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# Synopsis of the New World Genera of Anomalini (Coleoptera: Scarabaeidae: Rutelinae) and Description of a New Genus from Costa Rica and Nicaragua

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Ann. Entomol. Soc. Am. 96(4): 415-432 (2003)

**ABSTRACT** We describe a new genus of anomaline scarab, *Anomalorhina* (Coleoptera: Scarabaeidae: Rutelinae: Anomalini) from Costa Rica and Nicaragua. *Anomala turrialbana* Ohaus is transferred into this genus, and a new species, *Anomalorhina osaensis*, is described. *Anomalorhina* is characterized by the clypeal apex that is abruptly reflexed, the base of the frons that has prominent tubercles in males, the pronotum with a depressed fovea in males, and the pronotum with the apical bead posteriorly produced and V-shaped at the middle in females. We summarize the biological importance of the 16 genera of New World anomaline scarabs, including comments on agricultural pests, larvae, and natural history. We provide an overview and synopsis of each of the New World anomaline genera with comments on biology and characteristics for identification.

**RESUMEN** Se describe un género nuevo de escarabajos anomalinos, *Anomalorhina* (Coleoptera: Scarabaeidae: Rutelinae) de Costa Rica y Nicaragua. Se transfiere *Anomala turrialbana* Ohaus a este género nuevo, y se describe una especie nueva, *Anomalorhina osaensis*. *Anomalorhina* se caracteriza por tener el ápice del clipeo abruptamente elevado, los machos presentan dos tubérculos prominentes en la base frontal de la cabeza y una fovea en el pronoto, y las hembras tienen el pronoto con el área media del margen anterior proyectado posteriormente en forma de V. Se presenta un sumario sobre la importancia biológica de los 16 géneros de Anomalini del nuevo mundo que incluye comentarios sobre las plagas agrícolas, larvas e historia natural. Se provee una sinopsis de cada género de Anomalini del nuevo mundo con comentarios sobre su biología y características para su identificación.

**KEY WORDS** *Anomala*, *Popillia*, *Exomala*, *Phyllopertha*, scarab beetle

THE SCARAB TRIBE ANOMALINI contains one of the largest genera in the animal kingdom, the genus *Anomala* Samouelle, which includes ≈1,000 species worldwide. The tribe includes some species that are agricultural pests and some species that have the potential of becoming agricultural pests if introduced to new regions. With the addition of the new genus described herein, the New World Anomalini includes 16 genera and ≈320 species. Modern taxonomic treatments are available for three of these genera: *Dilophochila* Bates (six species, Morón and Howden 2001), *Strigoderma* Burmeister north of Panama (28 species, Bader 1992), and *Epectinaspis* Blanchard (nine species, Paucar-Cabrera 2003). The monotypic genera *Nayarita* Morón and Nogueira, *Yaaxkumukia* Morón and Nogueira, and *Mazahuapertha* Morón and Nogueira were recently created, and treatments for these are available (Morón and Nogueira 1999). The econom-

ically important genus *Anomala*, with ≈200 species in the New World and ≈800 in the Old World, has had no comprehensive taxonomic treatment. This lack of knowledge is significant because species of *Anomala* have become invasive, agricultural pests in countries where they are adventive. The size of this genus, in combination with high variability of characters, has led to 200 years of taxonomic neglect and paraphyly of taxa within the tribe.

In this paper, we describe a new genus of Anomalini from Costa Rica and Nicaragua, provide a key to the genera in the New World, and give a brief overview of each of the genera. It is our hope that this research will be used as a foundation for additional research on members of the Anomalini.

## Natural History of the Anomalini

Life histories of species of Anomalini are quite variable. Adult anomalines are both nocturnal and diurnal; nocturnal species are often attracted to lights at night. Some adults feed little or not at all (Ritcher 1958),

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while others feed on leaves, floral parts, and fruits of angiosperms and gymnosperms (see generic overviews).

Larvae of Anomalini are subterranean feeders on roots and organic material (Ritcher 1966). Larvae are described for only a handful of species (Böving 1921, Hayes 1921, Sim 1934, Gardner 1935, Ritcher 1943, 1945, 1966, Micó et al. 2003) in four of the anomaline genera (*Anomala*, *Callistethus* Blanchard, *Strigoderma*, and *Popillia* Dejean).

In the New World, three adventive species cause economic damage to agricultural crops and ornamental plants: *Popillia japonica* Newman, *Anomala orientalis* (Waterhouse), and *Anomala dubia* (Scopoli) (e.g., Zhang et al. 1994, Cowles and Villani 1996, Capinera 2002, Potter and Held 2002). In Latin American countries, larvae of several species of anomalines are part of the scarab larvae complex called "gallina ciega" or "joboto" that feed on roots and cause damage to crops (Maes and Tellez Robleto 1988, Pardo Lorcarno 1994, Morón 2001). Other species of anomalines feed on a wide variety of crops including corn, sugar cane, turfgrass, and soybeans (Ritcher 1966).

In the Old World, anomalines are also known to cause economic damage to horticultural and agricultural plants. *Phyllopertha horticola* (L.) causes damage to turfgrass in Europe (Smits et al. 1994). *Singhala tenella* (Blanchard) is reportedly destructive to young shoots of tea plants in Sri Lanka (Arrow 1917). *Pseudosinghala dalmanni* (Gyllenhal) is reportedly destructive in Chinese plantations (Arrow 1917). *Anomala rufocuprea* Motschulsky causes damage to soybean crops in Japan (Nakano et al. 1986). Suehiro (1960) reported that *Anomala sulcatula* Burmeister (a species from the Philippines) is adventive on Midway Atoll.

### