for the islands of Grand Cayman, Jamaica and Hispaniola. These records may be the result of recent natural overseas dispersal from northern South America, or they may be the result of human-mediated accidental introduction, or a combination of both. The southern Floridian (Nearctic) records for *T. laevigatus* probably represent a recent accidental introduction through commerce, followed by dispersal through flights of adults.

Introduction

A single specimen of the genus Tetragonoderus sent by Michael C. Thomas (FSCA) to us for identification set the wheels in motion that resulted in preparation of this paper. Collected in Dade County, Florida, this predominantly dark beetle had 2 pale spots on each elytron (Fig. 1A-C). Thus, it did not match any of the known Nearctic species of its genus, members of which have distinctly variegated elytral color, or are uniformly pale. But it did match the color pattern of a small unresolved Neotropical complex. The genitalia of this Florida specimen, a male, matched those of a Uruguayan male previously and tentatively identified by us as T. laevigatus Chaudoir. Dissections of additional similar specimens on hand in the Strickland Museum (UASM) were made to determine if phallic features might be specifically diagnostic. In fact, an additional 3 types of phalli were observed (Fig. 5A-H), 2 of which were associated with 2 additional named species (T. quadriguttatus Dejean and T. subfasciatus Putzeys), and 1 with a species that was unnamed and undescribed. This paper, then, treats the taxonomic aspects of 4 species, 3 of which are assigned to an informal quadriguttatus assemblage, identified by spotted (Fig. 2A-C) rather than fasciate elytra, and a fourth species with elytra that are either subfasciate, that is, the fascia is narrow compared to those of most other species of Tetragonoderus (cf. Fig. 2D) or spotted, with the fascia seemingly shorter than normal. That species is probably related to, or a member of, another yet-to-be established taxonomic assemblage.

Material, Methods, and Terms

Material

This study is based on examination of 319 *Tetragonoderus* adult specimens. Some of the material was available in the Strickland Museum, Department of Biological Sciences, University of Alberta (UASM). Additional material was borrowed from, or deposited in, the following institutions and private collections, noted in the text by the associated codens. Names of owners or curators are included, in parentheses.

- ABSC Archbold Biological Station Collection, P.O. Box 2057, Lake Placid, Florida, U.S.A. 32852-2057 (M.A. Deyrup)
- **AMNH** Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, U.S.A. 10024 (L.H. Herman)
- CASC Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118 (D.H. Kavanaugh, R. Brett)
- CMNC Canadian Museum of Nature, Entomology, P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4 (R.S. Anderson, F. Génier)
- CMNH Section of Entomology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania, U.S.A. 15213 (R.L. Davidson)
- **EMEC** Essig Museum, Division of Entomology and Parasitology, University of California-Berkeley, Berkeley, California, U.S.A. 94720 (K.W. Will)
- **FSCA** Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, P.O. Box 147100, Gainesville, Florida, U.S.A. 32614 (M.C. Thomas, P.E. Skelley)
- IAVH Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Claustro de San Augustin, Villa de Leyva, Colombia (E. Castillo)
- IJSM Science Museum, Institute of Jamaica, 12-16 East Street, Kingston, Jamaica (T.H. Farr)
- MCSN Museo Civico de Storia Naturale "Giacomo Doria", Via Brigita Ligurua 9, I-16121 Genoa, Italy (R. Poggi)
- MCZC Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. 02138 (P.D. Perkins, B.D. Farrell)
- MNHP Entomologie, Muséum National d'Histoire Naturelle, 45 rue Buffon, Paris, 75005, France (H. Perrin, T. Deuve)
- MZSP Museo de Zoologia da Universidade de São Paulo, Biblioteca, 7172, 01.051 São Paulo, Brazil (C. Costa)
- NMNH Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A. 20013-7012 (T.L. Erwin, W.E. Steiner)
- UASC Museo de Historia Natural Noel Kempff Mercado, Avenida Irala 565, Santa Cruz, Bolivia (J. Ledezema)
- **UDAE** S. L. Straneo Collection, Department of Entomology, University of Arkansas, Fayetteville, Arkansas, U.S.A. 72701 (J.B. Whitfield)
- VGIC Vincent Golia, 6095 Harbor Greens Drive, Lake Worth, Florida, U.S.A. 33467-7763
- WIBF West Indian Beetle Fauna Project, Department of Entomology, Montana State University, Bozeman, Montana, U.S.A. 59717 (M.A. Ivie).

Methods

Taxonomic concepts, principles, criteria for ranking, and general working methods follow those of Ball (1975, 1978) and Allen and Ball (1980).

Measurements. Measurements of external body parts were made with an ocular micrometer in a Wild M5 dissecting microscope. Measurements and abbreviations used for them in the text are:

Length of head (Hl): linear distance from base of left mandible to posterior margin of left compound eye;

Width of head (Hw): maximum distance across head, including the compound eyes;



Figure 1. Digital image illustrating dorsal habitus of *Tetragonoderus deuvei*, new species, female ("Jatahy, Goyaz", Brazil [MNHP]. SBL = 3.82 mm).

Length of pronotum (Pl): linear distance from anterior margin to posterior margin, measured along the midline;

Maximum width of pronotum (Pw): greatest linear transverse distance;

Length of elytra (El): linear distance from the basal ridge to apex, (of longer elytron), measured along the suture.

Standardized Body Length (SBL): used as an index of overall size, is the sum of Hl, Pl and El.

Preparation of material. See Shpeley and Ball (2000: 6-7). Photomicrographs of elytral microsculpture were made using a JEOL JSM6301FXV field emission scanning electron microscope. Line drawings of male genitalia were prepared using a camera lucida on a Wild M5 stereoscopic microscope, and elytra were photographed using a Nikon Coolpix 8400 camera, mounted on the same make of microscope. Final drawings, illustrations and plates were prepared using Adobe Photoshop CS 2.0.

