Revision and Phylogeny of the Neotropical genus *Cnemida* (Coleoptera: Scarabaeidae: Rutelinae)

Mary Liz Jameson

W-436 Nebraska Hall
University of Nebraska State Museum
Lincoln, Nebraska 68588-0514 U.S.A.
email: mjameson@unlinfo.unl.edu

Abstract: The scarab genus *Cnemida* includes eight species (including *C. gigantea* Jameson n. sp. from Colombia and *C. tristriata* Jameson n. sp. from Surinam) that inhabit tropical moist and premontane forests of South America, Central America, and Mexico. Keys to adults, diagnostic characters, descriptions, and distributions are presented. The larva of *C. intermedia* Bates is described and integrated into a key to larvae of the tribe Rutelini. A cladistic analysis among the species of *Cnemida* is based on 35 morphological characters and uses members of the genera *Pelidnota* and *Rutela* as outgroups. Four equally parsimonious cladograms are discussed.

Key words: Scarabaeidae, Rutelinae, phylogeny, New World tropics, larva

Introduction

The Neotropical genus *Cnemida* is a distinctive member of the scarab subfamily Rutelinae (tribe Rutelini). Species in the genus are characterized by a posteriorly triemarginate pronotum, dorsoventrally thickened body (height about equal to width), robust hind femora, exposed mesepimeron, moderate size (approximately 1 centimeter), and dark, shining dorsal surface. In nature, adults are found on flowers and vegetation. Some species have been observed reposing on their sides while on foliage, thus creating the appearance of detritus, withered fruits, or bird excrement (Ratcliffe 1990). This kind of behavioral deception has been reported in some Cerambycidae (Preston-Mafham 1993) and Orthoptera (pers. obs.). Within the Scarabaeoidea, this adaptation has been observed in two species: *Cnemida retusa* (Fabr.) and *C. intermedia* Bates.

The genus *Cnemida* was established by Kirby (1827), who brought together species that had been placed in the genera *Ometis* and *Rutela* (Rutelinae), as well as the genus *Trichius* (Cetoniinae). Kirby recognized that species in these fundamentally different genera were members of one distinctive group and united them in a new genus. Kirby defined the genus *Cnemida*, discussed the classification of the group (making comparisons to members in the subfamilies Dynastinae, Melolonthinae, and Cetoniinae), and discussed the possible natural history of species in the genus. Since the time of Kirby, little has been published aside from new species descriptions. Ohaus (1934), in his volume of the Genera Insectorum, did not provide keys or descriptions to the species in the genus. My research brings together the knowledge of the genus *Cnemida*. My objectives are to revise the genus *Cnemida*, describe two new species, describe the larva of *C. intermedia* (the first example of a larva in the genus), examine phylogenetic relationships within the genus, and to discuss geographical distribution of the species.

Methods and Definition of Taxonomic Characters

Taxonomic Material. Specimens examined for this study were provided by 37 institutions and private collections that loaned 908 specimens, including type specimens. Acronyms for loaning institutions follow Arnett *et al.* (1993).

AMNH American Museum of Natural History, New York, NY (Lee Herman)
ANSP Academy of Natural Sciences, Philadelphia, PA (Donald Azuma)
BCRC Brett C. Ratcliffe Collection, Lincoln, NE (Brett Ratcliffe)
BMNH The Natural History Museum, London, England (Malcolm Kerley)
CASC California Academy of Sciences, San Francisco, CA (Dave Kavanaugh, Roberta Brett)
DCCC David C. Carlson, Orangevale, CA (David C. Carlson)

CMNH Carnegie Museum of Natural History, Pittsburg, PA (Robert Davidson)
CNCI Canadian National Collection of Insects, Ottawa, ON, Canada (Jean McNamara, Josee Poirier)
CUIC Cornell University Insect Collection, Ithaca, NY (Richard Hoebeke)
DCCC Richard A. Cunningham Collection, Chino, CA (Richard A. Cunningham)
DJCC Daniel J. Curoe Collection, Palo Alto, CA (Daniel J. Curoe)
DBTC Donald B. Thomas Collection, Weslaco, TX (Don Thomas)
EMEC Essig Museum of Entomology, Berkeley, CA (John Chemsak, Cheryl Barr)
EGRC Edward G. Riley Collection, College Station, TX (Ed Riley)
FMNH Field Museum of Natural History, Chicago, IL (Alfred Newton)
FREY Georg Frey Collection at ZSMC, Munich, Germany (Gerhard Scherer, Max Kuhbander, Martin Baer)
FSCA Florida State Collection of Arthropods, Gainesville, FL (Bob Woodruff, Brenda Beck, Mike Thomas)
HAHC Henry and Anne Howden Collection, Ottawa, Canada (Henry Howden)
HPSC Henry P. Stockwell Collection, Balboa, Panama (Henry Stockwell)
INBC Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (Angel Solís)
JEWC James E. Wappes Collection, Bulverde, TX (Jim Wappes)
LAGO Paul Lago, University, MS (Paul Lago)
MCZC Museum of Comparative Zoology, Cambridge, MA (Stephan Cover)
MLPA Museo de La Plata, La Plata, Argentina (Ricardo Ronderos)
MNHN Museum National d'Histoire Naturelle, Paris, France (Jean Menier)
MNNC Coleccíon Nacional de Insectos, Santiago, Chile (Mario Elgueta)
MAMC Miguel A. Morón Collection, Xalapa, Mexico (Miguel A. Morón)
QBUM Museu Naçional, Rio de Janeiro, Brazil (Miguel Monné)
SEMC Snow Entomological Museum, University of Kansas, Lawrence, KS (Rob Brooks)
UMRM W.R. Enns Entomology Museum, University of Missouri, Columbia, MO (Robert Sites, Kristin Simpson)
UNAM Coleccíon Entomologia, Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Mexico, D.F. (Silvia Santiago)
UNSM University of Nebraska State Museum, Lincoln, NE (Brett Ratcliffe)
USNM United States National Museum, Washington, D.C. (Bob Gordon, Gary Hevel)
ZFMK Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (Michael Schmidt)
ZMHB Museum für Naturkunde der Humboldt Universitat zu Berlin, Berlin, Germany (Manfred Uhlig, Joachim Schulze)
ZMUC Zoological Museum, University of Copenhagen, Denmark (Olé Martin)
ZSMC Zoologische Staatssammlung des Bayerischen Staates, Munich, Germany (Gerhard Scherer, Max Kuhbander, Martin Baer)

Character Examination. Internal and external morphological features formed the basis for this work. Specimens were examined with a dissecting microscope (6.5 to 40 power) and fiber-optic lights. For better definition of cuticular sculpturing, a piece of opaque drafting film was used as a "screen" between the specimen and the light element. This simple procedure reduced the reflectivity on the beetle surface and enhanced visibility of microsculpture. Internal sclerotized structures were dissected by relaxing the specimen in hot water. Heavily sclerotized parts were soaked in a dilute solution (about 15 %) of potassium hydroxide and neutralized in a dilute solution (about 15 %) of acetic acid. Mouthparts, wings, and genitalia were studied and card-mounted or placed in a glycerin-filled vial beneath the specimen.

Species of the genus *Cnemida* were characterized by a combination of characters including form of the pronotum, legs, and tarsomeres, elytral striae, microsculpture (pronotal, elytral, and pygidial), and male parameres. For measurements, I used an ocular micrometer and the following standards: (1) Body length: measured from the apex of the clypeus to the apex of the pygidium; (2) Widest body width: measured at mid-elytra; (3) Puncture density: defined as dense if punctures are nearly confluent to less than 2 puncture diameters apart, moderately dense if punctures are between 2 to 6 puncture diameters apart, and sparse if punctures are separated by more than 6 puncture diameters; (4) Scutellum ratio: width and length ratios (W/L) were measured as follows: length was measured from elytral base to apex of scutellum (L), width was measured at base (W); (5) Elytral sutural length: measured from the base of elytral suture to apex, and; (6) Elytral discal striae: defined as the striae (complete or interrupted at mid-disc, extending from apex to mid-disc or base) located between the first elytral stria (laterad of the sutural stria) and the elytral humerus.

Natural History

Larvae of *Cnemida* are found in rotting wood, as are most species of rutelines. Ohaus (1909) reported *C. lacerata* (Germar) from a rotting cedar trunk along with passalids and termites (*Leucotermes* sp.), and Morón (1979) reared an adult of *C. aterrima* Bates from rotting wood. The only known larva in the genus, *C. intermedia* Bates, which I describe in this paper, was reared from the wood of *Hyeronima alchorneoides* Allemao (Euphorbiaceae) by F. Quesada (INBio, Costa Rica).

Adults have been collected on various flowering plants and from foliage. Label data indicate that individuals visit flowers of *Turnera ulmifolia* L. (Turneraceae), *Bixa orellana* L. (Bixaceae), *Mimosa invisa* Martius (Mimosaceae), *Inga* sp. (Mimosaceae), *Psychotria* sp. (Rubiaceae), and cotton (*Gossypium herbaceum* L. (Malvaceae)). Araújo e Silva (1968) reported *C. retusa* (Fabricius) from roses (Rosaceae). Adults are generally active from early morning to mid-day. This period of activity corresponds with the flowering period of recorded host plants. Flowers of *Turnera, Bixa, Inga,* and *Mimosa* generally bloom in early morning, and by midday the petals close and wilt (Janzen 1983, Koptur 1994, Elias *et al.* 1975).

I have observed that adults in the genus *Cnemida* do not fully lift and extend their elytra during flight, a feature shared with many cetoniine scarabs. Species of *Cnemida*, as well as most cetoniine scarabs, share two features that allow the hind wings to rotate into place for flight without the elytra being fully lifted: 1) a well-developed and enlarged mesepimeron that, in effect, braces and stabilizes the base of the elytron, and 2) the lateral margins of the elytra are emarginated (exposing lateral tergites), thus allowing the hind wings to unfold and extend. These adaptations facilitate speed and agility (Arrow 1925, Crowson 1981), especially important for day-flying flower visitors.

In addition to fast flight, species of *Cnemida* are able to evade predators with behavioral crypsis. Individuals of *C. retusa* and *C. intermedia* rest on their sides while on vegetation, thus disrupting their symmetry and appearing to be a bit of detritus, a bird dropping, or a withered fruit (Ratcliffe 1990, Wappes pers. comm.). Because individuals in the genus are fairly thickened (height is about equal to width), they can recline laterally on surfaces of leaves and use their appendages for balance. The irregular sculpturing of the elytra enhances the deception by further disrupting body symmetry. This type of behavioral crypsis also has been observed in *Aethomerus cretatus* Pascoe and *Ozodes* sp. (Cerambycidae) (Preston-Mafham 1993) and tropical Orthoptera (pers. observ.). Members of these taxa appear to mimic fecal material or debris when resting on vegetation in a manner similar to species of *Cnemida*.

Kirby (1827:149) commented on the presence of "farina" (which he differentiated from pollen) in the elytral striae and mouth parts of specimens of *Cnemida*. He conjectured that the pronotal and elytral sculpturing was used to gather farina: "...it is extremely probable that all the species of this genus of the New World collect some farinaceous substance, most likely from the plants that they frequent, for some purpose important to them in their peculiar economy." He further conjectured that individuals use this substance to feed their larvae as do bees. However, Kirby was incorrect. Instead, larvae feed on decaying organic matter (see larval description).

Much remains to be discovered about species in the genus *Cnemida*. Only one larva in the genus is known, pupae have not been described for any species, males are unknown for one species (*C. gigantea* n. sp.), and females are unknown for two of the species (*C. ephippiata* Ohaus and *C. tristriata* n. sp.).

Genus *Cnemida* Kirby 1827
(Figs. 1-22, 25-33)

Cnemida Kirby 1827:146. Type species: *Trichius retusa* (Fabricius) 1801:133.

Description. Form: Subovate, sides subparallel, dorsoventrally thickened, elytra shortened, pygidium exposed (Fig. 1, 6-13). Length 8.0-17.0mm; width at mid-elytra 4.0-8.0mm. **Head**: Surface punctate, punctostrigate, or strigate (Figs. 14-15). Frontoclypeal suture incomplete. Clypeus subequal in length to frons, laterally converging toward bidentate apex; apex weakly reflexed, beaded, emarginate, with 2 blunt teeth. Antenna with 10 antennomeres, club subequal to antennomeres 2-7. Labrum weakly exposed, bisinuate or rounded apically. Mandibles with 2 exposed, recurved, apical teeth and 2 small teeth basomedially; molar area robust. Maxilla with 6 teeth: 3 basal, 2 medial, 1 apical. Mentum bisinuate apically, length subequal to width. Interocular width 4.0-5.0 transverse eye diameters. **Pronotum**: Form at base trimarginate, laterally bisinuate (widest at middle and base)

(Figs. 16-19). Lateral margin beaded, bead lacking at base and mid-apex. Surface variably sculptured. Scutellum: Longer than wide (W:L ratio .55-.80 as measured from where elytral base meets scutellar base). Base not declivous at elytral base. Surface variably punctate. **Mesepimeron**: Broadly or narrowly exposed in dorsal view. Surface strigate. Elytra: Surface with or without weak foveae; striae irregularly depressed or not, variably impressed (Figs. 1-13). Epipleuron from base to middle rounded, with weak line at margin originating at mid-base; weakly incised from middle to apex, lateral tergites weakly exposed. Apex sinuate. Elytral sutural length 2-3 times length of scutellum. Propygidium: Partially or entirely exposed. Surface punctate. **Pygidium**: Shape semi-ovate. Surface variably strigate (Figs. 20-22). Margin with sparse setae; setae medium in length, tawny. Venter: Prosternal keel V-shaped; apex projecting at about 35° relative to plane of dorsal surface, produced to protrochanter, bluntly rounded; surface with moderately dense, tawny, moderately long setae. Mesometasternal keel broadly U-shaped in ventral view, produced weakly beyond mesocoxae; ventral surface parallel relative to plane of dorsal surface. Abdominal sterna variable in length. Sternum 5 of female with transverse row of sparse, decumbent setae near base; setae tawny, moderate in length. Last sternum of male and female rounded or with tooth; apex with sparse, tawny, moderately long setae. **Legs**: Surface strigate. Protibia with 3 teeth, basal tooth slightly removed from apical teeth; widest at middle in male, subparallel in female; tarsomere 5 of male a little longer than tarsomeres 1-4; foreclaw of male with lateral claw split apically, with or without apicomedial tooth, enlarged (twice as thick and 2-3 times wider than internal claw), mesal claw simple; foreclaws of female simple, subequal. Meso- and metatibiae slightly to greatly thickened with lateral carinae (slightly thicker in females, carinae more developed, and sculpturing more pronounced); apex biemarginate with or without corbel (Figs. 25 C1, C2, C3), 2 spurs interomedially, 1-4 spinules laterally; meso- and metatarsomere 4 of male with weakly developed, median, lobe-like projection between apical spinulae (Figs. 23d-25D); meso- and metatarsi with claws of male simple, lateral claw twice as thick and twice as wide as mesal claw; claws of female simple, lateral claw slightly thicker and wider than mesal claw; meso- and metatarsomere 5 of males with or without mesomedial tooth (Fig. 25d1-25d2); simple in females; empodium with apex hidden or weakly exposed, with 2 short, stout setae. **Metatrochanter**: Not produced beyond posterior border of femur. **Metacoxa**: Apex right-angled or weakly acute. **Hind wing**: Well-developed hooks on precostal membrane present. Veins AP_{3+4} and J lacking. Metendosternite: In posterior view, Y-shaped, robust, with 2 apical arms (Fig. 25B). **Male parameres**: Symmetrical or asymmetrical. Ventral plates sclerotized or not, symmetrical or asymmetrical, with or without prolonged lateral arms (Figs. 26-32).

Diagnosis. The genus *Cnemida* is separated from other genera in the tribe Rutelini by the following combination of characters: frontoclypeal suture obsolete medially, pronotum lacking basal bead, apex of metatibia without spinules on ventrolateral edge, pronotal base triemarginate, lateral edge of pronotum laterally bisinuate (widest at middle and base), epipleuron rounded (with weak line at margin), lateral margin of epipleuron strigate, apex of elytra sinuate, surface of pygidium strigate, male foreclaw thickened and split, mesepimeron broadly or narrowly exposed in dorsal view, basal veins (AP_{3+4} and J) of hind wing absent, subgalea slender.

Distribution (Fig. 33). Southern half of Mexico (south of the Tropic of Cancer), Central America, and South America (north of 30° S latitude). Found at elevations ranging from sea level to 1,500 m.

Key to species of *Cnemida*

[Males have claws of foretarsus unequal in size, outer claw greatly enlarged and split apically; females have claws of foretarsus subequal in size, not split apically.]

1. Color of elytra, pronotal margins, and venter testaceous; pronotal disc, scutellum and pygidium metallic green. Pronotum moderately densely punctate (not strigate), punctures moderately large (Fig. 18). Male parameres as in Fig. 30. .... *C. leprieuri* Arrow

1'. Color of elytra, pronotum, venter, and pygidium black or castaneous; elytra with or without orange or testaceous markings. Pronotum finely punctate-strigate (Fig. 19) *or* moderately densely punctate (punctures small) with few strigae in anterior angle (Figs. 16-17). Male parameres not as in Fig.30. 2

2. Pygidial apex with strigae forming 2 separate concentric circles each side of midline (Fig. 21). Elytral disc with 1 large, orange macula (Figs. 2, 9)... .... *C. gigantea* Jameson n. sp.

2'. Pygidial apex with strigae forming 1 concentric circle (Figs. 20, 22). Elytral disc black, black with testaceous markings, or primarily orangish. 3

3. Pronotum strigate, strigae extending from anterior angle to posterior angle of pronotum and from lateral margin to near middle of pronotum (Fig. 19). Male parameres not as in Fig. 26. 4

3'. Pronotum finely punctate, at most with narrow patch of strigae extending from anterior angle to near middle, not extending to posterior angle (Fig. 16-17). Male parameres as in Fig. 26. .... *C. aterrima* Bates

4. Elytral disc with 3 striae uninterrupted at mid-disc (Fig. 5). Pygidial disc with strigae at midline complete (Fig. 22). Male parameres as in Fig. 32. .... *C. tristriata* Jameson n. sp.

4'. Elytral disc with 4 striae (Figs. 1, 3, 4) usually interrupted at mid-disc. Pygidial disc with strigae at midline complete or incomplete (Figs. 20, 22). Male parameres not as in Fig. 32. 5

5. Surface of frons strigate, strigae coalescing in a V-shaped discal depression (Fig. 15). Elytral striae at base coalescing and rugose. Metasternum of male with dense, yellow setae. Male parameres as in Fig. 29. *C. lacerata* (Germar)

5'. Surface of frons strigate, strigae not coalescing in a V-shaped discal depression (Fig. 14). Elytral striae at base separated, distinct (Figs. 1, 3, 4). Metasternum of male without dense, yellow setae. Male parameres not as in Fig. 29. 6

6. Surface of pygidium at midline smooth, strigae not continuous (Fig. 20). Surface of pronotum lacking metallic green reflections. Elytra black, with or without single, transverse orange band. Male parameres as in Fig. 28. .... *C. intermedia* Bates

6'. Surface of pygidium with strigae continuous or nearly so at midline, not smooth. Surface of pronotum with or without metallic green reflections. Elytra castaneous or black with testaceous markings, or testaceous with castaneous margins. Male parameres not as in Fig. 28. 7

7. Color of elytra castaneous to black with orange markings throughout (Fig. 12). Elytra at subapex with transverse strigulae terminating before the lateralmost discal stria. Surface of pygidium with strigae finely impressed and closely spaced along midline (strigae separated by 1-3 strigal widths). Male parameres as in Fig. 31. .... *C. retusa* (Fabr.)

7'. Color of elytra primarily orangish, margins castaneous (Fig. 7). Elytra at subapex with transverse strigulae extending beyond the lateralmost discal stria. Surface of pygidium with strigae moderately impressed and more distantly spaced along midline (strigae separated by 3-4 strigal widths). Male parameres as in Fig. 27. .... *C. ephippiata* Ohaus

Cnemida aterrima Bates
(Figs. 6, 16, 17, 20, 26, 33)

Cnemida aterrima Bates 1888:272. Lectotype, lectoallotype, and 7 paralectotypes designated. Lectotype male at BMNH labeled a) "Type" (round with red circle), b) "sp. figured," c) "Chontales, Nicaragua. T. Belt," d) "Cnemida aterrima Bates" (Bates' handwriting), e) "B.C.A. Col. II (2)," and my lectotype label. Lectoallotype female at BMNH labeled a) "Type" (round with red circle), b) "Panzos, Vera Paz. Conradt. Cnemida aterrima Bates" (Bates' handwriting), c) "B.C.A. Col. II (2)," and my lectoallotype label. Paralectotype females (4) at BMNH all with the label "B.C.A. Col. II (2)," and the following locality data: 1) "Chontales, Nicaragua. Janson," 2) "Chacoj, Vera Paz. Champion," 3) "Santecomapan," 4) "Chontales, Nicaragua. T. Belt." One male paralectotype at BMNH labeled a)"Mexico, Sallé Coll.," b) "Ex. Coll. J. Sturm," c) "Mexico. Cnemida aterrima. Mihi." One female paralectotype at ZSMC labeled a) "Chontales, Nicaragua. Janson," a) "B.C.A. Col. II (2) Cnemida aterrima Bates," and my paralectotype label. One female paralectotype at ZMHB labeled a) "Misantla, Mexico. Höge," b) "ex. Museo H.W. Bates," c) "Cnemida aterrima Bates co-type" (Ohaus' handwriting on red label), and my paralectotype label.

Description. Length 9.9-12.4mm. Greatest width 5.2-6.5mm. **Color**: Dorsum, venter, and appendages shining black, dark brown, or castaneous, with castaneous or orangish markings on elytra (Fig. 6). **Head**: Surface of frons at mid-disc moderately densely punctate; base, apex, and margins punctostrigate, strigae coalescing in a U-shaped median depression; punctures .02-.05mm, transverse; strigae separated by about 1 strigal width. Surface of clypeus basomedially densely punctate to confluently rugopunctate or punctostrigate medially and apically. **Pronotum**: Form at base triemarginate; emargination at mid-base (anterior to scutellum) pronounced (Fig. 25a2). Basal angle right-angled or acute. Surface of disc moderately densely punctate, occasionally with a narrow patch of strigae extending from apex to near middle, not extending to margin (Figs. 16-17); punctures minute to .03mm. **Scutellum**: Longer than wide (W/L ratio = .74). Surface sparsely or moderately densely punctate; punctures .01-.03mm. **Mesepimeron**: Apex broadly produced beyond elytral base in dorsal view (Fig. 25a2). **Elytra**: Surface with weak, longitudinal depressions and punctate striae. One depression at mid-base mesad of humerus coalesces with another depression at base or disc, 1 anterior of apical callus (nearly obsolete), 1 mesad and anterior to apical callus (nearly obsolete), 1 lateral of humerus. Striae irregularly depressed, in irregular rows, interrupted at mid-disc: 1 next to sutural (stria reaching apex or entirely obsolete, marked only by a longitudinal depression), 3 on disc (none reaching base or apex, all interrupted at mid-disc), 2-3 laterad of humerus in foveate area only; punctures of first stria (next to sutural stria) longitudinal; punctures of discal striae elongate, inverse U-shaped (making striae appear closely paired), crescent-shaped, ocellate, or simple; striae separated in depressed area at base. Intervals variable in width, moderately to sparsely punctate; punctures minute to .02mm. Lateral margin not transversely strigulate. Elytral sutural length about 2.3 times length of scutellum. **Pygidium**: Surface punctate and strigate; mid-disc sparsely to moderately densely punctate, punctures minute to .02mm; strigae at apex forming 1 concentric circle, not closed at base; strigae separated by 3-4 strigal widths (Fig. 20). **Venter**: Metasternum at middle glabrous. Last sternite of male subapically quadrate, surface at base without weak vermiform striations laterad of midline. Last sternite of female apically entire, rounded, with weak strigulae at lateral margin; apex laterally with sparse, tawny, moderately long setae. **Legs**: Foreclaw with medioapical tooth (male); empodium not exposed beyond tarsomere 5. Meso- and metatarsomere 5 of male with mesomedial projection well developed (Fig. 25d2); simple in female. Mesotibia broadest at middle; lateral edge carinate in apical 1/3 and basal 1/3; apex biemarginate with 2 teeth: 1 medial, 1 lateral, both produced to tarsomere 2 or 3; 2 spinulae next to spurs. Metatibia broadest at middle, subequal in width to femur; mesal edge with few, moderately long, tawny setae; lateral edge carinate in apical 1/3 and basal 1/3, carinae more pronounced in female; apex with corbel produced to middle of tarsomere 3 or 4. Metacoxa: Apex right-angled. **Parameres**: Fig. 26.

Diagnosis. *Cnemida aterrima* is easily separated from others in the genus by a pronotal disc that lacks strigulae (occasional specimens may have a narrow patch of strigulae that extends from the apex to near the middle of the pronotum) (Figs. 16-17). Other characters that will serve to separate this species are: elytral disc with only 3 discal striae, lateral margin of elytra not transversely strigulate (shared with *C. leprieuri*, *C. intermedia*, and *C. gigantea*). Male parameres are also diagnostic.

In regions where *C. aterrima* and *C. intermedia* are sympatric (southern Nicaragua and northern Costa Rica), sculpturing of the pronotum of *C. aterrima* may range from nonstrigulate to strigulate (Figs. 16-17). Other characters are not variable in the region of overlap, and the 2 species are readily separated by the following characters: 3 elytral striae (4 in *C. intermedia* (Fig. 3)), mid-disc of the pygidium lacking strigae (Fig. 20) (mid-disc with strigae present in *C. intermedia*), and male parameres (Fig. 26).

Distribution. Tropical moist forests of southern Mexico to northern Costa Rica. Recorded from 150 to 1,400 m elevation.

Locality Data (Fig. 33). 85 specimens examined from AMNH, BMNH, CASC, CNCI, EMEC, FREY, HAHC, INBC, LAGO, MNHN, MAMC, SEMC, UMRM, UNAM, UNSM, USNM, ZMHB, ZSMC.

Costa Rica (9). Alajuela (1): Est. San Ramon (Parque Nacional Guanacaste). Guanacaste (8): Est. Cacao (lado suroeste del Vol. Cacoa), Est. Maritza (lado oeste Vol. Orosi), Est. Pitilla (9 km S Santa Cecilia).

El Salvador (1). Cuscatlan (1): no data.

Guatemala (7). Alta Vera Paz (3): Panzos, Chacoj. San Marcos (4): Tumbador.

Honduras (3). Intibuca (1): Choloma. Yoro (1): Progreso. Atlantida (1): La Cieba, Col. Naranjal.

Mexico (52). Chiapas (12): Santo Domingo (15 mi SE Simojovel), Cuidad Cuauhtemoc, 7.7 mi N. Frontera Comalapa, Raneno Alegre, Parque Laguna Belgica, Amatán, Tuxtla Gutierrez. Oaxaca (1): no data. San Luis Potosi (1): Tamazunchale. Veracruz (24): Minatitlán, Misantla, Alazan, Presidio, Est. Biol. Los Tuxtlas, Rancho Hanover, Cordoba (9 mi. NE), Sontecomapan, Playa Vicente, Misantla, Medellin, Tlacotalpan, no data. Yucatán (1): X-Can. No data (13).

Nicaragua (9). Chontales (9): no data.

No Data (4).

Temporal Data. January (1), March (2), April (2), May (13), June (8), July (8), August (5), October (1).

Remarks. Bates (1888) described *C. aterrima* from "many examples," including those from the Sallé collection. Bates retained the specific epithet, *aterrima*, that Sallé used in his collection. I located nine type specimens and designated lectotypes and paralectotypes.

Adults have been collected at flowers of *Inga* sp. (Mimosaceae). Morón *et al.* (1988) collected adults from rotting logs and from wood that was being used to maintain *Megasoma elephas* (Fabr.) in the laboratory (Morón 1979). In Chiapas, Mexico, this species was collected in lowland rain forest, montane rain forest, and tropical deciduous forest (Thomas 1993).

Cnemida ephippiata Ohaus
(Figs. 7, 32, 33)

Cnemida ephippiata Ohaus 1912:295.
Holotype male at ZMHB with labels a) "Amazonas, S. Andon d. Iça, 23.9.06. A. Ducke S." (newer label), b) "S. Antonio do Iça, 23.9.1906. Ducke" (older label), c) male parameres card-mounted, d) "Typus!" (rectangular red label), e) "Cnemida ephippiata Ohs." (handwritten on red paper), and my lectotype label.

Description. Length 10.1mm. Greatest width 5.2mm. **Color**: Head, pronotum, scutellum, pygidium, legs, and venter shining dark brown to black, with greenish reflections. Elytra shining ochraceous, with castaneous margins, and 2 castaneous markings on disc (Fig. 7). **Head**: Surface of frons at mid-disc moderately densely punctate; base, apex, and margins punctostrigate; strigae forming 2 adjacent, concentric circles, coalescing apically in medial depression (Fig. 14); punctures .02-.04mm; strigae separated by 1 or fewer strigal widths. Surface of clypeus confluently punctostrigate. **Pronotum**: Form at base triemarginate; emargination at mid-base (anterior to scutellum) pronounced (Fig. 25a2). Basal angle acute. Surface of disc punctate and strigate; strigae present laterad of midline to near margin and from apex to base, strigae separated by less than 1 to 1 strigal width; punctures present at midline from apex to base, wider from middle to base, region moderately densely punctate, punctures .01-.02mm, some transverse near strigate area. **Scutellum**: Longer than wide (W/L ratio = .67). Surface moderately densely punctate near margins; punctures .01-.03mm. **Mesepimeron**: Apex broadly exposed beyond elytral base in dorsal view (Fig. 25a2). **Elytra**: Surface with weak depressions and punctate striae. One depression at mid-base mesad of humerus, 1 at base of disc (somewhat transverse), 1 laterad of humerus. Striae irregularly depressed, in irregular rows, interrupted at mid-disc; 1 next to sutural stria reaching apex but not base, 4 on disc (2 inner striae reaching apex, 2 lateral striae reaching near callus and coalescing with striae laterad of humerus, none reaching base), striae laterad of humerus not in defined rows; punctures of first stria (adjacent to sutural stria) longitudinal, forming a broken line; punctures of disc broadly crescent-shaped or broadly inverse U-shaped, disordered in depression at elytral base. Intervals variable in width, moderately punctate; punctures about .01-.02mm. Lateral margin from metacoxa to apex transversely strigulate. Elytral sutural length about 2.3 times length of scutellum. **Pygidium**: Surface strigate; mid-line with strigae continuous; strigae at apex forming 1 concentric oval; apical strigae separated by 3-4 strigal widths. **Venter**: Metasternum at middle glabrous. Last sternite of male subapically quadrate, surface from base to preapex strigulate; apex setigerously punctate, punctures .01mm, setae moderate in length, tawny. **Legs**: Foreclaw with medioapical tooth; empodium not exposed beyond tarsomere 5. Meso- and metatarsomere 5 with mesomedial projection well developed (Fig. 25d2). Mesotibia broadest at middle; lateral edge weakly carinate in apical 1/3; apex biemarginate with 3 produced teeth: 1 mesal (weakly produced), 1 mediolateral, and 1 lateral (both produced to tarsomere 2), 2 spinulae between spurs and mediolateral tooth. Metatibia broadest at middle, femur slightly wider than tibia; mesal edge with moderately dense, moderately long, tawny setae; lateral edge with pronounced carinae, 1 in apical 1/3 and 1 in basal 1/3; apex with corbel produced to middle of tarsomere 4. **Metacoxa**: Apex right-angled. **Parameres**: Fig. 27.

Diagnosis. In overall body sculpturing, *C. ephippiata* is most similar to *C. retusa*. However, the coloration of the elytra (primarily orange in *C. ephippiata* rather than castaneous with orange or tan maculae as in *C. retusa*) serves to separate these species. Microsculpture characters also separate these taxa: in *C. ephippiata* the transverse strigulae at the subapex of the elytra extend past the lateralmost discal stria, whereas in *C. retusa* the lateral strigae terminate before the lateralmost discal stria at the humerus; the pygidial strigae of *C. ephippiata* are separated by 3 to 4 strigal widths, whereas in *C. retusa* the pygidial strigae are separated by 1 to 3 strigal widths. Male parameres are also diagnostic (Fig. 27).

Distribution. Western Amazon River near the Peruvian and Colombian border.

Locality Data (Fig. 33). 1 specimen (holotype) from ZMHB. **Brazil** (1). Amazonas (1): San Antonio do Iça.

Temporal Data. September.

Remarks. Only the holotype for this species is known; females, larvae, natural history, and variation are unknown.

Cnemida gigantea Jameson, new species
(Figs. 2, 9, 21, 33)

Cnemida gigantea Jameson new species; Holotype female deposited at the MNHN labeled, a)"New Granada" (handwritten), b) "Sta. Rosa" (handwritten), c) "Ex. Musaeo H.W. Bates 1892," d) "Museum Paris ex Coll. R. Oberthur 1952," and with my holotype label.