Species recognition and descriptions. Because of the distinct shortage of defining character states (habitus of all of the species treated is well represented in Fig. 1), the descriptions are notably short, including reference to measurements and ratios, elytral microsculpture (Fig. 3) and 4) and color, and male genitalia (Fig. 5). Color is of use principally as a group character. Microsculpture mesh patterns, although useful as shown by the SEM images, are not that easily perceived at ordinary magnifications. Specific differences between "isodiametric" and "slightly transverse" are obscured, primarily because in the isodiametric condition the longitudinally oriented microlines are less distinct than the microlines oriented transversely. Absence of many of the

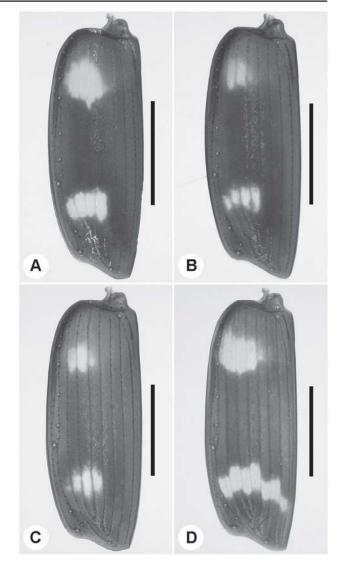


Figure 2. Digital image, left elytron of *Tetragonoderus* species. **A)** *T. laevigatus* Chaudoir. **B)** *T. deuvei*, new species. **C)** *T. quadriguttatus* Dejean. **D)** *T. subfasciatus* Putzeys. Scale bar = 1 mm.

former provides the distinction between isodiametric and slightly transverse. Thus, if one fails to see the longitudinal microlines, a misidentification is likely.

Label data. For type material, the information on each label is reproduced as exactly as is possible using ordinary type. Quotation marks indicate text of each label. A slash mark (/) indicates the end of each line of text. Semicolons and or quotation marks indicate the end of a label. Enclosed in square brackets is information about color of label paper (other than white), or printing (other than black), form of the label (other than rectangular), and coden for collection in which the type specimens are housed.

For other material, sex, locality data, habitat or collecting method, collector(s) and codens are given.

Terms

Box labels. In the species treatments, this term refers to a label in the Chaudoir/Oberthür Collection (MNHP), pinned to the bottom of a specimen box with a banknote pin (Ball and Erwin, 1983: 490, Fig. 6

and 7), on which is written a specific epithet, name of describer, country of specimen origin, and collector. The label refers to the pinned specimen(s) that immediately precedes it. Most of the labels attached to the pins with the specimens state only "Ex Musaeo Chaudoir" (in red type). The box labels, then, are vital for establishing identity and locality, and, in conjunction with the published descriptions, in determining the probable nomenclatural status of the specimens.

Male genitalia. Phalli were recognized as left pleuropic-anopic, with the ostium laterad, but more toward the dorsal surface. The phalli, illustrated in dorsal (Fig. 5A, 5C, 5E and 5G) and right lateral (Fig. 5B, 5D, 5F and 5H) aspects, with base toward the top of the page, exhibit interspecific differences in form. These differences are seen readily as overall patterns ('Gestalt') but are not so easily described, except with notation of differences in size and shape of the distal area. To provide the basis for a more analytical verbal description, two principal regions are distinguished (Fig. 5A), the shaft (sh) and basal lobe (bl). The latter is the swollen area set at an angle to the ventrally curved shaft, surrounding the basal opening (bo).

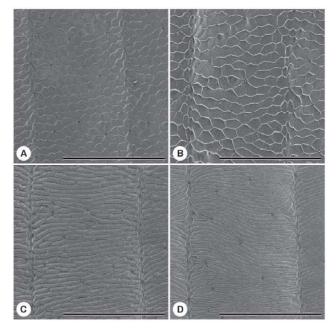


Figure 3. SEM photographs, left elytron of *Tetragonoderus* species, illustrating microsculpture mesh pattern. **A)** *T. laevigatus* Chaudoir. **B)** *T. deuvei*, new species. **C)** *T. quadriguttatus* Dejean. **D)** *T. subfasciatus* Putzeys. Scale bars = 100 m.

Three areas of the shaft are recognized: a more distal periostial area (**poa**), subtending the ostial membrane (**om**), which surrounds the ostium (**oo**, Fig. 4E), marking the place of egress of the endophallus during copulation; a more proximal middle area (**ma**) extended from the base of the periostial area to the basal lobe; and an apical area (**aa**) extended distally from the periostial area to the apex of the phallus. The armature of the endophallus (**ea**) consists of a patch of microtrichia of various extent and form.

Taxonomic Treatment

Key to Western Hemisphere genera of long-spurred lebiomorphs, and species groups of subgenus *Peronoscelis* Chaudoir (modified from Ball and Shpeley 2002: 274)

- Labial mentum toothed. Tibial spurs of middle and hind legs fimbriate (Ball 1983: 523, cf. Fig. 6K-L). Mandible basally with dorsolateral and ventrolateral margins in line, or explanate, with lateroventral margin distinctly laterad laterodorsal margin
- 2(1). Head posteriad eyes constricted in form of narrow neck. Tarsal claws prominently pectinate.

 Mandible basally explanate, lateroventral margin extended distinctly laterad dorsolateral margin

 Tribe Lebiini, *Nemotarsus* LeConte

Pronotum with posterior margin approximately straight. Paraglossae joined apically by a transligular membrane intersectus species group

Synopsis of classification of Tetragonoderus Dejean in the Western Hemisphere

Ball (2000: 190) recognized the Western Hemisphere taxa of *Tetragonoderus* (sensu latissime) as a monophyletic group, ranked as a subgenus, named *Peronoscelis* Chaudoir, with its postulated adelphotaxon being the Eastern Hemisphere tropical subgenus *Tetragonoderus* (sensu stricto) (for a recent and more traditional arrangement and excellent habitus illustration, see Martinez 2005: 217-219). The species of *Peronoscelis*, in turn, were arrayed by Ball in two species groups: the figuratus and the intersectus groups, the latter being the Western Hemisphere equivalent of *Tetragonoderus* (sensu Chaudoir, 1876). Chaudoir (1876: 35-55) recognized in a key-like arrangement of the text several unnamed assemblages. Four of Chaudoir's assemblages, those predominantly or exclusively Western Hemisphere in distribution, are treated here as infrasubgeneric informal "complexes" of convenience, and here designated respectively pictipennis, viridis, tesselatus, and intersectus.

The intersectus complex (Chaudoir 1876: 44-47) is characterized as having mid-tarsomeres 1-4 of males with adhesive vestiture and notched medial apical margin of abdominal sternum VII (referred to as "anus" by Chaudoir), and tarsal claws of both sexes in most species denticulate. Females with abdominal sternum VII rounded, not notched. Chaudoir (1876: 44) also characterized this complex as having a simple (unmargined) prosternal intercoxal process, but this is erroneous: in fact, this process is finely margined. To this complex Chaudoir assigned species with spotted, variegated-fasciate, and unicolorous (black) elytra. The spotted species and South American specimens exhibiting unicolorous elytra are the subject of this paper, and are here referred to as "the spotted assemblage ", or quadriguttatus assemblage. Additionally, we treat one species, *T. subfasciatus* Putzeys exhibiting dark, narrowly fasciate elytra, some specimens of which may be confused with members of the spotted assemblage.