Description. Length 16.2mm. Greatest width 8.0mm. **Color**: Dorsum, venter, and appendages shining black with castaneous undertones, with 1 large, orange macula on center of disc of each elytron (Fig. 29). **Head**: Surface of frons at mid-disc moderately densely punctate; base, apex, and margins punctostrigate, strigae coalescing in V-shaped medial depression (Fig. 15); punctures .02-.05mm, transverse; strigae separated by 1-2 strigal widths. Surface of clypeus basomedially densely punctate to confluently, rugopunctate or punctostrigate medially and apically. **Pronotum**: Form at base triemarginate; pronounced emargination at midbase (anterior to scutellum) (Fig. 24a2). Basal angle right-angled. Surface of disc moderately densely punctate, some punctures transverse, these present apically to middle third of disc, a few at marginal line occasionally coalescing to form short strigulae; punctures .01-.03mm, a little larger at margin. **Scutellum**: Scutellum longer than wide (W/L ratio = .76). Surface sparsely or moderately densely punctate; punctures .01-.02mm. **Mesepimeron**: Apex broadly exposed beyond elytral base in dorsal view (Fig. 25a2). **Elytra**: Surface with weak, somewhat longitudinal depressions, weakly raised macula, and punctate strigae. One depression at midbase mesad of humerus, 1 laterad of humerus. Striae irregularly depressed, in irregular, obscure rows, interrupted at mid-disc by raised macula (Fig. 2, 9): 1 next to sutural stria reaching apex but fading at mid-disc, 3 at base (1 inner stria that borders macula and reaches apex, 1 at middle interrupted by macula, but reappearing at posterior edge of macula and continuing to apex, 1 laterad that is interrupted by macula), 3 laterad of humerus in obscure, incomplete rows; punctures crescent-shaped near apex, inverted U-shaped at mid-disc and base, simple or crescent-shaped laterad of humerus; punctures .01-.05mm. Intervals variable in width, moderately densely punctate; punctures minute to .02mm, some crescent-shaped (especially at apex). Lateral margin not transversely strigulate. Elytral sutural length about 2.3 times length of scutellum. **Pygidium**: Surface strigate; mid-disc smooth, lacking strigae; strigae at apex forming 2 adjacent, concentric circles (Fig. 21); apical strigae separated by 3-4 strigal widths. **Venter**: Metasternum at middle glabrous. Surface of last sternite weakly strigulate and punctate; punctures .02-.04mm; apex entire (although worn). **Legs**: Foreclaw with empodium not exposed beyond tarsomere 5. Mesotibia nearly parallel (weakly convergent in apical 1/3); lateral edge with nearly obsolete carina in apical 1/3 and basal 1/3; apex biemarginate with 3 produced teeth: 1 mesal (weakly produced), 1 mediolateral, 1 lateral (both produced to tarsomere 2), 2 spinulae next to spurs and mediolateral, apical tooth. Metatibia nearly parallel (convergent in apical 1/3); femur wider than tibia; lateral edge with carinae, 1 in apical 1/3 and 1 in basal 1/3; corbel produced to base of tarsomere 4. **Metacoxa**: Apex weakly acute.

Diagnosis. *Cnemida gigantea* is separated from its congeners by its large size (1.5 to 2.0 times larger than any other species) and its single, large macula on each elytron (Figs. 2, 9). Other characters that serve to separate it are: pronotal disc that is punctate or with few transverse punctures (similar to *C. aterrima*) rather than strigate, elytral disc with only 3 striae (shared with *C. tristriata*, *C. aterrima*, and *C. leprieuri*), and apical strigae of the pygidium that form 2, adjacent, concentric circles (Fig. 21).

Distribution. Colombia.

Locality Data (Fig. 33). 1 specimen (holotype) from MNHN. Colombia (1). Guainía (1): Santa Rosa.

Temporal Data. Unknown.

Remarks. The holotype specimen of *C. gigantea* originally came from the H.W. Bates collection, was later bought by R. Oberthur, and was deposited at the Paris Museum (MNHN). In the Biologia, Bates (1888) remarked that several new species of *Cnemida* were known in collections, yet he described only *C. intermedia* and *C. aterrima*. Bates may have been referring to this specimen (and *C. leprieuri* Arrow, a species that he collected in the Amazon) when he made this statement.

The locality "Santa Rosa" in New Granada is a commonly encountered place-name in older collections. I conjecture that the type locality, "Santa Rosa," refers to the locale in Colombia. Santa Rosa, Guainía, is located on the Rio Guaviare, which is a tributary of the Rio Orinoco.

Only the female holotype specimen is known of this species.

Etymology. The specific epithet, *gigantea*, refers to the large size of the holotype, a feature characteristic of the species.

Cnemida intermedia Bates
(Figs. 3, 8, 14, 25c2, 28, 33)

Cnemida intermedia Bates 1888:272. **Lectotype** and lectoallotype designated. One syntype not located. Lectotype male at BMNH labeled a) "Type" (round label with red circle), b) "Tolé, Panama. Champion," c) "Cnemida intermedia Bates" (handwritten in Bates' hand)," d) "B.C.A. Col. II (2)," and my lectotype label. Lectoallotype female at BMNH labeled a) "Type" (round with red circle), b) "Chontales, Nicaragua. T. Belt," c) "Cnemida intermedia Bates" (Bates' handwriting), d) "B.C.A. Col. II (2)," and my lectoallotype label.

Description. Length 8.2-12.4mm. Greatest width 4.2-6.3mm. **Color**: Dorsum, venter, and appendages shining black, dark brown, or castaneous, with castaneous or orangish markings on elytra (Fig. 3, 8). **Head**: Surface of frons at mid-disc moderately densely punctate; base, apex, and margins punctostrigate, forming 2 adjacent circles of concentric strigae and that coalesce in discal depression (Fig. 14); punctures .03-.06mm; strigae separated by fewer than 1-2 strigal widths. Surface of clypeus basomedially confluently rugopunctate or punctostrigate medially and apically. **Pronotum**: Form of pronotum at base triemarginate; pronounced emargination at mid-base (anterior to scutellum) (Fig. 25a2). Basal angle right-angled or acute. Surface of disc punctate and strigate; strigae present laterad of midline from apex to middle and from lateral margin to near mid-disc, strigae separated by fewer than 1 to 2 strigal widths; punctures present at mid-disc extending from apex to base, this region moderately densely punctate; punctures .01 to .05mm, some transverse near foveate region. **Scutellum**: Longer than wide (W/L ratio = .68). Surface sparsely or moderately densely punctate; punctures .01-.03mm. **Mesepimeron**: Apex broadly exposed beyond base of elytra in dorsal view (Fig. 25a2). **Elytra**: Surface with weak depressions and punctate striae. One depression at mid-base mesad of humerus coalesces with another at base of disc, 1 anterior to apical callus, 1 lateral and anterior to apical callus, 1 laterad of humerus. Striae irregularly impressed, in irregular rows (Fig. 3): 1 next to sutural stria (reaching apex but obscure at mid-suture), 4 on disc (all interrupted at mid-disc, none reaching base, 2 inner striae reaching apex, 1 or 2 lateral striae reaching callus, lateral-most stria often reduced or lacking from base to mid-disc), 3-4 laterad of humerus; punctures of first stria (adjacent to sutural stria) longitudinal, forming a continuous line; punctures of disc elongate, inverse U-shaped or slightly crescent-shaped (making striae appear closely paired), striae distinct or slightly disordered at base in depressed regions. Intervals variable in width, moderately to sparsely punctate; punctures minute to .02mm. Lateral margin from metacoxa to apex transversely strigulate. Elytral sutural length about 2.1 times length of scutellum. **Pygidium**: Surface punctate and strigate; punctures present at mid-disc, moderately dense, minute to .02mm; strigae at apex forming 1 concentric oval, strigae not joined at base; apical strigae separated by 1-3 strigal widths. **Venter**: Metasternum glabrous. Last sternum of male subapically quadrate, surface at base laterad of midline with weak, vermiform strigae. Last sternum of female apically entire, rounded, with vermiform strigae at apex. **Legs**: Foreclaw with medioapical tooth (male); empodium not exposed beyond tarsomere 5. Meso- and metatarsomere 5 of male with mesomedial projection well developed (Fig. 25d2); simple in female. Mesotibia broadest at middle; lateral edge carinate in apical 1/3 and basal 1/3; apex biemarginate with 3 produced teeth: 1 mesal (weakly produced), 1 mediolateral, and 1 lateral (both produced to tarsomere 2 or 3), 2 spinulae next to spur and mediolateral, apical tooth. Metatibia broadest at middle (Fig. 25c2), nearly as wide as femur; mesal edge (male) with setae moderately long, sparse to moderate in density; lateral edge with carinae, 1 in apical 1/3 and 1 in basal 1/3, more pronounced in female; apex with corbel produced to middle of tarsomere 4 or 5. **Metacoxa**: Apex right-angled. **Parameres**: Fig. 28.

Diagnosis. *Cnemida intermedia* is most similar to *C. lacerata*, but is separated based on: a lack of dense, tawny, setae on the middle of the metasternum of the male (present in *C. lacerata*); the elytral striae which, at the base, are not confused and rugose as in *C. lacerata*; and the strigae of the frons which form 2, adjacent, concentric circles that meet in a median, discal depression (Fig. 14) (in *C. lacerata*, the strigae coalesce in a V-shaped, median, discal depression and do not appear as 2 adjacent circles (Fig. 15)). This species is separated from

C. retusa, C. ephippiata, and *C. tristriata* by sculpturing of the pygidium and pronotum. In *C. intermedia* the mid-disc of the pygidium is punctate (rather than strigate as in the other 3 species) and the punctate region of the pronotum in *C. intermedia* is wider from mid-disc to base (Fig. 20), whereas in *C. retusa, C. tristriata,* and *C. ephippiata* the punctate region is narrower or lacking (Fig. 22). It is separated from *C. aterrima* by the sculpturing of the pronotal disc which is strigate in *C. intermedia* and punctate (or with few strigae) in *C. aterrima.*

Distribution. Nicaragua to northwestern South America, including 1 record from Bolivia (possibly erroneous). Recorded from elevations of 20 to 1,200 m.

Locality Data (Fig. 33). 180 specimens examined from BCRC, BMNH, DCCC, CASC, CMNH, RACC, DJCC, EGRC, FMNH, FSCA, HAHC, HPSC, INBC, JEWC, MCZC, MNHN, SEMC, USNM, ZMHB.

Bolivia (1). No data (1).

Colombia (25). Antioquia (5): Valle de Cauca. Boyaca (2): Antioquia. Magdalena (3): Bonda, Aracataca, no data. Valle (2): Sevilla, Rio Dagua. No data (13).

Costa Rica (61). Alajuela (2): Pilón de Bijagua, Sector San Ramon. Cartago (2): Turrialba, Hitoy Cerere. Guanacaste (33): P.N. Santa Rosa, Est. Maritza (lado oeste Vol. Orosi), Cerro El Hacha (12 km SE La Cruz), 24 km NW Cañas (hacienda COMELCO), P.N. Barra Honda (3 km N Nacaome), Est. Murcielago (8 km SW Cuajiniquil), Est. Las Pailas (P.N. Rincon de la Vieja), Rio San Lorenzo, Est. Los Almendros. Limon (2): Bananito. Puntarenas (10): Punta Banco, Est. Esquinas, Sta. Elena (4-6 km S), Peninsula de Osa (Rancho Quemado), Lindora (Res. Biol. Monteverde), Res. Biol. Bonita (Est. Queb. Bonita), P. N. Manuel Antonio. San José (5): San José, nr. Quesada, San Isidro del General. No data (7).

Ecuador (4). Loja (2): no data. No data (2).

Nicaragua (3). Chontales (2): no data. No data (1).

Panama (72). Bocas del Toro (1): Gualaca-Chiriqui Grande Hwy (4 km N cont. div.). Chiriqui (7): Tolé, David, no data. Colon (2): 6 km E Maria Chiquita (9°26' N 79°42' W), 34 km E. Portobelo. Darien (1): Morti (8°50' N 77°59' W). Panama (59): Cerro Campana (8°40' N 49°56' W), Majé Station (9°09' N 78°47' W), El Llano (11-15 km N; 10 km N; km 8-15), El Llano-Carti Rd (km 8-11; km 8 N; km 9 N; 7-13 km), Barro Colorado Island (Lago Gatun), Chorrera. No Data (2).

Venezuela (9). Apure (2): Sarare. Distrito Federal (4): Caracas. No Data (3).

No Data (5).

Temporal Data. February (2), March (7), April (5), May (36), June (10), July (3), August (11), September (2), October (6), November (7), December (9).

Remarks. Bates (1888) named *C. intermedia* based on 3 specimens, and he was unsure whether it was, in fact, a true species: "In sculpture, this species or subspecies more nearly resembles the South-Brazilian *C. lacerata* (Germ.) than the *C. retusa* of Guiana and the Amazons (sic) valley" (p. 272). Only 2 specimens from the type series were located. One remaining type specimen, collected by Champion in David, Panama remains to be located. The Ohaus collection in Berlin (ZMHB) contains 2 female specimens with Ohaus' cotype labels and "ex. Museo H.W. Bates" labels. However, because the label data do not correlate with Bates' description (the specimens are from "V.d. Chiriqui" rather than David and do not bear a Champion label), I believe that Ohaus erroneously placed cotype labels on these specimens.

Adults visit flowers and are most active in the early morning. Label data indicate that beetles have been collected between 7:10 and 9:50 am on *Turnera ulmifolia* L. (Turneraceae), *Bixa orellana* L. (Bixaceae), *Mimosa invisa* Martius, and *Mimosa* sp. (Mimosaceae). Adults have also been collected on flowers of *Psychotria* sp. (Rubiaceae). Similar to the behavioral deception that was described in *C. retusa* (Ratcliffe 1990), Wappes (pers. comm. Jan. 1994) observed individuals of *C. intermedia* resting on their sides while on vegetation.

Individuals of *C. intermedia* and *C. aterrima* occur sympatrically in southern Nicaragua and northern Costa Rica. Within this narrow region of overlap, there is a wide range of pronotal sculpturing in *C. aterrima*. Despite this variation, the 2 species are distinct and easily separated (see remarks section under *C. aterrima*).

The larvae of *C. intermedia*, the only larvae known in the genus, were collected and reared by F. Quesada (INBio, Costa Rica). Larvae of *C. intermedia* were found in rotting wood of *Hyeronima alchorneoides* Allemao (Euphorbiaceae) in the Osa Peninsula, Costa Rica.

Cnemida lacerata (Germar)
(Figs. 10, 15, 25c3, 29, 33)

Rutela lacerata Germar 1824:119. Type not found in ZMHB or elsewhere.
Cnemida curtisi Kirby 1827:148. Type not found.
Cnemida sparshalli Kirby 1827:148. Holotype male at BMNH labeled a) "Type" (round label with red circle), b) "6350" (round, blue label), c) "(2) sparshalli" (handwritten), and my holotype label.

Description. Length 10.8-13.5mm. Greatest width 5.2-6.8mm. **Color**: Dorsum, venter, and appendages shining black, dark brown, or castaneous (pronotum, scutellum, elytral suture often margined with red-brown), with orange or red-brown markings on elytra (Fig. 10). **Head**: Surface of frons at mid-disc moderately densely punctate; base, apex and margins punctostrigate, strigae coalescing in V-shaped medial depression (Fig. 15); punctures .02-.05mm; strigae separated by 1 or fewer strigal widths. Surface of clypeus basomedially confluently rugopunctate or punctostrigate medially and apically. **Pronotum**: Form at base triemarginate; pronounced emargination at mid-base (anterior to scutellum) (Fig. 25a2). Basal angle right-angled or acute. Surface of disc punctate and strigate; strigate present laterad of midline from apex to base and from lateral margin to near mid-disc, strigae separated by 1 strigal width or less; punctate region at mid-disc (basally to apically), moderately densely punctate, punctures .01 to .02mm, some transversely punctostrigate near strigate region. **Scutellum**: Longer than wide (W/L ratio=.72). Surface sparsely to moderately densely punctate; punctures minute to 0.01mm. **Mesepimeron**: Apex broadly exposed beyond elytral base in dorsal view (Fig. 25a2). **Elytra**: Surface with weak depressions and punctate striae. One depression at mid-base mesad of humerus coalesces with another at base of disc, 1 anterior to apical callus, 1 laterad and anterior to apical callus, 1 laterad of humerus. Striae irregularly depressed, in irregular rows, interrupted at mid-disc; 1 next to sutural stria reaching apex but not base, 4 on disc (2 inner striae reaching apex, 2 lateral striae reaching callus, none reaching base, all interrupted at mid-disc), 3-4 laterad of humerus; punctures of first stria (adjacent to sutural stria) longitudinal, forming a continuous line; punctures of disc elongate, inverse U-shaped or crescent-shaped (making striae appear closely paired), disordered and rugose at elytral base in depressed regions. Intervals variable in width, moderately to sparsely punctate; punctures minute to .02mm. Lateral margin from metacoxa to apex transversely strigulate. Elytral sutural length about 2.3 times length of scutellum. **Pygidium**: Surface strigate except at midline (smooth), apex with strigae forming 1 concentric circle, separated by 1-3 strigal widths. **Venter**: Metasternum at middle with dense, tawny, yellow setae; setae moderate in length. Last sternum of male subapically quadrate, surface at base with weak, vermiform strigae laterad of midline. Last sternum of female apically entire, rounded, with vermiform strigae at apex. **Legs**: Foreclaw with medioapical tooth (male); empodium not exposed beyond tarsomere 5. Meso- and metatarsomere 5 of male with mesomedial projection well developed (Fig. 25d2); simple in female. Mesotibia broadest at middle; lateral edge carinate in apical 1/3 and basal 1/3, apex bi-emarginate with 3 produced teeth: 1 mesal (weakly produced), 1 mediolateral (produced to tarsomere 2 or 3), 1 lateral (produced to tarsomere 2 or 3), 1-2 spinulae next to spur and mediolateral, apical tooth. Metatibia broadest at middle, wider than femur; mesal edge with dense, tawny, moderately long setae; lateral edge carinate in apical 1/3 and basal 1/3, carinae more pronounce in female; apex with corbel produced to middle of tarsomere 4 or 5. **Metacoxa**: Apex right-angled. **Parameres**: Fig. 29.

Diagnosis. *Cnemida lacerata* is distinct from other species of *Cnemida* based on the dense field of tawny setae in the middle of the metasternum in the male (absent in other species); the strigae of the frons that coalesce in a V-shaped discal depression (Fig. 15) [rather than strigae forming adjacent, concentric circles (Fig. 14)]; the mesal edge of the metatibia with dense, tawny setae (Fig. 25c3); the mid-disc of the pygidium that lacks strigae; and a metatibia that is wider than the femur. Females of *C. lacerata* can be readily separated from females of *C. retusa* and *C. intermedia* based on the punctures of the elytral striae that are disordered at the base in *C. lacerata* (in *C. retusa* and *C. intermedia* the punctures are distinct, not disordered). Additionally, the pygidial strigae in females of *C. lacerata* are diagnostic. In *C. lacerata*, the pygidial strigae form a complete concentric circle at the apex, whereas in *C. intermedia* the circle is incomplete. In *C. lacerata* the pygidial strigae at mid-disc are incomplete, whereas in *C. retusa* the strigae at mid-disc are complete.

Distribution. Eastern Brazil, coastal Venezuela, and coastal French Guiana. The only records for elevation are 300 to 500 m.

Locality Data (Fig. 33). 131 specimens examined from AMNH, ANSP, BMNH, CASC, CMNH, CNCI, CUIC, FMNH, FREY, HAHC, MCZC, MLPA, MNHN, QBUM, USNM, ZMHB, ZSMC.

Argentina (2). Jujuy (1): no data. Misiones (1): Igazú.

Brazil (99). Bahia (1): no data. Distrito Federal (2): Brasilia. Espirito Santo (9): St. Leopoldina, no data. Paraná (4): Rolandia, no data. Rio de Janeiro (41): Rio de Janeiro, Corcovado. Santa Catarina (17): Nova Teutonia (27°11', 52°23'), Corupá, Joinville, Blumenau, no data. No Data (25).

French Guiana (3). Cayenne (3): Cayenne.

Paraguay (2). Alto Parana (2): Bella Vista.

Venezuela (1). Distrito Federal (1): Caracas.

No Data (24).

Temporal Data. January (2), February (1), March (3), April (1), July (1), October (11), November (20), December (15).

Remarks. Several authors (Burmeister 1844, Gemminger and Harold 1869, Ohaus 1918 and 1934, Machatschke 1972) list *C. retusa* LaPorte as a synonym of *C. lacerata* (Fabr.). This synonymy is in error. LaPorte (1840:123) described 2 new species (*C. cartissi* and *C. francilloni*), synonymized *C. sparshalli* Kirby (under *C. retusa* (Fabr.)), and compared his new species to *C. retusa* (Fabr.). Evidently, this was mistakenly interpreted as a description of a new species, "*Cnemida retusa* LaPorte." Burmeister (1844) was the first to place "*C. retusa* Laporte" as a synonym of *C. lacerata* and, since this time, this error has been perpetuated.

Nearly half the specimens of *C. lacerata* are older, 1800's specimens, and label data are absent or record only the country where the specimen was collected. Thus, although I examined 128 specimens, the range and temporal data for this species is scanty. It is distributed from northern South America (Venezuela and French Guiana, 4 specimens) to east and southeastern Brazil (Bahia to Santa Catarina) and Paraguay (75 specimens). There is an absence of locality data from the Amazon Basin and northeastern Brazil. These distributional data indicate that there is a wide gap between the species' northern and southern distributions. Additional specimens with accurate locality information are needed to address whether this disjunct distribution is real or whether it is an artifact of collecting.

The only ecological information indicates that individuals were collected from buds and flowers.

Cnemida leprieuri Arrow
(Figs. 11, 18, 25A-D, 30, 33)

Cnemida leprieuri Arrow 1899:367.**Lectotype**, lectoallotype, and 1 paralectotype designated. One syntype not located. Lectotype male at BMNH labeled a) "Type" (round on red circle), b) "male symbol," c) "Ega, Brazil" (handwritten), d) "Cnemida leprieuri, Arrow type male symbol," and my lectotype label. Lectoallotype female at BMNH labeled a) "female symbol," b) "Type" (round on red circle), c) "Amazons," d) "Bowring. 63-47," 4) "Cnemida leprieuri, Arrow type female symbol," and my lectoallotype label. Paralectotype male at BMNH labeled a) "Amazons male symbol" (handwritten), b) "Cnemida leprieuri, Arrow. Co-type," c) "Nevinson Coll. 1918-14," and with my paralectotype label.

Description. Length 10.4-12.9mm. Greatest width 5.2-6.5mm. **Color**: Head, disc of pronotum, and scutellum dull, metallic green; margins of pronotum, elytra, venter, and appendages shining tan (Fig. 11); pygidium in males and females dull, metallic green, with or without tan margins; elytral margin at middle with darkened macula in females (absent in males). **Head**: Surface of frons at base and mid-disc densely punctate, mid-apex confluently punctate to rugopunctate, base laterally punctostrigate; punctures about .05mm; puncto-strigae fine, separated by 1 strigal distance. Surface of clypeus at base densely punctate and confluently punctate or rugopunctate medially and apically; punctures .04-.05mm. **Pronotum**: Form at base triemarginate; weak emargination at mid-base (anterior to scutellum) (Fig. 25a1). Basal angle right-angled or slightly acute. Surface of disc moderately densely punctate at base and mid-disc and moderately densely to confluently punctate at apex and margins; punctures of base and disc .01-.03mm, punctures at apex and margins .03-.10mm, some punctures forming punctate striae at margins. **Scutellum**: Longer than wide (W/L ratio = .77). Surface moderately, densely punctate; punctures .02-.04mm, more dense at base, some transverse. **Mesepimeron**: Apex narrowly exposed beyond elytral base in dorsal view (Fig. 25a1). Elytra: Surface with linear, punctate striae: 1 next to sutural stria (nearly reaching apex and base), 4 on disc (2 inner striae nearly reaching apex, 2 lateral striae reaching apical umbone, none reaching base), 3-4 laterad of humerus (reaching neither apex nor base); punctures .01 (at apex) to .13mm (at base), ocellate or not, some confluent at base. Intervals variable in width, moderately densely punctate;

punctures .01-.05mm. Lateral margin from metacoxa to apex strigulate. Elytral sutural length about 2.8 times length of scutellum. **Pygidium**: Surface with strigae forming 1 concentric circle at apex (male) or semi-circular (female); strigae continuous at mid-disc. **Venter**: Metasternum at middle glabrous. Last sternum of male at subapex quadrate, surface at mid-apex with vermiform strigae. Last sternum of female apically with medial tooth (present or not); if present, surface laterad of tooth weakly declivous, with vermiform strigae; if tooth absent, surface apically declivous, with vermiform striae. **Legs**: Foreclaw with medioapical tooth not evident (male); empodium weakly exposed beyond tarsomere 5. Meso- and metarsomere 5 without mesomedial projection (Fig. 25d1). Mesotibia with sides subparallel; lateral edge with carina in apical 1/3 (may be obsolete); inner apex produced to middle of tarsomere 2 or base of tarsomere 3, 2-4 spinulae between spurs and lateral edge. Metatibia with sides subparallel, widest at middle (Fig. 25c1), not as wide as femur; mesal edge without dense setae; lateral edge with carinae in apical 1/3; apex laterally with weak corbel produced to middle of tarsomere 2 or base of tarsomere 3. Meso- and metatibia of female slightly thicker than male, carinae more developed, sculpturing heavier. **Metacoxa**: Apex acute or right-angled. Parameres: Fig. 30.

Diagnosis. *Cnemida leprieuri* is easily distinguished from other species in the genus by its coloration (pronotum, scutellum, and pygidium dull metallic green; elytra and margins tan rather than castaneous or black with orange to tan maculations). It also differs by the following characters: meso- and metatarsomere 5 lacking internal medial tooth (Fig. 25d1) (present in other species of *Cnemida* (Fig. 25d2)), base of pronotum anterior to scutellum weakly emarginate (Fig. 25a1) (deeply emarginate in other species (Fig. 25a2), and pronotum moderately densely punctate (Fig. 18) (strigate or finely punctate in other species of *Cnemida*).

Distribution. Amazon Basin region. The only recorded elevation is 290 m.

Locality Data (Fig. 33). 49 specimens examined from BCRC, BMNH, CMNH, FREY, FSCA, MNHN, USNM, ZMHB, ZSMC.

Brazil (33). Amazonas (26): Tefé, no data. Pará (5): no data. Roraima (1): Limão. No Data (1).

Bolivia (1). La Paz (1): Coroico.

French Guiana (8). Cayenne (8): Cayenne, no data.

Peru (1). Madre de Dios (1). Rio Tambopata Res. (30 km [air] SW Puerto Maldonado).

Surinam (1). No data (1).

No Data (5).

Temporal Data. October (1). No other temporal data are available.

Remarks. Arrow (1899) described *C. leprieuri* from specimens collected by H.W. Bates in the Amazon region. According to Arrow (1899), he described this species based on 3 female specimens and 1 male specimen. However, I located 2 male syntypes and 1 female syntype (1 syntype was not located). It is possible that Arrow misidentified the gender of the specimens in the type series. In his description Arrow incorrectly stated that differences in pygidial coloration were due to gender. However, in *both* males and females the coloration of the pygidium ranges from entirely dull metallic green to dull metallic green with wide, tan margins, and these differences are not gender-specific. Instead, males and females are separated by the foreclaws (claws of male with outer claw greatly enlarged and split, subequal in size and simple in females) and a mid-lateral elytral macula present in females and lacking in males.

Cnemida retusa (Fabricius)
(Figs. 1, 4, 12, 19, 31, 33)

Trichius retusa Fabricius 1801:113. Lectotype and paralectotype designated. Lectotype male at ZNUC with male parameres card-mounted labeled with a) small, green square label, b) "Type" (red label), c) "Essequibo. Smidt. Mus. J. Lund. Trichius retusus F." (handwritten [not Fabricius' writing] on bordered paper), and my lectotype label. Paralectotype male at ZMUC with male parameres card-mounted at ZMUC and labeled with a) small, green, square label, b) "Type" (red label), and my paralectotype label.

Cnemida cayennensis Laporte 1840:123. Type not located. No specimen with this name at MNHN and no mention of this taxon in the accession books.

Cnemida francilloni Kirby 1827:147. (Not *Ceemida* as in Machatschke 1974.) Holotype male at BMNH labeled a) "Type" (round with red circle), b) "Kirby," c) "6350" (round, blue label), d) "(1) Francilloni," and my holotype label.

Ometis picta Guérin-Meneville 1844:92. Type not located.

Description. Length 8.1-12.2mm. Greatest width 4.0-5.9mm. **Color**: Dorsum, venter, and appendages shining black, dark brown, or castaneous, with or without metallic green reflections, and with tan or orange markings on elytra (Fig. 1, 4, 12). **Head**: Surface of frons at mid-disc moderately densely punctate; base, apex, and margins punctostrigate, forming 2 adjacent, concentric circles that coalesce at apex in weak, medial depression (Fig. 14); punctures .02-.04mm; strigae separated by 1-2 strigal widths. Surface of clypeus basomedially confluently, rugopunctate and confluently rugopunctate or punctostrigate medially and apically. **Pronotum**: Form at base triemarginate; pronounced emargination at mid-base (anterior to scutellum) (Fig. 25a2). Basal angle right-angled or acute. Surface of disc punctate and strigate; strigae present laterad of midline from apex to base and from margin to mid-disc, strigae separated by 1 strigal width or less; punctate area present at mid-disc (basally to apically), moderately densely punctate, punctures .01-.05mm, some transversely punctostrigate near strigate region. **Scutellum**: Longer than wide (W/L ratio = .66). Surface moderately densely punctate near margins; punctures .01-.03mm. **Mesepimeron**: Apex broadly exposed beyond elytral base in dorsal view (Fig. 25a2). **Elytra**: Surface with weak depressions and punctate striae. One depression at mid-base mesad of humerus, 1 basodiscally (slightly transverse), 1 anterior of apical callus (longitudinal), 1 laterad of humerus. Striae irregularly depressed, in irregular rows (Figs. 1, 4): 1 next to sutural stria reaching apex but not base, 4 on disc (2 inner striae reaching apex, 2 lateral striae reaching callus, none reaching base), 3-4 lateral of humerus; punctures of first stria (adjacent to sutural stria) longitudinal, nearly continuous; punctures of disc elongate, inverse U-shaped or crescent-shaped (making striae appear closely paired), disordered and confluent at elytral base in depressed regions. Intervals variable in width, moderately punctate; punctures .01-.02mm. Lateral margin from metacoxa to apex transversely strigulate. Elytral sutural length about 2.2 times length of scutellum. **Pygidium**: Surface strigate; strigae partially effaced or broken at midline, separated by more than 3 strigal widths, more effaced in female; strigae at apex forming 1 concentric oval, separated by 1-3 strigal widths. **Venter**: Metasternum at middle glabrous. Last sternum of male subapically quadrate, surface at base with weak vermiform strigae; subapex to apex of male with reduced sclerotization. Last sternum of female apically entire, rounded, with vermiform strigae. **Legs**: Foreclaw with medioapical tooth (male); empodium not exposed beyond tarsomere 5. Meso- and metatarsomere 5 of male with mesomedial projection well developed (Fig. 25d2); simple in female. Mesotibia broadest at middle, as wide as femur; mesal edge with sparse, moderately long, tawny setae (may be worn) in male; lateral edge with carinae in apical 1/3 and basal 1/3 (obsolete in males); apex biemarginate with 3 teeth: 1 mesal (weakly produced), 1 mediolateral (produced to apex of tarsomere 2 or middle of tarsomere 3), 1 lateral (produced to tarsomere 2 or middle of tarsomere 3), 1-2 spinulae next to spur and mediolateral, apical tooth. Metatibia broadest at middle; males with mesal edge setose; setae sparse to moderately dense, tawny, moderately long; lateral edge carinate in apical 1/3 and basal 1/3, more carinate and sculptured in female; apex with corbel produced to middle of tarsomere 4. **Metacoxa**: Apex right-angled. **Parameres**: Fig. 31.

Diagnosis. *Cnemida retusa* is most similar to *C. ephippiata* and *C. tristriata* but is separated by the following character states: elytra castaneous or black with orange or tan maculae (elytra primarily orangish in *C. ephippiata*, castaneous in *C. tristriata*); elytral disc with 4 striae (Fig. 4) (shared with *C. ephippiata*) rather than 3 striae as in *C. tristriata* (Fig. 5); the apicomedial margin of the elytra without strigulae extending to the lateralmost discal striae (whereas strigulae extend to lateralmost discal striae in *C. ephippiata*). *Cnemida retusa* differs from *C. lacerata* due to the absence of a dense field of tawny setae in the middle of the metasternum in the male, strigae of the frons not coalescing in a V-shaped area (strigae of *C. retusa* form 2, adjacent, concentric circles (Fig. 14)), and pygidium with strigae more or less continuous at the mid-disc (punctate or smooth in *C. lacerata*).

Distribution. South America north of Argentina. Elevation records for this species are 350, 400, and 750 m.

Locality Data (Fig. 33). 460 specimens examined from AMNH, BCRC, BMNH, CASC, CMNH, CNCI, CUIC, DJCC, FMNH, FREY, HAHC, MCZC, MNHN, MNNC, QBUM, UNSM, USNM, ZMHB, ZMUC, ZSMC.

Brazil (332). Amapa (2): Porto Santana, Serro do Navio. Acre (1): Rio Humaitá. Amazonas (40): Tefé, Manaus, Manacapuru, BR 319 km 275, Rio Javari, São Paulo do Olivença, Rio Tonantins, Rio Juruá, Fonte Boa, no data. Bahia (30): Mucuri, no data. Espirito Santo (22): Linhares, Linhares (P.N. Sooretama), Santa Leopoldina, no data. Goias (67): Jatahy, Rio Verde, Trinidade. Mato Grosso (14): Chapada dos Guimaraes, Gleba Arinos, Reserva Humboldt (10° 11'S, 59°48'W). Mato Grosso do Sul (10): Corumbá, Urucum. Minas Gerais (5): no data.

Pará (80): Obidos, Obidos (Canta Galo), Colonia Rio Branco, Mocajuba, Est. Cruz Alta (Rio Trombetas), Santarem, Itaituba, Ilha de Marajo, Cameta, Mosquiero (Rio de Para), Amazonas Faro, no data. Rio de Janeiro (9): Jurujuba, Corcovado, no data. Rondonia (6): Porto Velho (Rio Madeira), Ouro Preto do Oeste. No Data (46).

Bolivia (9). Beni (1): Villa Bella. Chuquisaca (2): El Palmar (Yungas). Cochabamba (4): Rio Chapare. No Data (2).

Colombia (1). No data (1).

Ecuador (2). Imbabura (1): No data. Pastaza (1): Rio Cururay.

French Guiana (48). Cayenne (48): Cayenne, Roches de Kourou, Gourdonville, Charvein, Passoura (stream), no data.

Guyana (2). West Berbice (1): Blairmont. Mazaruni-Potaro (1): Kartabu.

Peru (20). Cuzco (1): Rio Vilcanota. Junin (1): 3-7 km SSW San Martin de Pangoa. Loreto (10): Ucayali R. Yarina Cocha, Rio Napo, Iquitos, Pucallpa (5 mi radius), Chambireyaci nr. Yurimaguas, Yurimaguas. San Martin (8): Mayobambo, Tarapoto.