Tetragonoderus quadriguttatus assemblage

Adults with character states of intersectus complex, further restricted as follows. Habitus as in Fig. 1. Size small, SBL 2.36-4.34 mm, ratio Hl/Hw 0.417-0.490, and ratio Pl/Pw 0.597-0.676. Dorsal surface

uniformly dark, deep brunneo-piceous to black, or elytra bicolored, with more or less circular subhumeral and preapical pale markings (Fig. 2A-C) dark to bright testaceous. Ventral surface uniformly dark; antennae, mouthparts, proepipleura, elytral epipleura and legs paler. Males with adhesive vestiture on fore-tarsomeres 1-3 broadly biseriate squamo-setae (Shpeley and Ball 2000: 30, cf. fig. 12B), and on mid-tarsomeres 1-4, dense pads of articulo-setae (Shpeley and Ball 2000: 30, cf. fig. 12E) Tarsal claws with evident denticulations, easily visible at 50X magnification. Phallus slightly left anopic-pleuropic.

Geographical distribution (Fig. 6 and 7). The range of this group extends throughout South America east of the Andes, and northward in the Greater Antilles, and southern Florida.

Relationships. We postulate that the quadriguttatus assemblage is monophyletic, based on overall similarity and chorological affinity of the included species. Chaudoir (1876: 44-49) included this assemblage in the intersectus complex.

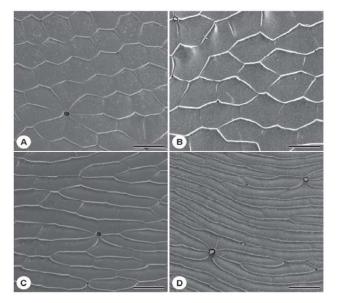


Figure 4. SEM photgraphs, left elytron of *Tetragonoderus* species, illustrating microsculpture mesh pattern. **A)** *T. laevigatus* Chaudoir. **B)** *T. deuvei*, new species. **C)** *T. quadriguttatus* Dejean. **D)** *T. subfasciatus* Putzeys. Scale bars = 10 m.

Also included were *T. subfasciatus* and additional species, males of which exhibit the abdominal sternal and tarsal features noted above, and which have the elytral color pattern variegated, with extensive pale markings.

The species of the quadriguttatus assemblage are very similar to one another in external features. Male genitalia, however, are distinctive, and should be examined to provide a certain identification.

The basis for postulating species relationships is the transformation series of the elytral microsculpture mesh pattern from isodiametric, to slightly transverse, to markedly transverse, exhibited respectively by *T. laevigatus*, *T. deuvei*, and *T. quadriguttatus* (Fig. 3A-C and 4A-C). We suggest that *T. subfasciatus* is a relative of the quadriguttatus assemblage, but not a member.

Key to adults of the Tetragonoderus quadriguttatus assemblage and T. subfasciatus Putzeys

- Elytron with discal setigerous punctures small; microsculpture mesh pattern isodiametric to distinctly transverse (Fig. 3A-C, and 4A-C); dorsal surface rather shiny or with sericeous luster; with two spots, preapical one in intervals 5-8 only (Fig. 2A, 2B and 2C), or unicolorous black. Phallus various (Fig. 4A-F). Specimen from South America (east of the Andes), West Indies or North America (Florida)
- 2(1). Elytron with mesh pattern distinctly transverse (Fig. 3C and 4C), dorsal surface with more or less sericeous luster, and two-spotted. Phallus in dorsal aspect with apical portion short rather broad, apical margin broadly rounded (Fig. 5E), in lateral aspect projected dorsad (Fig. 5F). Geographical range: South America, from Paraguay northward to Colombia, and the West Indian islands of Grand Cayman, Jamaica, and Hispaniola T. quadriguttatus Dejean

Tetragonoderus laevigatus Chaudoir

Fig. 2A, 3A, 4A, 5A-B, 6 and 7

- Tetragonoderus laevigatus Chaudoir: 1876: 46. **Type Material:** HOLOTYPE, male, labeled: "TYPE" [red paper]; "Tetragonoderus/ laevigatus/ J. Mateu det. 1979" [MNHP]. **Type Area:** Montevideo, Uruguay. Csiki 1932: 1298.— Blackwelder 1944: 52.— Lorenz 2005: 453.
- Tetragonoderus unicolor Chaudoir: 1876: 47. **Type Material:** LECTOTYPE (here designated) male, without labels (see "Notes about type material" below). **Type Area:** state of Rio de Janeiro, Brazil. Junior homonym of Tetragonoderus unicolor Gemminger and Harold: 1868: 144. Csiki 1932: 1296.—Blackwelder 1944: 52.—Lorenz 2005: 453.
- Tetragonoderus chaudoiri Liebke: 1928: 129. Replacement name for Tetragonoderus unicolor Chaudoir: 1876: 47. Csiki 1932: 1296. Blackwelder 1944: 52. Lorenz 2005: 453. NEW SYNONOMY.

Notes about type material. In the MNHP is a single specimen associated with the box label "laevigatus Chaudoir Montevideo Livori Mus de Genoa" which is the holotype. Additionally, in the MNHP associated with the box label "unicolor Chaud. Brésil Mines Geraës Squires" are two specimens, a male and a female. Chaudoir in his original description stated he had two examples from the province of Rio de Janeiro, collected by Squires. The specimens associated with the box label were collected by Squires, and the assumption is that the wrong locality data were placed on the box label (Mines Geraës [sic], rather than Rio de Janeiro Province). The male specimen is selected and here designated as LECTOTYPE. The male lectotype of T. unicolor was dissected, and the genitalia match those of T. laevigatus. Additionally, the elytral microsculpture of T. unicolor matches that of *T. laevigatus*. Hence these names are synonymous.

Recognition. See the key, and figures noted above. The broad phallus with broadly triangular apical area is definitive. Specimens of this species with unicolorous elytra could be confused with other southern South American *Tetragonoderus* species exhibiting this feature, for example, *T. viridis* Dejean and *T. chalceus* Chaudoir. However, specimens of these two species have dark legs, rather than the pale ones characteristic of the quadriguttatus assemblage. Further, males of *T. viridis* and *T. chalceus* have only midtarsomeres 1-3 with adhesive vestiture (tarsomeres

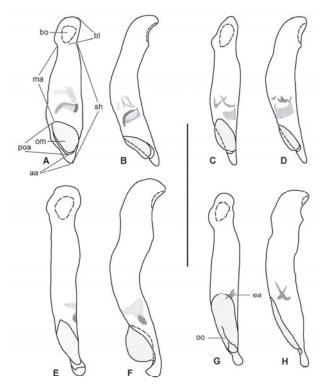


Figure 5. Line drawings of male genitalia of *Tetragonoderus* species. A, C, E and G, dorsal aspect; B, D, F and H, right lateral aspect. A-B) *T. laevigatus* Chaudoir. C-D) *T. deuvei*, new species. E-F) *T. quadriguttatus* Dejean. G-H) *T. subfasciatus* Putzeys. Legend: aa, apical area; bl, basal lobe; bo, basal opening; ea, endophallic armature; ma, median area; om, ostial membrane; oo, ostial opening; poa, periostial area; and sh, shaft. Scale bar = 1 mm.

1-4 of mid-tarsus with adhesive vestiture in the quadriguttatus assemblage), and abdominal sternum VII is slightly emarginate medially in *T. viridis* (distinctly notched in quadriguttatus assemblage males). Male specimens of *T. chalceus* have abdominal sternum VII rounded, not notched.

Description. See Table 1 for values for standardized body length (SBL) and ratios Hl/Hw and Pl/Pw. **Elytra.** Bicolored (Fig. 2A) or uniformly dark, with microsculpture mesh pattern isodiametric, sculpticells relatively uniform (Fig. 3A and 4A); discal setigerous punctures relatively small, not foveate.

Male genitalia. Phallus (Fig. 5A and 5B) in dorsal aspect broad, relatively straight, medial area of shaft widened from its base to periostial area, and narrowed markedly distad rather broadly triangular short apical area, apex obtusely pointed; periostial area short, less than one third length of shaft; in lateral aspect shaft moderately angled, surface without or with parallel ridges (indicated in Fig. 5A by scalloped margins of distal part of median area and proximal part of periostial area), apical area short, moderately triangular; ventral surface smooth. Endophallus, inverted, with prominent microtrichial field, band-like in appearance in both dorsal and right lateral aspects, within medial area.

Notes about variation. A single specimen of T. *laevigatus* from Paraguay exhibits the same type of elytral microsculpture mesh pattern as observed in *T. quadriguttatus*. The Paraguay specimen is a male, and the species determination was established on the basis of its genitalic features.

Of the total material examined, only two specimens from Brazil and four from Paraguay had the pale markings of the elytra much darker than typical (Fig. 2A), and the holotype of *T. unicolor* and five

Montevideo, Uruguay specimens had completely dark elytra with no visible pale markings.

Collecting notes and habitat. In Florida, one specimen was taken on a *Datura* Linnaeus (Solanaceae) plant, others in a residential backyard, and in a sandy/grassy community area. In Bolivia, specimens were collected during daylight in an unshaded sand pit, resting among the roots of dead, standing plants, and in tropical transition forest, in leaf litter. These sites were about a kilometer from the nearest permanent water source. Other Floridian and South American specimens were taken at UV and mercury vapor lights.

Geographical distribution. (Fig. 6-7). The natural geographical range (Fig. 5) of this species extends from southern Uruguay and central Argentina northward to mid-central Brazil on the Atlantic coast, and along the southern and western edges of the Amazon basin. The Florida records (Fig. 7) probably represent a recent point introduction, probably through commerce, with subsequent dispersal by flight. We postulate then, that *T. laevigatus* is established in Florida, with the likelihood of further range expansion.

Chorological affinities. The range of *T. laevigatus* is mostly overlapped by that of its close relative, *T. quadriguttatus*, and partially overlapped by that of *T. deuvei*.

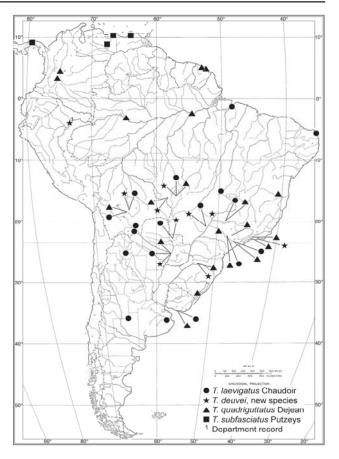


Figure 6. Map illustrating known distribution of *Tetragonoderus* quadriguttatus complex in Central and South America.

Material examined. In addition to type material, we have seen a total of 114 specimens.

UNITED STATES. Florida. Dade. 1 male, Miami, 21.III.2007, on *Datura* sp., H. Escobar (FSCA). 1 female, Miami, 23.IV.2008, A. Johnson et al, CAPS Tile Warehouse Survey (FSCA). Palm Beach. Lake Worth, Harbour Greens Drive, black light, V. Golia: 1 female, 1 male, 3.VI.2007 (ABSC); 1 male, 1 female, 21.VI.2007 (VGIC); 1 male, 1 female, 22.VI.2007 (UASM); 1 female, 22.VI.2007 (VGIC); 2 male, 3 females, 8.VII.2007 (VGIC); 1 female, 3.X.2007 (VGIC); 1 female, 17.X.2007 (VGIC); 1 female, 20.VI.2008 (VGIC). 1 female, Lake Worth, Harbour Greens Drive, mercury vapor light, 16.VI.2007, V. Golia (FSCA).

ARGENTINA. Buenos Aires. 1 male, 1 female, Rosas, F. C. Sud, 1968, J. B. Daguerre (NMNH). Salta. 1 male, 3 km W Cabra Corral Dam, 30.I.1982, H. & A. Howden (UASM). 1 female, Juramento, 25°S 65°W, 17.I.1963, Werner (MCZC). San Luis. 1 female, 18 km S Arizona, 18-23.I.1982, H. & A. Howden (UASM).