Surinam (2). Para (1): Dist. 13 Zanderij Area. No data (1).

Venezuela (14). Bolivar (7): Rio Caura. Distrito Federal (6): Caracas. No data (1).

No Data (30).

Temporal Data. January (11), February (8), March (10), April (11), May (11), June (15), July (14), August (2), September (5), October (23), November (25), December (5).

Remarks. *Cnemida retusa* is the most commonly collected species of *Cnemida* in South America, but little natural history information is available. Adults have been observed feeding on the buds and flowers of roses in the Rio de Janeiro district (Araujo e Silva *et al.* 1968).

Cnemida tristriata Jameson, new species
(Figs. 5, 13, 22, 32, 33)

Cnemida tristriata. Holotype male at ZMHB labeled a) "Surinam. Stark" (handwritten, green label), b) "12448" (typed), and my holotype label.

Description. Length 10.2mm. Greatest width 5.1mm. **Color**: Head, pronotum, scutellum, pygidium, legs, and venter shining black, with greenish reflections. Elytra shining black, with tan markings on disc (Fig. 5, 13). **Head**: Surface of frons at mid-base moderately densely punctate; base, mid-disc, apex, and margins punctostrigate, strigae forming 2, adjacent, concentric circles that coalesce at mid-disc (Fig. 14); strigae separated by 1 or fewer strigal widths; punctures .02-.04mm. Surface of clypeus confluently punctostrigate. **Pronotum**: Form at base triemarginate; pronounced emargination at mid-base (anterior to scutellum) (Fig. 25a2). Basal angle acute. Surface of disc punctate and strigate; strigae present laterad of midline from apex to base (region wider from middle to base) and from margin to mid-disc, strigae separated by 1 or fewer strigal widths; punctate area present at mid-disc (from base to apex), moderately densely punctate, punctures .01 to .05mm, some transversely punctostrigate near strigate area. **Scutellum**: Longer than wide (W/L ratio = .58). Surface moderately densely punctate near margins; punctures .01-.03mm. **Mesepimeron**: Apex broadly exposed beyond elytral base in dorsal view (Fig. 25a2). **Elytra**: Surface with weak depressions and punctate striae. One depression at base of disc (slightly transverse), 1 laterad of humerus. Striae irregularly impressed, in irregular rows, not interrupted at mid-disc (Fig. 5): 1 next to sutural stria reaching apex but not base, 3 on disc (2 inner striae nearly reaching apex, 1 lateral stria nearly reaching callus, none reaching base), 2 striae laterad of humerus coalescing with transverse stigae at lateral margin; punctures of first stria (adjacent to sutural stria) longitudinal and simple, not forming a continuous line; punctures of disc elongate, inverse U-shaped or crescent-shaped; punctures laterally crescent-shaped to strigulate. Intervals variable in width, moderately densely punctate; punctures .01-.02mm or crescent-shaped. Lateral margin from metacoxa to apex strigulate. Elytral sutural length about 2.3 times length of scutellum. **Pygidium**: Surface strigate, strigae continuous (not effaced) at midline; strigae separated by 3-5 strigal widths forming 1 concentric oval at apex (Fig. 22). **Venter**: Metasternum at middle glabrous. Last sternum of male subapically quadrate, surface weakly punctostrigulate to strigulate, surface at preapex moderately densely punctate, some punctures setigerous; punctures .01mm, setae moderate in length, tawny. **Legs**: Foreclaw with medioapical tooth; empodium not exposed beyond tarsomere 5. Meso- and metatarsomere 5 with mesomedial projection well developed (Fig. 25d2) (worn on metatarsomere). Mesotibia broadest at middle; lateral edge carinate in apical 1/3; apex biemarginate with 3 teeth: 1 mesal (weakly produced), 1 mediolateral, 1 lateral (both produced to tarsomere 2), 2 spinulae next to spurs and mediolateral, apical tooth. Metatibia broadest at middle, subequal in width to femur; mesal edge with moderately dense, tawny, moderately long setae; lateral edge with weak carinae in apical 1/3 and basal 1/3; corbel produced to middle of tarsomere 4. **Metacoxa**: Apex right-angled. **Parameres**: Fig. 32.

Diagnosis. *Cnemida tristriata* resembles *C. retusa* and *C. ephippiata* in pronotal sculpturing and general elytral pattern. *Cnemida tristriata* is separated from *C. retusa* and *C. ephippiata* based on the elytral discal striae and the strigae at the mid-disc of the pygidium: the elytral disc in *C. tristriata* has 3 discal striae (Fig. 5) (*C. retusa* (Fig. 4) and *C. ephippiata* have 4 discal striae), and in *C. tristriata* the strigae of the mid-disc of the pygidium are continuous (Fig. 22) (in *C. retusa* and *C. ephippiata* the strigae are partially effaced). *Cnemida tristriata* shares the character state of 3 discal striae with *C. gigantea* and *C. aterrima*, but in *C. tristriata* the striae are more continuous at mid-disc; in both *C. gigantea* (Fig. 2) and *C. aterrima* the elytral discal striae are interrupted at mid-disc.

Distribution. Surinam.

Locality Data (Fig. 33). 1 specimen (holotype) from ZMHB.

Surinam (1). No Data.

Temporal Data. Unknown.

Remarks. Only the holotype is known for this species. Natural history and the female are also unknown.

Etymology. The specific epithet, "tristriata," refers to the 3 uninterrupted discal striae on each elytron.

Larva of *Cnemida*

Based on the larva of *C. intermedia*, the larvae of *Cnemida* are most similar to those of *Rutela* and share the following characteristics: antenna with well-defined scape; labrum oval; 2 to 3 frontal setae; ocelli absent; epipharynx lacking zygum and epizygum, pedium and gymnoparia well defined, plegmatia lacking; and respiratory plate with a maximum of 17 to 18 holes across any width. The larva of *C. intermedia* differs from those of *Rutela* based on the following characters: antenna with 4 dorsosensory spots (3 in *Rutela*); width of labrum subequal to length (wider than long in *Rutela*), left mandible with 3 scissorial teeth (2 in *Rutela*); epipharynx with clithra and beak-like haptomeral process (both lacking in *Rutela*); claws with 1 apical seta (2 on the pro- and mesothoracic legs, 2 or 3 on the metathoracic leg of *Rutela*). The description of *C. intermedia* is based on 4 cast skins, all of which are distorted posteriorly, thus making it impossible to observe abdominal segments VIII to X.

The key to the larvae of the Rutelini (Jameson *et al.* 1994) is modified as follows to include the larvae of *C. intermedia*.

Key to the American Genera of Rutelini Based on Third-Stage Larvae

(Modified from Jameson, Ratcliffe, and Morón 1994)

1. Left mandible with 2 teeth in scissorial region (including sharp tip) 3
1'. Left mandible with 3 well-defined teeth in scissorial region 2

2. Lacinia of maxilla with 2 unci, subequal in size or 1 reduced or represented by a short, stout seta. 6
2'. Lacinia of maxilla with 1 uncus, reduced or well-developed 9

3. Epipharynx with plegmata well developed. Septula present 4
3'. Epipharynx without plegmata. Septula absent 5

4. Septula short, ovate. Lacinia of maxilla with 2 unci, subequal in size. Maximal width of cranium 3.6mm .... *Calomacrapis*
4'. Septula elongate, extended across venter of last segment and lower anal lip. Lacinia of maxilla with 1 reduced uncus. Maximal width of cranium 4.9mm .... *Parastasia*

5. Spiracles of abdominal segments VII and VIII noticeably larger than preceding spiracles. Tarsal claws slightly reduced. Maximal width of cranium 5.8mm .... *Paracotalpa*
5'. Spiracles of abdominal segments VI, VII, and VIII noticeably smaller than preceding spiracles. Tarsal claws not reduced. Maximal width of cranium 6.9mm .... *Cotalpa*

6. Septula irregularly defined on lower anal lip. Lacinial unci different in size; internal unci reduced, truncate, with a short stout seta. Maximal width of cranium 5.6mm .... *Rutelisca*
6'. Septula absent. Lacinial unci subequal in size. Maximal width of cranium variable 7

7. Epipharynx with epizygum. Spiracles of abdominal segments VII and VIII similar in size to preced-

ing spiracles. Maximal width of cranium variable 8

7'. Epipharynx without epizygum. Spiracles of abdominal segments VII and VIII noticeably larger than preceding spiracles. Maximal width of cranium 7mm .... *Pelidnota*

8. Last antennal segment with 7-13 dorsal sensory spots. Maximal width of cranium 10mm *Chrysina*

8'. Last antennal segment with 2-5 dorsal sensory spots. Maximal width of cranium 6.0-7.2mm .... *Plusiotis*

9. Clithra of epipharynx present, symmetrical .... *Cnemida*

9'. Clithra of epipharynx absent 10

10. Septula absent. Lacinial uncus vestigial, represented by small sclerotized plate with small, stout seta. Maximal width of cranium 4.7mm .... *Rutela*

10'. Septula present. Lacinial uncus reduced but not vestigial. Maximal width of cranium greater than 5.0mm 11

11. Last antennal segment with 4-6 dorsal sensory spots. Metathoracic tarsal claws reduced and weakly sclerotized relative to pro- and mesothoracic claws. Maxillary stridulatory area with row of 8 large, sharp, pointed, recurved teeth. Maximal width of cranium 6mm*Macraspis*

11'. Last antennal segment with 2 dorsal sensory spots. Metathoracic tarsal claws subequal in size and similarly sclerotized relative to pro- and mesothoracic claws. Maxillary stridulatory area with row of 5-6 small, sharp, pointed, recurved teeth. Maximal width of cranium variable . 12

12. Lobes of respiratory plate separated. Maxillary stridulatory area with a row of 6 teeth. Fore- and mesotarsal claws with 2-5 long, stout setae. Maximal width of cranium 6-8mm .... *Macropoides*

12'. Lobes of respiratory plates contiguous. Maxillary stridulatory area with row of 5 teeth. Fore- and mesotarsal claws with 2 long, stout setae. Maximal width of cranium variable 13

13. Metathoracic tarsal claws reduced. Spiracles of abdominal segments I-VIII progressively smaller. Head capsule dark reddish-brown. Maximal width of cranium 9mm .... *Heterosternus*

13'. Metathoracic tarsal claws not reduced. Spiracles of abdominal segments I-V progressively smaller and segments VI-VIII progressively larger. Head capsule bicolored, dark brown to reddish-yellow. Maximal width of cranium 5mm .... *Parisolea*

Cnemida intermedia Bates
3rd Instar Larva
(Figs. 34-47)

Larvae of *C. intermedia* were found and reared in decaying wood of *Hyeronima alchorneoides* Allemao (Euphorbiaceae) by F. Quesada (INBio). The adults, third instar exuviae, and 1 pupal exuvium were collected. Terminology used for the larval description follows that of Ritcher (1966) and Jameson *et al.* (1994).

Description. Based on 4 exuviae and associated adults with the following data: "Rancho Quemado, 200m, Peninsula de Osa, Prov. Puntarenas, Costa Rica, Dic. 1992, P. Quesada, L-S 292500, 511000," INBio bar code "INBio CR 1000920576." Two specimens (card-mounted together) are labeled as above but with the date "Nov. 1992" and INBio bar code "INBio CR 1000910081." Two additional specimens were labeled as above, but with the date, "Ago 1992," INBio bar codes "INBio CR 1000889571" and "INBio CR 1000889569" and field labels "157. P. Quesada 92.1" and "157. P. Quesada 92.2." One cast skin was mounted on a card next to the adult, the remaining 3 cast skins were stored in alcohol. The following information is archived with numbers 153: "20 de julio. Larvas tipo jogoto. Mide 1 cm, come zapatero donde Chucho. 5 oct. encontre adulto. 22 oct. nace otro. 26 nov. encontre dos desechos. 13 dic. nace otro."

Cranium (Fig. 34): Width of head capsule 2.7mm. Surface finely roughened, light yellow-brown, preclypeus and mandibles piceous. Frons, on each side, with single large anterior frontal seta, 2 smaller setae at apex. Dorsoepicranium apparently without setae. Epicranial, frontal, and clypeofrontal sutures broken. Ocellus absent. **Clypeus**: Form trapezoidal. Postclypeus mediolaterally setigerously rugopunctate; setae moderately long, tawny; punctures moderately dense. Preclypeus glabrous. **Labrum**: Form suboval, symmetrical. Surface at apex and margins moderately densely punctate, punctures setigerous; setae short or moderately long (apex) to moderately long (sides), tawny. **Antenna** (Fig. 35-36): 4 antennomeres with well-defined scape; scape 1/2 length of first antennomere, 1-3 subequal in length, antennomere 4 two-thirds length of 1. Apical antennomere oval with 4 dorsal sensory spots (Fig. 35) and 3 ventral sensory spots (Fig. 36). **Mandibles** (Fig. 37-38): Form falcate, asymmetrical. Left mandible (Fig. 38) with 3 scissorial teeth (second tooth reduced), each separated by narrow scissorial notch; dorsum (external surface) with 2 setae at apex and 3 moderately long setae at base, surface finely rugose. Venter (internal surface) granulose distally; stridulatory area elongate-oval with 14-16 ridges (smaller at apex and base); molar area bilobed, dorsomolar area with 5 dorsomolar setae; basomedial angle with brustia consisting of 3 moderately long setae; basolateral angle with preartis. Right mandible (Fig. 37) with 2 scissorial teeth separated by narrow notch; dorsum (external surface) with 2 long setae at apex, 2 at base; surface finely rugose. Venter (internal surface) granulose distally; stridulatory area elongate-oval with 13-15 ridges (smaller at apex and base); molar area with 3 differentiated lobes, distal lobe weak, and with 3 dorsomolar setae; basolateral angle with preartis. **Maxilla** (Fig. 39-41): Cardo subquadrate. Stipes longer than wide. Galea with uncus and many stout setae. Lacinia with uncus and many stout setae (Fig. 40). Maxillary palpus with 4 segments; segments 1-3 subequal in size, segment 4 subequal to segments 2 and 3; stridulatory area (Fig. 41) with 8 slightly elongate, acute, curved spines well separated from truncate process. **Labium** (Fig. 42): Margins with few moderately long setae. Internal surface of glossa with numerous short and moderately long setae. Hypopharyngeal sclerome asymmetrical, concave, with raised tubercle on right side. **Epipharynx** (Fig. 43): Form suboval, apex asymmetrical. Haptomerum with beak-like process, without zygum or epizygum. Clithra present. Acanthoparia with 2-3 short setae. Plegmatia lacking. Gymnoparia well developed. Chaetoparia with about 30 stout setae; setae short laterally, longer medially. Pedium well defined. Laeotorma and dexiotorma nearly symmetrical. Nesium not developed. **Legs**: Subequal in length. Trochanter, femur, and tibiotarsus with numerous setae; setae stout, moderately long to long. Claws (Fig. 44) yellowish-brown, constricted toward blunt apex; apex with 1 seta placed off-center. **Body vestiture**: Pronotum with about 120 slender setae generally distributed, not in apparent rows. Prothorax and mesothorax with about 30 long setae (LS) and 20 short setae (SS), metathorax with about 20 LS and 20 SS. Abdominal terga with setae generally distributed, not in obvious rows; short, spinose setae (ShSp) increasingly numerous and stout up to terga VI, decreasingly numerous and stout to terminal segment. Terga I-IV with 18-24 LS, 140-160 ShSp; tergum V with 24 LS, 200 ShSp; tergum VI with 20 LS, 120 sclerotized ShSp; tergum VII with 24 LS, 14 ShSp; tergum VIII and X distorted, not observable. Sterna I-VII with 10-12 LS generally distributed; sternum VIII-X distorted, not observable. **Spiracles** (Figs. 45-47): Thoracic spiracle .38mm high by .25mm wide. Abdominal spiracles (Figs. 45-46) with spiracles 1 and 8 largest, decreasing in size to spiracle 4; spiracle 1 and 8 each 3.6mm high by .20mm wide, spiracle 4 .12mm high by .10mm wide. Each spiracle with C-shaped respiratory plate surrounding bulla; plate widest at top and bottom (about 17 respiratory holes in width), narrowest at center (about 10 respiratory holes in width). Center of bulla with weakly raised knob. Respiratory holes irregularly suboval or roundish (Fig. 47).