BOLIVIA. Santa Cruz. 1 female, Boyuibe to Charagua, via Cueva, 15.VII-1.XI.1920, G. L. Harrington (NMNH). Santa Cruz, Andrés Ibañez. 1 male, 1 female, Villecito, 4-5.X.1994, R. D. Ward (CMNH). 1 male, 1 female, Potrerillo del Guenda, Terebinto, 17°40′20″S 63°27′25″W, 3-4.X.1994, P. Bettella (CMNH). Santa Cruz, Ichilo. Buena Vista, 400 m, mercury vapor light, R. Ward (CMNH): 1 female, 2.X.1994; 1 female, 3.X.1994. 1 male, 1 female, 3 km SE Buena Vista, Río Surutu, 17-29S 63-42W, 310 m, 15.II.1994, R. Ward (CMNH). 1 female, Hotel Flora y Fauna, UV light trap, 01-53, 14.XI.2001, G.E. Ball (UASM). 4 females, 3.7km sse Buena Vista/ Hotel Flora y Fauna/ 17°29.949′S, 63°33.152′W, 5-15.11.2001, ca. 430 m/ M.C. Thomas & B. Dozier (UASM). Santa Cruz, Ignacio Warnes. 7 males, 1 female, 5 km ESE Warnes, Hotel Río Selva, 17°33.809′S/63°12.109′W. 450m, 04.XI.2001, G.E. Ball and M.C. Thomas 01-31 (UASM); 2 males, same, except 17°33.695N, 63°11.481′W. 450 m, forest leaf litter &/ beating vegetation,

Pl/Pw **Species** N **SBL SBL** H1/Hw H1/Hw Pl/Pw Mean Range Mean Range Mean Range T. subfasciatus 2^1 3.61 3.50-3.72 0.478-0.488 0.483 0.656 0.645-0.667 males T. subfasciatus 1² 3.96 0.458 0.636 females T. quadriguttatus 10^{3} 4.06 3.78-4.20 0.462 0.423-0.490 0.642 0.629-0.676 males T. quadriguttatus 10^3 4.15 3.98-4.34 0.462 0.440 - 0.4800.639 0.620-0.662 females T. laevigatus 10^{4} 3.32 2.84-3.74 0.464 0.429-0.488 0.639 0.606-0.667 males T. laevigatus 10^{4} 3.38 2.36-3.84 0.446 0.417-0.458 0.638 0.621-0.655 females T. deuvei 10^{5} 3.55 3.24-3.94 0.464 0.447-0.479 0.617 0.597-0.644 males T. deuvei 7^{5} 3.69 3.56-3.82 0.459 0.417 - 0.4780.621 0.609-0.656 females

Table 1. Standardized body lengths of Tetragonoderus species,

substrate sand, 03.11.2001 G.E. Ball, M.C. Thomas 01-31 (UASM). **Santa Cruz, Tarija.** 1 female, Palmar Grande, nr. Yquiba (= Yacuiba), 16.X1920 (NMNH).

BRAZIL. Goias. 1 male, 3 females, Mt. Corumbá, 21-23.II.1954, C. Gans, F. Pereira (MZSP). Mato Grosso. 5 males, 2 females, Caraca, 5-8.III.1963, F. Werner (MCZC). 1 female, Chapada (CMNH). 3 males, 7 females, Mt. Tres Lagoas, Rio Sucuriu, Faz. Canae, X.1966, F. Lane (MZSP). Pará. 1 female, Pará (= Belém) (CMNH). São Paulo. Campinas, Mogi Guaçu, 29-31.XII.1969, J. M. & B. A. Campbell (CMNC). Piracicaba, blacklight, C. A. Triplehorn (UASM): 2 females, 3.II.1963; 1 male, 1 female, 10.II.1963.

PARAGUAY. Amambay. 2 males, A. Schulze (MCZC). Central. 1 female, 15 km NE Asuncion. 21.VI.1969, P. & P. Spangler (NMNH). 1 female, San Antonio (UADE). San Lorenzo, UV light, J. Kochalka (CMNH): 1 male, 7.XI.1986; 4 males, 30.XII.1987. Concepción. vic. Horqueta, A. Schulze (MCZC): 1 male, VII; 1 female, 27.IV.1934.

URUGUAY. Montevideo. Montevideo: 2 females (CMNH); 2 males, 2 females, 14, sex not determined, Sivori (MCSN, UASM).

Tetragonoderus deuvei, new species

Fig. 1, 2B, 3B, 4B, 5C-D and 6

Type material. HOLOTYPE male, labeled: "Matto Grosso/ Cuijaba"; "ex Coll./ R. Oberthur" [pale green paper]; "Tetragonoderus/ deuvei n. sp./ J. Mateu det. 1995" [MNHP]. 22 additional PARATYPES, 16 males and 6 females, labeled as follows. 1 male, 1 female, "BOLIVIA: Santa Cruz/ Hotel Flora y Fauna/ 4.4 km SSE Buena/ Vista. 440m./ 17°29'57" 63°33'09"W"; "near residences/ in grass/ 06-09.XII.2005 05-27/ George E. Ball coll." [UASC]. 1 male, "BOLIVIA Santa Cruz/ Prov. 5 km ESE Warnes/ Hotel Rio

¹ Panama

² Venezuela

³ Paraguay

⁴ Brazil

⁵ Bolivia, Brazil, Paraguay

Selva/ 17°33.809'S/ 63°12.109'W. 450m"// sand pit; in clusters of/ dead vegetation at/ bases of standing plants/ 04.XI.2001 G.E. Ball/ M.C. Thomas 01-31" [UASM]. 1 male, "Chapada" [AMNH]. 1 male, 1 female, "Três Lagôas Mt/ marg.esq. Rio Sucuriu/ Faz Canaã X.1966/ F.Lane col." [MZSP]. 2 males, "Matto Grosso/ Cuijaba"; "ex Coll./ R. Oberthur" [pale green paper] [MNHP]. 1 male, "S.Antonio da Barra/ Pr de Bahia/ Gounelle 11-12-88"; "Museum Paris/ ex Coll./ R. Oberthur" [pale green paper] [MNHP]. 1 male, 1 female, "Jatahy/ (GOYAZ)" [MNHP]. 1 male, "Rio/ Jan."; "Ex-Musaeo/ H.W.BATES/ 1892" [1892 is at right angle to other printing] [MNHP]. 1 male, "Nova Teutonia/ Santa Catarina/ BRAZIL VIII-30-52/ Fritz Plaumann" [MCZC]. 1 male, "Nova Teutonia/ Sta.Cat.,Brazil/ 27 Apr./ F. Plaumann" [MCZC]. 1 female, "Nova Teutonia/ Sta.Cat.,Brazil/ 23 Mar. 48/ F. Plaumann" [MCZC]. 2 males, 1 female, "vic.Horqueta/ Paraguay/ A. Schulze" [MCZC]. 1 male, "vic.Horqueta/ Paraguay/ I-29-34/ A. Schulze" [MCZC]. 1 female, "P. 00920"; "Paraguay Central/ P. Germain/ 1885."; "T. laevigatus/ Chaud./ Mateu det. 1995"; "Museum Paris/ ex Coll./ R. Oberthur" [pale green paper] [MNHP]. 1 male, "MUSEUM PARIS/ Pébas (Ht. Amaz.)/ Castelnau 9-47" [pale green paper] [MNHP].

Notes about type material. For the holotype, we chose the same specimen that Joaquin Mateu had chosen to represent this new species.

Specific epithet. The word "deuvei" is a Latinized genitive eponym, based on the surname of Thierry Deuve, Curator of Coleoptera, Muséum National d'Histoire Naturelle, Paris, France. Mateu recognized specimens of this species as representing a new species in 1995 and labeled them as "Tetragonoderus deuvei n. sp.", but neglected to publish the description. We propose the same name to honor Dr. Deuve, as Dr. Mateu had intended.

Recognition. See the key, and figures noted above. Some specimens of *T. deuvei* share unicolorous elytra with the southern South American *T. viridis* and *T. chalceus*. But the latter two species have dark legs, whereas those of *T. deuvei* are pale. Some male features differ also, among these species, as noted above (*T. laevigatus*, "Recognition").

Description. Habitus as in Fig. 1. See Table 1 for values for standardized body length (SBL) and ratios Hl/Hw and Pl/Pw.

Elytra. Bicolored or uniformly dark, with microsculpture mesh pattern slightly transverse, sculpticells slightly wider than long (Fig. 3B and 4B).

Male genitalia. Phallus (Fig. 5C-D) in dorsal aspect slender, shaft subsinuate, distally curved to right, narrowed toward periostial area; latter relatively long, more than one third length of shaft; apical area short, slender, apex narrowly rounded; in lateral aspect shaft relatively straight, apical area short, slender; ventral surface smooth, not ridged. Endophallus, inverted, with prominent microtrichial field, band-like in appearance in both dorsal and right lateral aspects, within medial area.

Notes about variation. Of the 23 specimens in the type series, a single specimen from Bolivia had the pale markings of the elytra much darker than typical (Fig. 1B), and 2 specimens from Brazil had completely dark elytra, in other words, no visible pale markings.

Notes about habitat. The Bolivian specimens of *T. deuvei* were collected in a cultivated grassy area near residences, and in a sand pit, among the roots of dead, standing plants.

Geographical distribution. (Fig. 6). The geographical range of this species is southern, extending from eastern Brazil westward to Paraguay and Bolivia, and northward to Amazonian Peru.

Chorological affinities. The range of this species is overlapped by that of *T. quadriguttatus* and mostly overlapped by that of *T. laevigatus*. Specimens of the latter and of *T. deuvei* were collected in the same place, at the same time, thus indicating that these 2 species are syntopic in at least part of their common range.

Material examined. We have seen only the type series, of 23 specimens. For details, see "Type material", above.

Tetragonoderus quadriguttatus Dejean

Fig. 2C, 3C, 4C, 5E-F, 6 and 7

- Tetragonoderus quadriguttatus Dejean 1829: 509. **Type Material:** Dejean's type most likely lost, NEO-TYPE here designated (see "Notes about type material" below). **Type Area:** Brazil. Csiki 1932: 1298.— Blackwelder 1944: 52.— Lorenz 2005: 453.
- Tetragonoderus columbicus Steinheil 1875: 140. Type Material: HOLOTYPE, male, labeled: "TYPE" (red paper); "Ambalema" (handwritten); "Columbie/ coll E. Steinheil"; "columbicus/ Steinh" (handwritten); "Tetragonoderus/ columbicus Steinh/ (=lacordairei Chd)/ J. Mateu det. 1989" [MNHP]. Type Locality: Ambalema, Tolima Department, Colombia. Csiki 1932: 1296.— Blackwelder 1944: 52; Lorenz 2005: 453. NEW SYNONOMY
- Tetragonoderus lacordairei Chaudoir 1876: 45. Type Material: LECTOTYPE (here designated), male, labeled: "TYPE" [red paper]; "Cayenne/Lacordaire"; "Tetragonoderus/lacordairei/ Chd/ J. Mateu det. 1979" [MNHP]. Type Area: Cayenne, French Guiana. Csiki 1932: 129. Blackwelder 1944: 52. Lorenz 2005: 453. NEW SYNONOMY.
- Tetragonoderus tetragrammus Chaudoir 1876: 46. **Type Material:** HOLOTYPE, female, labeled: "82"; square (yellow paper). **Type Locality:** Ega (= Tefé, Amazonas, Brazil). Csiki 1932: 1299.— Blackwelder 1944: 52.— Lorenz 2005: 453. **NEW SYNONOMY.**

Notes about type material. Dejean's type of *T. quadriguttatus* could not be located, and is presumed lost. Chaudoir (1876: 46) states that he possessed two specimens: the type of Dejean, and another specimen collected by M. Sahlberg in Cantagallo (State of Rio de Janeiro, Brazil). In the MNHP associated with the box label "4guttatus Dej Brésilo c. Dejean" is a single male (head and prothorax missing) labeled "Cantagallo Sahlberg jun." and is selected and here designated as NEOTYPE. Due to the poor condition of the specimen, it was not dissected to examine the male genitalia. The elytral microsculpture was the same as that observed in the holotypes of *T. columbicus*, *T. lacordairei* and *T. tetragrammus*.

The male holotype of *T. columbicus* was dissected, and the genitalia match those of *T. quadriguttatus*. Additionally, the elytral microsculpture of *T. columbicus* matches that of *T. quadriguttatus*.

In the MNHP associated with the box label "Lacordairei Chaud Cayenne C. Dejean" are 5 specimens. The third specimen, a male, is selected and here designated as LECTOTYPE. The male lectotype of T. lacordairei was dissected, and the genitalia match those of T. quadriguttatus. Additionally, the elytral microsculpture of T. lacordairei matches that of T. quadriguttatus.

The holotype of *T. tetragrammus* is a female. In the MNHP is another female specimen from Santarem, determined by J. Mateu as *T. tetragrammus*. The elytral microsculpture of this specimen matches that of both the holotype and *T. quadriguttatus*.

Recognition. This species is the largest of the three species in the quadriguttatus assemblage, with a mean SBL of 4.06 mm for males (range 3.78-4.20 mm) and 4.15 mm for females (range 3.98-4.34 mm). The transverse microsculpture (Fig. 3B) gives the elytra a satiny appearance.

Description. See Table 1 for values for standardized body length (SBL) and ratios Hl/Hw and Pl/Pw. **Elytra.** Bicolored, with pale markings markedly contrasting to subdued, with microsculpture mesh pattern transverse, sculpticells 3-5 times as wide as long (Fig. 3D and 4D).