Phylogenetic Analysis

Based upon prior phylogenetic analyses of the subtribe Rutelina (Jameson 1994) and on-going phylogenetic analyses in the tribe Rutelini (Jameson in prep.), members of the genera *Pelidnota* (subgenus *Pelidnota*) and *Rutela* (subgenus *Rutela*) were used as out-groups for the analysis. *Pelidnota*, *Rutela*, and *Cnemida* are closely related taxa and share the following character states: hind wing with well developed hooks on the leading edge of the precostal membrane, metendosternite robust and Y-shaped with apical branches bifurcate (Fig. 23b-25b), and meso- and metatarsomere 5 of male with median, lobe-like projection (Fig. 23d-25d). Historically, *Pelidnota* and the subtribe Pelidnotina have been separated from *Rutela* and *Cnemida* based on the presence of a pronotal basal bead (pronotal basal bead lacking in *Cnemida* and *Rutela*). However, within some Pelidnotina (**e.g.** *Pelidnota* and *Homothermon*) the basal bead may be partially effaced or entirely absent. The loss or gain of a pronotal basal bead is not uncommon between closely related species and within a genus. For example, in the genus *Pelidnota*, the pronotal basal bead is a generic character, although in *P. polita* Latr. the bead is entirely lacking. Within the genus *Plusiotis* the pronotal basal bead varies from complete to incomplete (Morón 1990). In the subtribe Heterosternina the basal bead is usually complete with the exception of the genus *Plesiosternus* (Morón and Howden 1992). These examples of variability of the basal bead within groups of Rutelinae demonstrate that this character may be evolutionarily vagile and its states may shift readily. This type of character should not be used to separate higher level taxa or in higher level classification and phylogeny. Character states that effectively separate *Pelidnota* from the *Rutela/Cnemida* clade are: scutellum in *Pelidnota* abruptly declivous at the base of the pronotum (Fig. 23a) (whereas in *Rutela* and *Cnemida* the surface of the scutellum is flat where it meets the base of the scutellum (Fig. 25a)); and presence of an epipleural ridge in the Pelidnotina (the epipleuron is rounded and lacks a ridge in *Rutela* and *Cnemida*). *Rutela* and *Cnemida* are sister taxa and share the following character states: maxilla with 6 teeth (3 basal, 2 medial, 1 apical), fifth protarsomere with empodium hidden, and metendosternite with mesal, apical branches robust and thick (Fig. 25b). Additional analyses are currently being conducted to address the relationships and higher classification of the tribe Rutelini.

Relationships among the species in the genus *Cnemida* were analyzed using PAUP version 3.1 (Swofford 1993) and character state distributions were investigated using MacClade version 3.01 (Maddison and Maddison 1992). Thirty-five internal and external morphological characters formed the basis of this analysis (Table 1) and were polarized using the out-group comparison method (Watrous and Wheeler 1981, Maddison *et al.* 1984, Brooks and McLennan 1991). Character states (Table 2) were unweighted and unordered. For taxa where character states were unknown (males or females not known or behavior not known) character states were scored as ambiguous (?).

Based on the character analysis, an exhaustive search yielded 4 equally parsimonious cladograms with a consistency index of .93 (rescaled consistency index of .87, tree length of 60). Two tree topologies with identical species groups resulted; Figure 48a (1 of 2 topologies) and Figure 48b (1 of 2 topologies). The relatively high consistency index is due to the number of consistent synapomorphs that support the *Cnemida* clade (branch 1) and the *Cnemida* minus *C. leprieuri* clade (branch 2). Fewer consistent synapomorphs support natural groups within the *Cnemida* minus *C. leprieuri* clade, and because of this, homoplasy and conflicting tree topologies resulted. Identifying unknown character states in the data matrix (? or 0/1), for example for unknown males and females and for unknown behavioral states, will help to resolve the phylogenetic hypothesis.

Each of the 4 cladograms (Figs. 48a and b) placed *C. leprieuri* as the most primitive species in the genus and supported 2 species groups; the *C. aterrima*-group (branch 8: *C. aterrima, C. gigantea, C. intermedia*, and *C. lacerata*) and the *C. retusa*-group (branch 4: *C. retusa, C. ephippiata*, and *C. tristriata*). Within the *C. retusa*-group (*C. retusa, C. tristriata*, and *C. ephippiata*, branches 4 and 5) *C. tristriata* is consistently shown as derived, although its sister taxon (*C. retusa* or *C. ephippiata*) is unresolved (branch 5). Because *C. tristriata* and *C. ephippiata* are known from only male holotypes, females and additional specimens in these two taxa will help to resolve the ambiguity in this clade. Within the *C. aterrima*-group (*C. aterrima, C. gigantea, C. intermedia, C. lacerata*, branches 6-8), *C. aterrima* and *C. gigantea* are consistently hypothesized to be sister taxa, sharing the characters of tristriate elytral disc, non-strigulate pronotum, and lateral subapical margin of the elytra without stigulae. However, due to the paucity of unambiguous characters at the base of the *C. aterrima*-clade (branches 6 and 7), the phylogenetic positions of *C. intermedia* and *C. lacerata* are unresolved. *Cnemida leprieuri*, the most basal member of the clade (branch 1), shares several plesiomorphic characters with *Rutela* including: metatarsus 5 without a medial tooth (Fig. 25d1), ventral sclerite of the male parameres membranous (not heavily sclerotized) (Fig. 30b), elytral disc without irregularly depressed striae, and metatibia without a well-developed corbel (Fig. 25c1).

Distribution

Species in the genus *Cnemida* are widely distributed from central Mexico to South America in low to mid elevation (0 to 1,500 m), tropical moist habitats. *Cnemida aterrima* is distributed from the state of San Luis Potosi in Mexico, through Guatemala, Honduras, El Salvador, Nicaragua, and into northernmost Costa Rica. In the region of the Nicaraguan depression (southern Nicaragua), populations of *Cnemida aterrima* are sympatric with populations of *C. intermedia*. In areas of sympatry there is a great amount of intraspecific variation in *C. aterrima*. For example, at the Estacion Maritza in Guanacaste, Costa Rica, pronotal sculpturing of *C. aterrima* varies from nonstrigulate to strigulate (Fig. 16-17). Other characters are not variable in this narrow zone. Intraspecific variability may suggest interactions between the 2 populations of *C. aterrima* and *C. intermedia*.

Cnemida intermedia is distributed from northern Costa Rica, through Panama, and into areas of Colombia, Venezuela, and Ecuador. The most widespread species in the genus, *C. retusa*, is distributed east of the Andes from northern Venezuela to southern Brazil. Locality data indicate that the species is found in a variety of habitats: lowland rain forest, caatinga, cerrado, and Atlantic forest.

Cnemida lacerata is distributed along the northern periphery of South America (Venezuela and French Guiana) and the eastern periphery of Brazil (Bahia to Santa Catarina) as well as southeastern Paraguay. The distribution records of *C. lacerata* is not continuous; a lack of distributional data in the Amazon Basin and northeastern Brazil seemingly divides the species into northern populations and southern populations in South America. Although this disjunction correlates with the distribution of caatinga habitat in Brazil, the gap could be a function of inadequate collection data. Only 4 specimens were available from the northern range of *C. lacerata* (1 from Venezuela and 3 from French Guiana), and these specimens show no differences in character traits. If, in fact, the 2 populations of *C. lacerata* are disjunct and isolated, I would expect to find character differences. Additional specimens and locality data are needed in order to address this disjunction.

Cnemida leprieuri is widely distributed in the lowlands from Surinam and French Guiana to the Amazon Basin and southward in Peru and Bolivia. For 3 species in the genus, little distributional data exist (aside from the type localities); *C. gigantea* (Santa Rosa, Colombia), *C. ephippiata* (San Antonio do Iça, Brazil), and *C. tristriata* (Surinam).

The widespread distribution of species in the genus *Cnemida* (lack of endemicity), the unresolved phylogeny of the genus (Fig. 48a and b), and scanty distributional records for several species do not provide a robust data set for biogeographic hypotheses.

Acknowledgments

I am grateful for loans of specimens and assistance that were provided by each of the curators, collections managers, and other individuals listed in "Taxonomic Materials" section. I extend my gratitude to Steve Ashe (University of Kansas) for supervision during this dissertation research, to Brett Ratcliffe (University of Nebraska) for suggestions and advise, and to Dan Schmidt (Schuyler, NE) for excellent illustrations and habitus drawings. I thank F. Quesada (INBio) for rearing the larvae of *C. intermedia,* Angel Solís for archival information (INBio), and Jim Wappes (Bulverde, TX) for behavioral information for *C. intermedia.* I am grateful to Steve Ashe (University of Kansas), François Genier, Henry Howden (both at the Canadian Museum of Nature), Brett Ratcliffe (University of Nebraska), and Bob Woodruff (Florida State Collection of Arthropods) for providing helpful suggestions on the manuscript. Partial support for the completion of this paper was provided by a University of Kansas Graduate Student Summer Fellowship, the University of Kansas Department of Entomology and Snow Entomological Museum, and the University of Nebraska State Museum. Contribution number 3168 of the Snow Entomological Museum.

References

Arnett, R. H., Jr., G. A. Samuelson, and G. M. Nishida. 1993. The insect and spider collections of the world, 2nd edition. Flora and fauna handbook No. 11. Sandhill Crane Press, Inc., Gainesville, FL. 310 pp.

Arrow, G. J. 1925. The fauna of British India, including Ceylon and Burma: Coleoptera, Lamellicornia (Cetoniinae and Dynastinae). Dr. W. Junk, The Hague. 387 pp.

Araújo e Silva, G. Aristoteles, C. R. Gonçalves, D. M. Galvão, A. J. L. Gonçalves, J. Gomes, M. do Nascimento Silva, and L. de Simoni. 1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil, seus parasitos e predadores. Parte 2, Vol. 1 (insetos, hospedeiros e inimigos naturais). Ministerio da Agricultura, Laboratorio Central de Patalogia Vegetal, Rio de Janeiro. 622 pp.

Arrow, G. J. 1899. Notes on the classification of the coleopterous family Rutelidae. Annals & Magazine of Natural History (series 7) 4:363-370.

Bates, H. 1888. Pectinicornia and Lamellicornia, pp. 1-432. *In* F.D. Godman & O. Salvin (eds), Biologia Centrali Americana. Insecta, Coleoptera vol. 2, part 2.

Brooks, D. R. and D. A. McLennan. 1991. Phylogeny, ecology, and behavior: a research progam in comparative biology. University of Chicago Press, Chicago. 434 pp.

Burmeister, H. C. C. 1844. Handbuch der Entomologie, vol. 4, part 1. Theod. Enslin, Berlin. 588 pp.

Crowson, R. A. 1981. The Biology of Coleoptera. Academic Press, New York, New York. 802 pp.

Elias, T. S., W. R. Rozich, and L. Newcombe. 1975. The foliar and floral nectaries of *Turnera ulmifolia* L. American Journal of Botany 62(6):570-576.

Fabricius, J. C. 1801. Systema eleutheratorum, vol. 2. Kiliae. 687 pp.

Gemminger, M. and B. Harold. 1869. Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus, Scarabaeidae. 4: 979-1346. Monachii.

Germar, E. F. 1824. Insectorum species novae aut minus cognitae, descriptionibus illustratae, vol. 1. Halae.

Guerin-Meneville, M. F. E. 1844. Iconographie du regne animal de G. Cuvier ou représentation d'après nature de l'une des espèces les plus remarquables et souvent non encore figurees, de chaque genre d'animaux. J. B. Baillère, Paris. 576 pp.

Jameson, M. E. 1994. What is the Rutelina (Coleoptera: Scarabaeidae)? Defining the subtribe for the 21st century, p. 35 (abstract). International Symposium on Biodiversity and Systematics in Tropical Ecosystems. Bonn, Germany, 2-7 May.

Jameson, M. L., B. C. Ratcliffe, and M. A. Morón. 1994. A synopsis of the Neotropical genus *Calomacraspis* Bates with a key to larvae of the American genera of Rutelini (Coleoptera: Scarabaeidae: Rutelinae). Annals of the Entomological Society of America 87(1):43-58.

Janzen, D. (ed.). 1983. Costa Rican natural history. University of Chicago Press, Chicago. 816 pp.

Kirby, W. 1827. A description of some new genera and species of petalocerous Coleoptera. Zoological Journal 3:146-148.

Koptur, S. 1994. Floral and extrafloral nectaries of Costa Rican *Inga* trees: a comparison of their constituents and composition. Biotropica 26(3):276-284.

de Laporte, F. L. N. C. (Comte de Castelnau) 1840. Histoire naturelle des insectes Coléopteres. P. Duménil, Paris.

Machatschke, J. W. 1972. Scarabaeoidea: Melolonthinae, Rutelinae. Coleopterorum Catalogus Supplementa 66:1-361. W. Junk, Gravenhage.

Maddison, W. P. and D.R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Sunderland, MA. 398 pp.

Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Out-group analysis and parsimony. Systematic Zoology 33:83-103.

Morón, M. A. 1979. Fauna de coleopteros lamelicornios de la estacion de biologia tropical, "Los Tuxtlas", Veracruz, UNAM. Mexico. Anales del Instituto Biologia Universidad Nacional Autonomia Mexico 50, ser. Zoologia (1):375-454..

Morón, M. A. 1990. Los Coléopteros del mundo. Volume 10: Rutelini Première Partie. Sciences Nat, Venette, France. 145 pp.

Morón, M. A. and H. F. Howden. 1992. A second species of *Plesiosternus* Morón with notes on other Heterosternina (Coleoptera: Scarabaeidae: Rutelinae). Coleopterists Bulletin 46(10):15-19.

Morón, M. A., J. Valenzuela, and R. A. Terron. 1988. La macro-coleopterofauna saproxilofila del Soconosco, Chiapas, Mexico. Folia Entomologica Mexicana 74:145-158.

Ohaus, F. 1909. Bericht über eine entomologische Studienreise in Südamerika. Stettiner Entomologische Zeitung 70:3-139.

Ohaus, F. 1912. Beitrage zur Kenntnis der Ruteliden X. Stettiner Entomologische Zeitung 73: 273-319.

Ohaus, F. 1918. Scarabaeidae: Euchirinae, Phaenomerinae, Rutelinae. Coleopterorum Catalogus 20:1-241. W. Junk, Berlin.

Ohaus, F. 1934. Genera Insectorum, Coleoptera, fam. Scarabaeidae: subfam. Rutelinae, erster teil, fasc. 199A, pp. 1-172. L. Desmet-Verteneuil, Bruxelles.

Preston-Mafham, R. and K. Preston-Mafham. 1993. The encyclopedia of land invertebrate behavior. MIT Press. 320 pp.

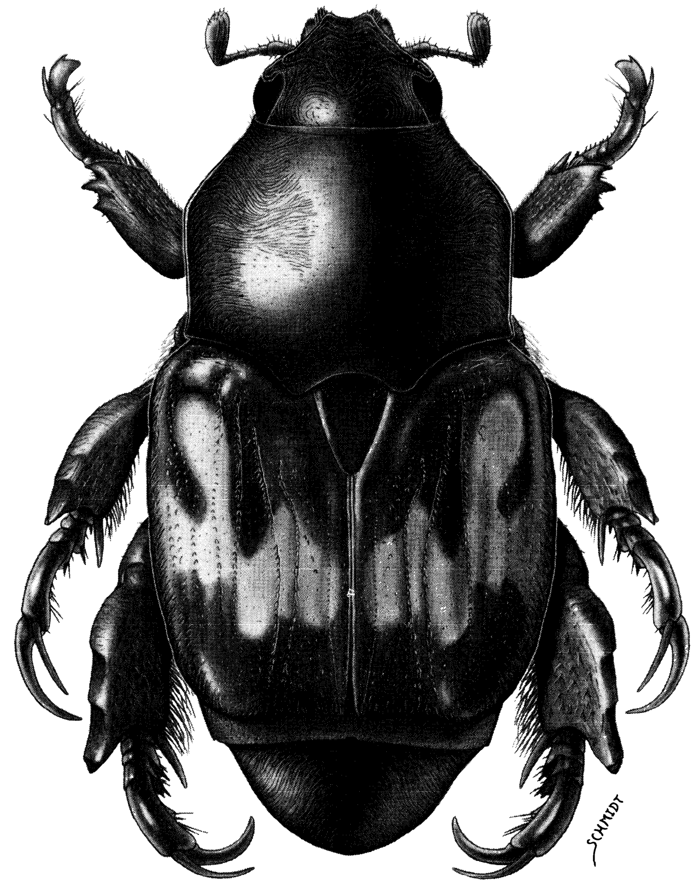
Ratcliffe, B. C. 1990. Unusual method of pattern disruption in an Amazonian scarab beetle. Boletin Museo Paraense Emilio Goeldi, series Zoologia 6(2):109-113.

Ritcher, P. O. 1966. White grubs and their allies: a study of North American scarabaeoid larvae. Studies in Entomology No. 4. Oregon State University Press, Corvalis.

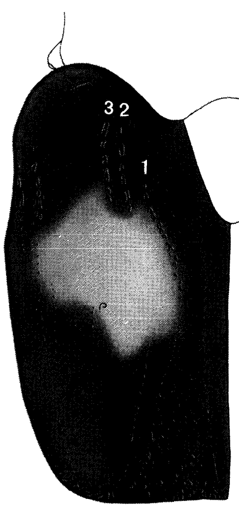
Swofford, D. L. 1991. Phylogenetic analysis using parsimony (PAUP), version 3.0. Illinois Natural History Survey, Champaign. 257 pp.

Thomas, D. B. 1993. Scarabaeidae of the Chiapanecan forests: a faunal survey and chorographic analysis. Coleopterists Bulletin 47(4):363-408.

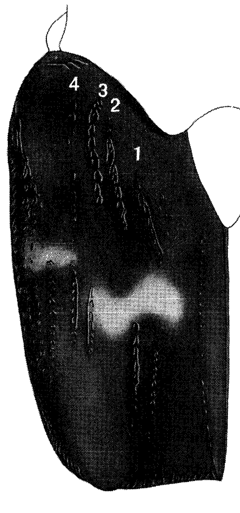
Watrous, L. E., and Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Systematic Zoology 30:1-11.