Male genitalia. Phallus (Fig. 5E-F) in dorsal aspect slender, shaft subsinuate, distally curved to right, narrowed toward periostial area; latter relatively short, about one third length of shaft; apical area short, slender, subspatulate, nearly globose; apex narrowly rounded; in lateral aspect shaft markedly sinuate, apical area broad, projected dorsad; ventral surface smooth, not ridged. Endophallus, inverted, with microtrichial patch (somewhat band-like) right lateral, and slightly proximad the periostial area.

Collecting notes and habitat. Several specimens were taken at UV light. Most of the specimens collected in Tayrona National Park, northern Colombia, were resting during the heat of the day, on white

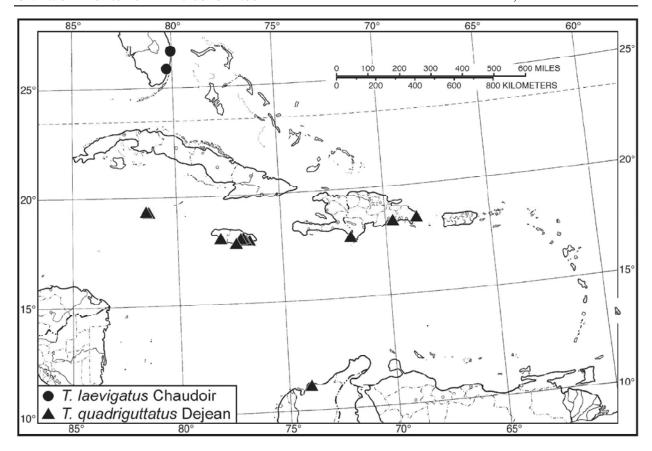


Figure 7. Map illustrating known distribution of *Tetragonoderus* quadriguttatus complex in southern Florida, the West Indies and northern Colombia.

sand, beneath shrubs growing on the flood plain of a wide river (Río Piedras), about 50 m from the water's edge. One specimen was collected in the same general area, on a gravel road, but well removed from the river.

Geographical distribution. (Fig. 6 and 7). The geographical range of this species extends through much of South America (southern Uruguay to northern Colombia) (Fig. 6), and into the West Indian islands (Fig. 7) of Grand Cayman, Jamaica and Hispaniola. We believe the West Indian records indicate a relatively recent arrival of *T. quadriguttatus*, either naturally by oversea immigration from northern South America, or by accidental introduction, through commerce.

Chorological affinities. The range of this species completely overlaps that of T. deuvei, mostly overlaps that of T. laevigatus, and partially overlaps that of T. subfasciatus.

Material examined. In addition to type material, we have seen a total of 185 specimens.

BOLIVIA. Santa Cruz. Andres Ibanez. 2 females, Villecito, 4-5.X.1994, R. D. Ward (CMNH).

BRAZIL. Bahia. 1 male, Encruzilhda, 960 m, XI.1972, J. Nègre (MNHP). Mato Grosso. 2 males, Caraca, 5-8.III.1963, F. Werner (MCZC). Chapada: 9 females, (CMNH); 1 male, 2 females, VIII (AMNH). 1 female, Cuijaba (MNHP). Minas Gerais. 1 male, 1 female, Env. De Passa-Quatro, Bords du Rio Las Pedras, 1000 m, 1903, E. R. Wagner (MNHP). Pará. Santarem: 1 female (MNHP); 1 male, 2 females (CMNH). Santa Catarina. Nova Teutonia, F. Plaumann: 2 females, XII.1975 (CASC); 1 female, X.1976 (CASC); 1 male, XI.1976 (CASC); 1 female, XII.1976 (CASC); 2 males, II.1977 (CASC); 4 males, 7 females, XII.1970 (NMNH). Nova Teutonia, 300-500 m, F. Plaumann (NMNH): 1 female, X; 1 female, IX.1972; 2

females, XI.1972; 14 males, 10 females, XII.1972; 1 female, I.1973. **Rio de Janeiro.** 2 males, Mendes, IV, Le Moult (MNHP). **Rio Grande do Sul.** 1 male, Pelotas, 30.X.1956, C. Biezanko (AMNH). **São Paulo.** 1 male, Cachoeira de Emas, XII.1944 (MZSP). 1 female, Garca 27.I.1950 (MZSP). 1 female, Itu, II.1959, U. Martins (MZSP). 1 male, Piracicaba, blacklight, 5.XI.1965, C. A. Triplehorn (UASM).

COLOMBIA. Huila. 1 male, Villavieja, III.1945 (CASC). Magdalena. PNN Tayrona, 11°20'N 74°02'W, Sector Naranjos, C. Martinez, G. E. Ball (IAVH, UASM): 1 male, 30.VI.2002, gravel road margin, 12-02; 5 males, 3 females, 1.VII.2002, flood plain, Río Piedras, on sand, beneath live vegetation 14-02. FRENCH GUIANA. Roches de Kourou, VI.1905, E. Le Moult (MNHP).

PARAGUAY. Central. San Lorenzo, UV light, J. A. Kochalka (CMNH): 3 females, 7.XI.1986; 1 male, 4 females, 18-19.XI.1986; 8 males, 14 females, 23-24.XI.1986; 4 males, 5 females, 30.XII.1987.

URUGUAY. Montevideo. Montevideo: 1 female, Sivori (MCSN). WEST INDIES

CAYMAN ISLANDS. Grand Cayman. 2 females, Georgetown UCCI, at light, 8.VI.2008, R.H. Turnbow (FSCA). 1 male, "Grand Cayman", UV light, VI.1992, P. Fitzgerald (FSCA). 1 male, Hell, 19°23'N 81°24'W, 24.II.1993, W.E. Steiner, J.M. Swearingen (NMNH). Rum Point, 19°22'N 81°16'W, W.E. Steiner, J.M. Swearingen (NMNH): 1 male, 1 female, 22.II.1993; 1 female, 24.II.1993. West Bay (Town Hall Crescent), 21.VII-1.VIII.1986, D. Gicca (FSCA): 4 males, 1 female; blacklight trap, 11 males, 5 females.

DOMINICAN REPUBLIC. La Altagracia. 1 female, vic. Oyo Clara, 18°33'48"N 68°26'50"W, UV light, 24.VII-5.VIII.2002, K. Will & C. Chaboo (EMEC). **Pedernales**. 1 male, Cabo Rojo, car net after storm, near sea level, 26.VIII.1988, M. Ivie, Phillips and Johnson (WIBF). **San Pedro.** 1 female, 13 km E Boca Chica, mv + bl, 17.V.1992, R. Turnbow (UASM).

JAMAICA. Clarendon. 2 males, 4 females, Portland Ridge, PWD Fishing Club, UV light, 20.VII.1969, Woodruff (FSCA). Saint Andrew. 1 female, Kingston, T.H. Farr (IJSM): Palisadoes, 8.XII.1963; 41 Sunrise Crescent off Red Hills Road, 25.VI.1979. Saint Catherine. 1 female, Caymanas Estate, UV light trap, 10.V.1970, J. H. Frank (UASM). 1 female, Port Henderson, UV trap, 12.VII.1970, E. G. Farnsworth (FSCA). Spanish Town, E. G. Farnsworth (FSCA): 1 female, UV light, 10.VII.1970; 1 female, Twickenham Park, mosq. light trap, 18.V.1970. Spanish Town, Jamaica School Agr., UV trap, E. G. Farnsworth (FSCA) 1 male, 11.IV.1970; 1 female, 14.IV.1970. Saint Elizabeth. Black River: 1 male, UV trap, 14.VII.1970, E. G. Farnsworth (FSCA); 1 male, at light, 7.VI.1969, J. H. Frank (UASM). Saint Thomas. 1 male, 1 female, Yallahs, UV trap, 25.VI.1970, E. G. Farnsworth (FSCA).

Tetragonoderus subfasciatus Putzeys

Fig. 2D, 3D, 4D, 5G-H, 6

Dromius subfasciatus Putzeys 1846: 376. **Type Material:** LECTOTYPE (here designated), male, labeled: "Dromius/Putz" [MNHP]. **Type Area:** Cumana, Venezuela.

Tetragonoderus subfasciatus; Chaudoir 1876: 47; Csiki 1932: 1299; Blackwelder 1944: 52; Lorenz 2005: 453.

Notes about type material. In the original description, Putzeys (1846: 376) referred to 4 specimens from Cumana, Venezuela. Chaudoir (1876: 47) stated "I have the Putzeys type from Cumana (Venezuela)." The single specimen associated with box label "subfasciatus Putzeys Venezuela Cumana Putzeys" in the MNHP is selected and here designated as LECTOTYPE.

Recognition. Readily separated from the three species of the quadriguttatus assemblage by the markedly transverse elytral microsculpture, which renders the elytra subiridescent.

Description. See Table 1 for values for standardized body length (SBL) and ratios Hl/Hw and Pl/Pw. **Elytra.** Bicolored, with mesh pattern distinctly transverse, sculpticells very wide, with few longitudinal edges (Fig. 3C and 4C).

Male genitalia. Phallus (Fig. 5G-H) in dorsal aspect slender, medial part of shaft parallel-sided, with apical portion curved to right; periostial area relatively long, more than one third length of shaft; apical area narrow, short, flat, slightly spatulate; in lateral aspect shaft slightly curved, apical area

thicker apically. Endophallus, inverted, with small microtrichial field to right of midline in dorsal aspect, and partially within the periostial area.

Notes about habitat. No specific label data are available regarding possible habitat. All three specimens with collection data were taken at UV light.

Notes about variation. Only one of the three specimens in the UASM has the elytral color pattern as in Fig. 2D. The other two specimens have reduced pale markings, so that they appear more like the other "four-spotted" species of the quadriguttatus assemblage.

Geographical distribution. (Fig. 6). This species is currently known only from northern Venezuela and Panamá. One would expect it to occupy Colombia as well.

Chorological affinities. The range of this species is partially overlapped by that of *T. quadriguttatus*.

Material examined. In addition to type material, we have seen a total of eight specimens.

PANAMÁ. Chiriqui. 1 male, 5.0 km S Concepcion, at Río Escarrea, UV light, 30.V.1972, T. L. & L. J. Erwin (NMNH). Panamá. 1 male, Tocumen, UV light, 17-21.VIII.1970, Navas, Diego (FSCA).

VENEZUELA. Capital District. 2 males, 2 females, Caracas (MNHP). **Guárico**. 1 female, 12 km S Calabozo, Est. Biol. Los Llanos, UV light, 6.II.1969, P. & P. Spangler (NMNH).

Concluding Remarks

Most of the Western Hemisphere *Tetragonoderus* species, 36 of the 43 recorded in T.L. Erwin's Western Hemisphere Carabidae list (pers. comm.), were described in the 19th Century. In the 20th Century, only 6 more species and one subspecies have been described, and one more species in the 21st Century. This seeming decline in taxonomic activity may be interpreted as indicating that an asymptote in species numbers is being approached. That may be so, but before a modern revision of the Western Hemisphere *Tetragonoderus* species in their entirety can be undertaken, much remains to be discovered about the described species, including name validation, classification, diel activity patterns, geographical range, chorological affinities, and phylogenetic relationships. Further, we expect that at least a few species remain to be discovered. Our paper, with its documentation of a small species assemblage, hopefully will make somewhat easier preparation of the more general treatment.

Acknowledgments

We are pleased to express our gratitude to Michael C. Thomas, whose knowledge of carabids and his enthusiasm for knowing the insect fauna of Florida induced him to seek our opinion about a possible new state record—the enquiry that led to the preparation of this paper.

We thank the curators listed in the Material section for their generous cooperation in making specimens available for this study. We also thank Vincent Golia for kindly donating two specimens to the UASM of *T. laevigatus* that he had collected in the backyard of his home, in Lake Worth, Florida.

We appreciate the cooperation of Thierry Deuve (Curator of Coleoptera, Paris Museum) who, with the building under reconstruction and entry markedly restricted, arranged for the junior author to re-examine the Chaudoir *Tetragonoderus* types.

We are grateful for the cooperation and assistance extended to us by our friend and colleague, George D. Braybrook (Department of Earth and Atmospheric Sciences, University of Alberta), operator of the scanning electron microscope used for the photomicrographs of elytral microsculpture.

The junior author extends his thanks to Michael Sharkey (University of Kentucky, Lexington, Kentucky) and to his Colombian associate, Fernando Fernandez (Universidad Nacional de Colombia, Santa Fé de Bogota, Colombia) who together made possible his trip to Colombia. While there he accompanied Claudia Martinez on several collecting forays to different parts of the country. On one of these, to Caribbean coastal Parque Nacional Tayrona, we learned something about habitat and probable diel activity of *Tetragonoderus quadriguttatus*.

A preliminary draft of this manuscript was reviewed by Douglas A. Craig (Department of Biological Sciences, University of Alberta) and Terry L. Erwin (Department of Entomology, Smithsonian Institution). We thank them for their comments which improved the manuscript appreciably. Finally, we thank M. C. Thomas and Paul E. Skelley for their editorial advice and important modifications to the manuscript.

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Received August 15, 2008; accepted September 22, 2008.