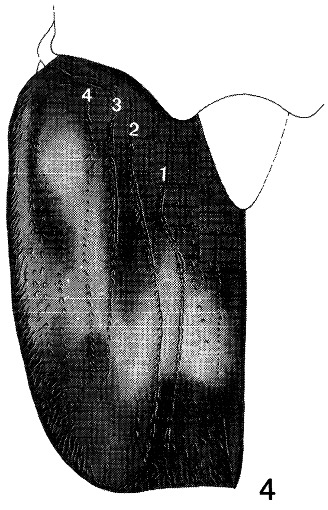
1



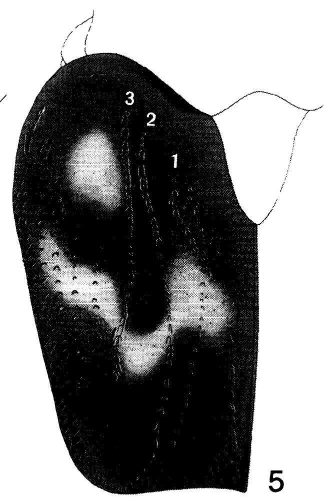
2



3

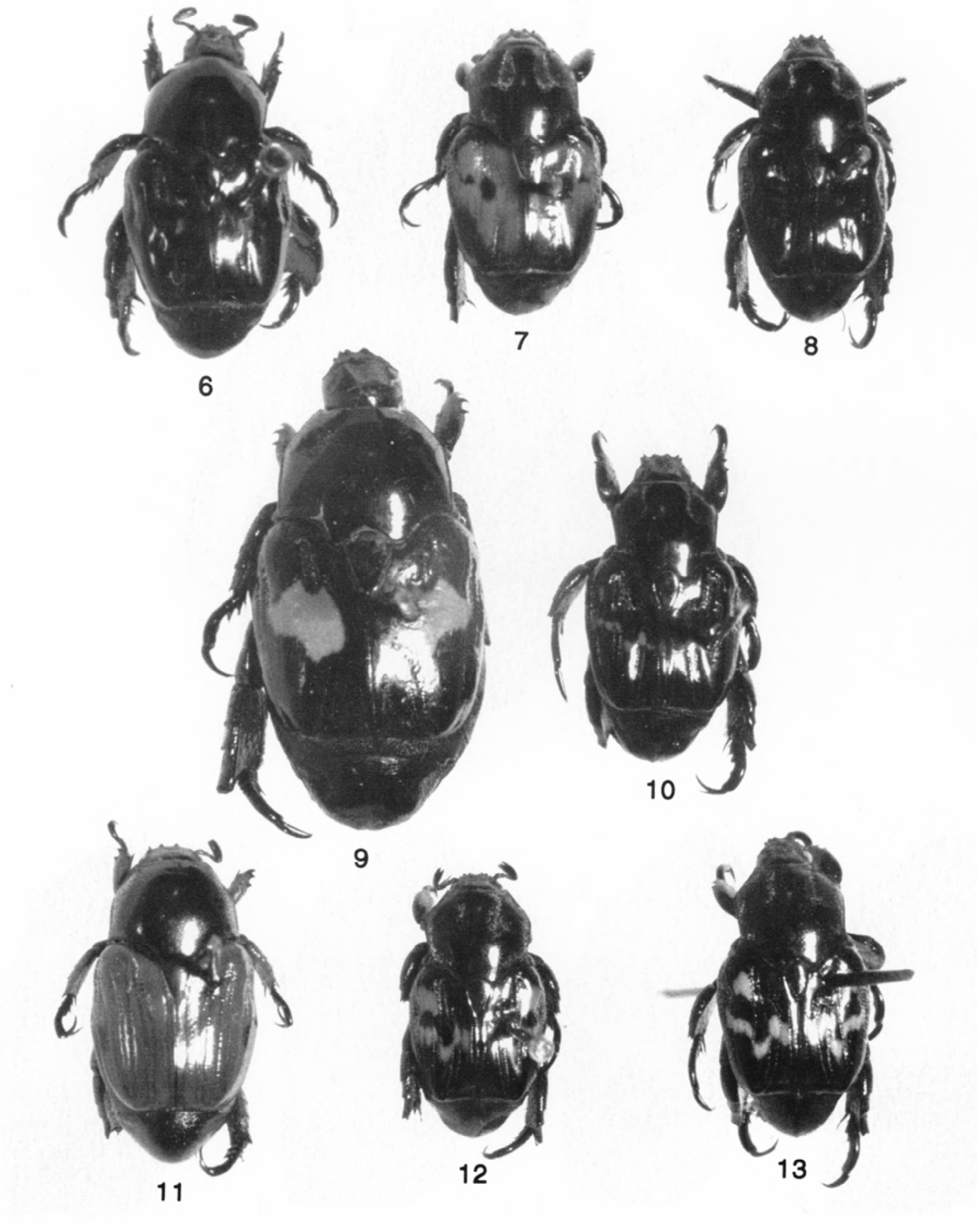


4

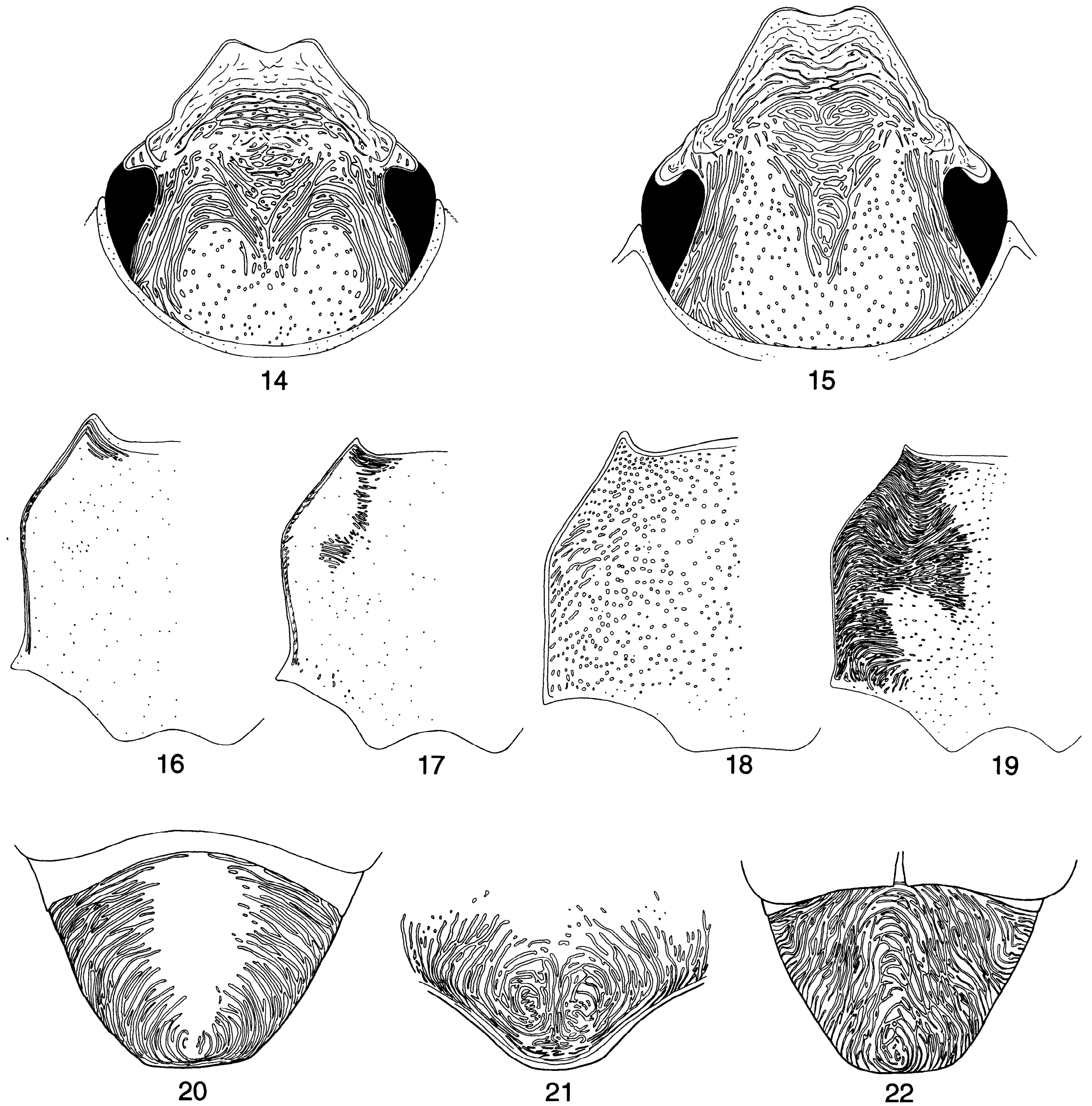


5

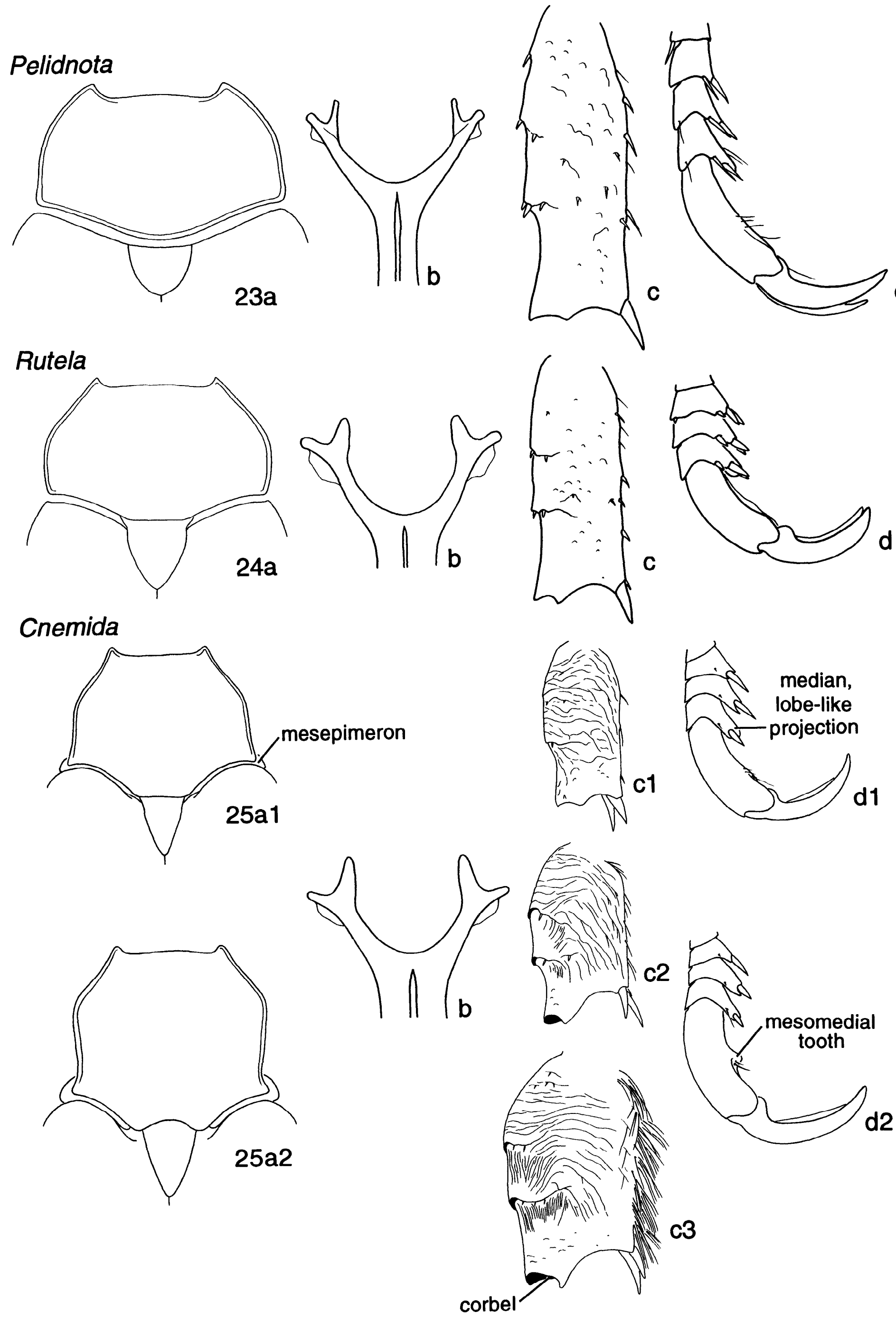
Figs 1-5. Fig. 1) Dorsal habitus of *Cnemida retusa* (Fabr.). Figs. 2-5). Dorsal view of left elytron showing sculpturing and striae. 2) *C. gigantea*. 3) *C. intermedia*. 4) *C. retusa*. 5) *C. tristriata*.



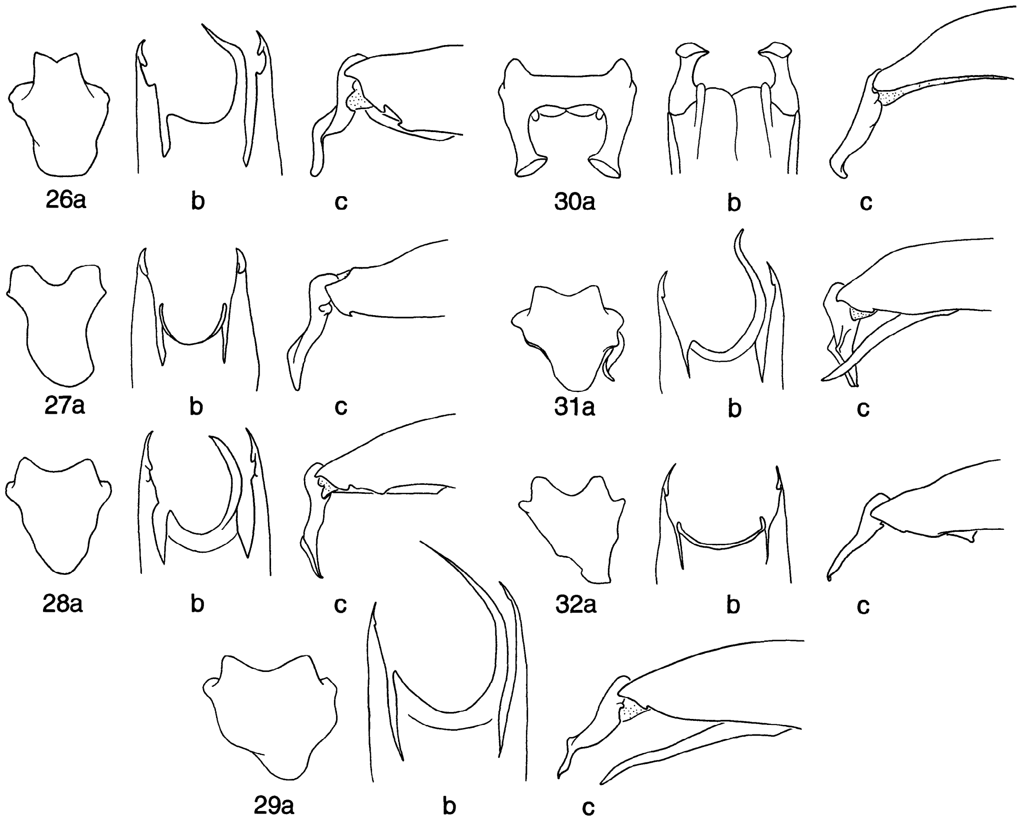
Figs. 6-13. Dorsal views of the species of *Cnemida*. 6) *C. aterrima* Bates. 7) *C. ephippiata* Ohaus. 8) *C. intermedia* Bates. 9) *C. gigantea* Jameson. 10) *C. lacerata* (Germar). 11) *C. leprieuri* Arrow. 12) *C. retusa* (Fabr.). 13) *C. tristriata* Jameson.



Figs 14-22. Figs 14-15. Dorsal view of the head showing sculpture patterns of 14) *C. intermedia* and 15) *C. lacerata*. Figs. 16-19. Dorsal view of the pronota showing form and sculpturing of 16-17) *C. aterrima*, 18) *C. leprieuri*, and 19) *C. retusa*. Figs 20-22. Views of the pygidium showing sculpturing: 20) posteriodorsal view of the pygidium of *C. aterrima*, 21) posterior view of the pygidium of *C. gigantea*, 22) posteriodorsal view of the pygidium of *C. tristriata*.



Figs 23-25. Diagnostic features of *Pelidnota* (*Pelidnota*) (23a-d), *Rutela* (*Rutela*), (24a-d) *C. leprieuri* (25a1-d1), and *C. retusa*-group (25a2, b2, c2, c3, d2) showing: a) dorsal view of the pronota and elytra showing form of pronotum (laterally bi-sinuate or evenly rounded, base triemarginate or evenly produced posteriorly), form of the scutellum (base declivous or not), and epimeron (hidden or exposed); b) metendosternite (posterior view); c) ventral view of the right metatibia showing sculpturing, elevated corbel (*C. intermedia* 25c2, *C. lacerata* 25c3), mesal edge with or without setae and; d) dorsal view of metatarsomere 5 of male with medial tooth lacking (22d, 23d, 24d, 25d1) or present (25d2).



Figs 26-32. Caudal (a), ventral (b), and lateral (c) views of the male parameres of *Cnemida*. 26) *C. aterrima*. 27) *C. ephippiata*. 28) *C. intermedia*. 29) *C. lacerata*. 30) *C. leprieuri*. 31) *C. retusa*. 32) *C. tristriata*.

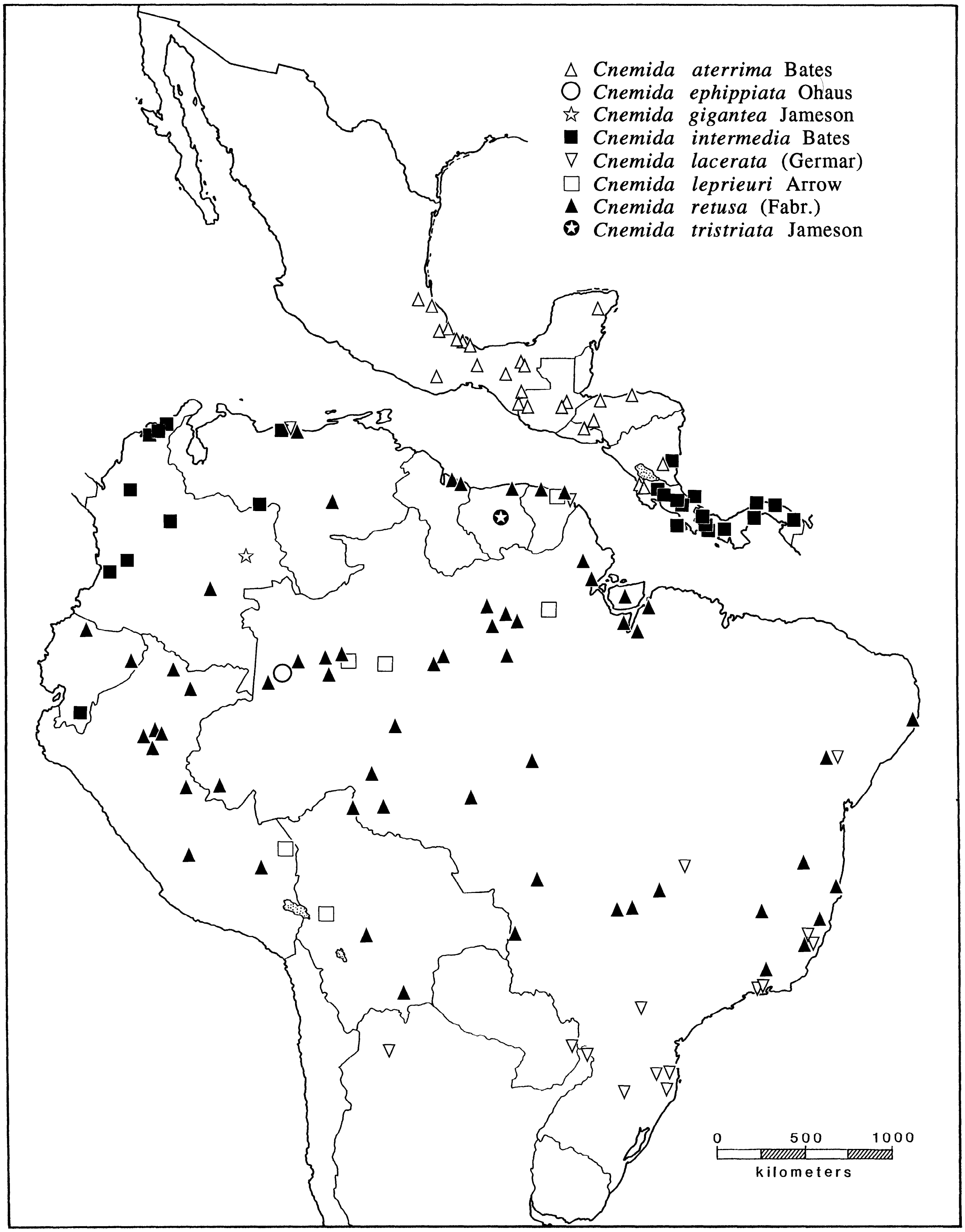
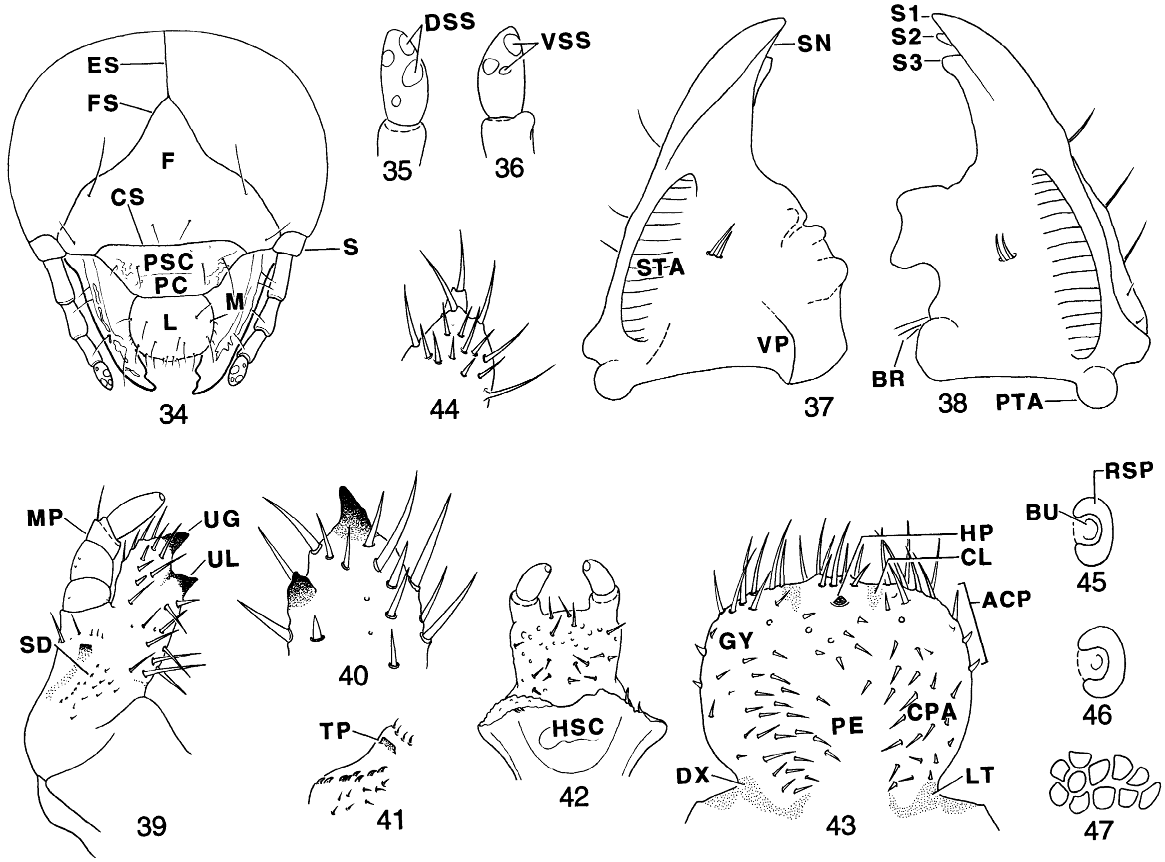


Fig. 33. Distribution of the species of *Cnemida*.



Figs 34-47. *Cnemida intermedia*, third stage larva. (34) Frontal view of cranium. CS, clypeofrontal suture; ES, epicranial suture; F, frons; FS frontal suture; M, mandibles; PC, preclypeus; PSC, postclypeus; L, labrum; S, scape. (35-36) Dorsal and ventral aspects, respectively, of apical antennal segment. DSS, dorsal sensory spots; VSS, ventral sensory spots. (37-38) Ventral aspect of right and left mandibles, respectively. S1-3, scissorial teeth; SN, scissorial notch; STA, stridulatory area, VP, ventral process; BR, brustia; PTA, preartis. (39) Dorsal aspect of maxilla. MP, maxillary palpus; SD, stridulatory teeth; UL, uncus of the lacinia; UG, uncus of the galea. (40) Apex of lacinia. (41) Stridulatory area of maxilla. TP, truncate process. (42) Dorsal view of labium. HSC, hypopharyngeal sclerome. (43) Epipharynx. ACP, acanthoparia; CPA, chaetoparia; DX, dexiotorma; HP, haptomeral process; LT, laeotorma; PE, pedium; CL, clithrum. (44) Form of the claws. (45-46) IV and VII abdominal spiracles, respectively. RSP, respiratory plate; BU, bulla. (47) Form of the holes in the respiratory plate.

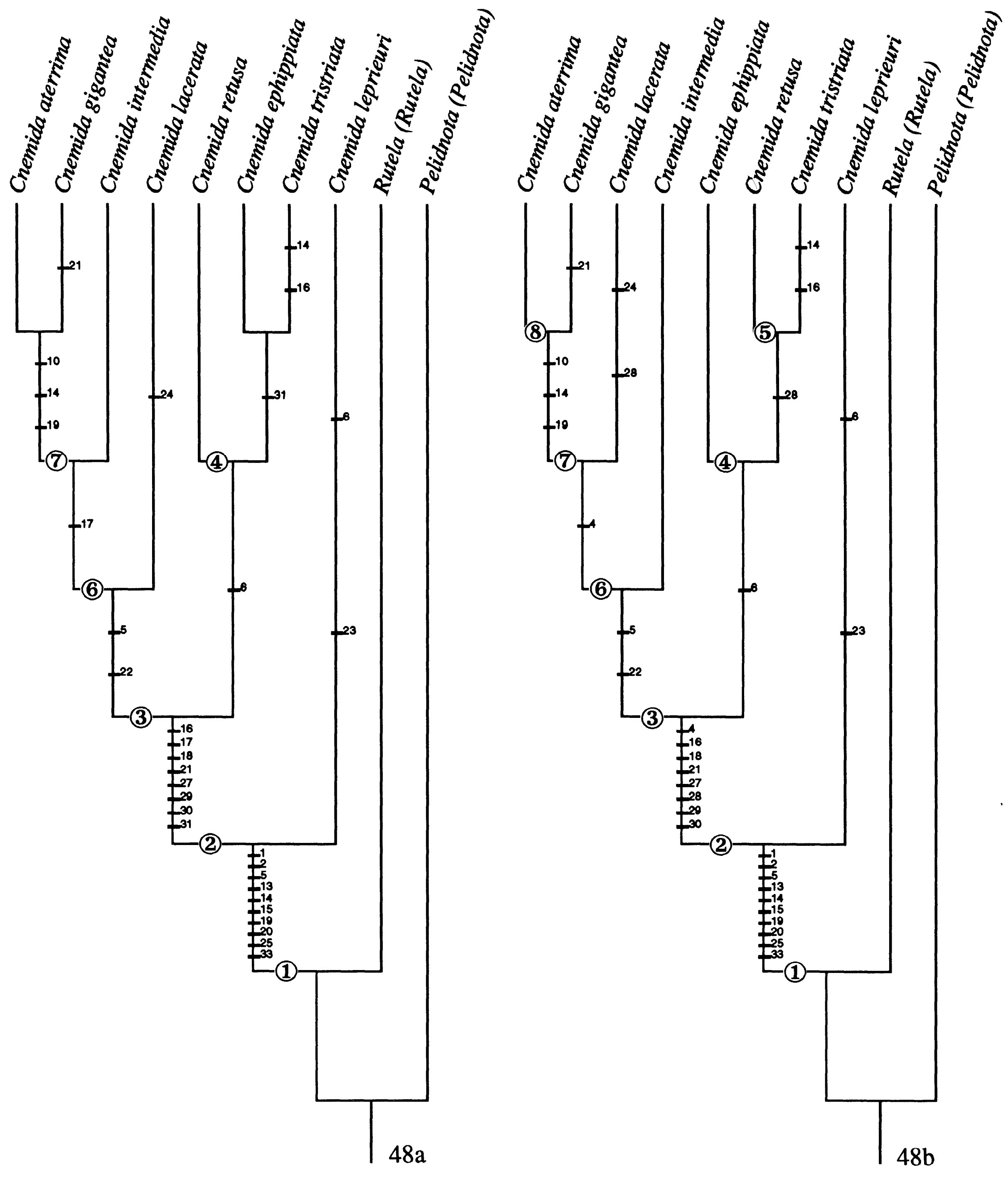


Fig. 48a and b. Two primary cladogram topologies that resulted from the phylogenetic analysis of *Cnemida* (consistency index equals .93, rescaled consistency index equals .87, tree length is 60). Unambiguous characters are traced on branches. Branches are indicated with circled numbers (see text).

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

Phylogenetic Characters and Character States

Plesiomorphic State	Apomorphic States
Head	
1. Mandibles bidentate at apex, teeth recurved 90° (0)	teeth recurved 45° (1).
2. Maxilla with stipes robust (0)	slender (1).
3. Maxilla with 6 teeth: 3 basal, 1 medial, 1 apical (0)	3 basal, 2 medial, 1 apical (1).
4. Sculpturing of frons punctate or confluently punctate (0)	strigate with strigae forming 2 adjacent, concentric circles (1), strigate with strigae forming two adjacent, concentric triangles (2).
5. Frons without medial depression (0)	with rounded depression (1), with V-shaped depression (2).
Pronotum	
6. Surface without metallic green reflections (0)	with metallic green reflections (1).
7. Base anterior to the scutellum rounded (0)	tri-angulate (1), tri-emarginate, nearly straight at mid-base (2), tri-emarginate with a pronounced emargination at mid-base (3).
8. Basal corner obtuse or rounded (0)	acute in both sexes (1), square in female, acute in male (2).
9. Lateral edge evenly rounded (0)	bisinuate, apex acute (1), bisinuate, apex and base acute (2).
10. Surface punctate (0)	finely punctate with few strigae (1), strigate, strigae lacking at middle and base (2), strigate, strigae evenly distributed (3).
11. Pre-basal margin without strigulae (0)	with few strigulae (1), with dense strigulae (2).
Epimeron	
12. Hidden in dorsal view (0)	exposed in dorsal view (1).
Scutellum	
13. Base of scutellum where it meets pronotum declivous (0)	flat (1).
Elytra	
14. Elytral disc without irregularly depressed striae (0)	with 3 irregularly depressed striae (1), with 4 irregularly depressed striae (2).
15. Discal punctures of elytra simple (0)	cresent-shaped, ocellate, or inverse U-shaped (1).
16. Striae at mid-disc punctate, not interrupted (0)	striate, not interrupted (1), striate, interrupted (2).
17. Coloration without confused vittae (0)	with confused orange and castaneous vittae (1), with one transverse orange macula (2).
18. Epipleuron horizontal (0)	rounded (1), rounded and with a raised line (2).
19. Lateral subapical margin not transversely strigulate (0)	transversely strigulate (1).
20. Apex rounded (0)	weakly sinuate (1).
Pygidium	
21. Surface strigulate, strigulae transverse (0)	strigate with 1 concentric circle at apex (1), strigate with 2 adjacent, concentric circles at apex (2).
22. Surface at mid-disc with strigulae complete(0)	with strigulae interrupted (1).
Venter	
23. Apex of last sternite of female rounded (0)	blunt (1).
24. Middle of metasternum of male without dense field of tawny setae (0)	with a dense field of tawny setae (1).
Appendages	
25. Mesal foreclaw of male simple (0)	split (2).
26. Fifth protarsomere with empodium exposed (0)	hidden (1).
27. Metatarsus 5 of male without medial tooth (0)	with medial tooth (1).
28. Mesal edge of male metatibia sparsely setose (0)	moderately setose (1), densely setose (2).
29. Metatibia with corbel not produced (0)	weakly produced (1), well produced (2).
Parameres	
30. In dorsal view symmetrical (0)	asymmetrical (1).
31. Ventral sclerite membranous (0)	heavily sclerotized, arms symmetrical (1), heavily sclerotized, arms asymmetrical (2).
Metanotum	
32. Apex quadrate and blunt (0)	produced, apices rounded (1), produced, apices angulate (2).
Hind Wing	
33. Veins AP 3+4 and J developed (0)	absent (1).
Metendosternite	
34. With mesal, apical branches thin and weak (0)	thick and robust (1).
Behavior	
35. Adults do not rest on their sides while on vegetation (0)	adults known to rest on their sides (1).

Table 2. Character matrix for the phylogenetic analysis of the species of *Cnemida.*

	Character						
		1	11111	11112	22222	22223	33333
Taxon	12345	67890	12345	67890	12345	67890	12345
Cnemida							
aterrima	11122	03121	12111	22201	11001	11121	2111?
ephippiata	11111	23123	22121	21211	10001	11121	1111?
gigantea	11122	03121	12111	22201	21001	11?21	?111?
intermedia	11112	03122	12121	22211	11001	11121	21111
lacerata	11122	03122	12121	21211	11011	11321	2111?
leprieuri	11101	12220	01121	00111	00101	10010	0211?
retusa	11111	23123	22121	21211	10001	11221	21111
tristriata	11111	23123	22111	11211	10001	11221	1111?
Rutela							
(s.g. *Rutela*)	00100	01010	00000	00100	00$^{0}/_{1}$00	1001$^{0}/_{1}$	00010
Pelidnota							
(s.g. *Pelidnota*)	00000	00000	00000	00000	00000	00000	00000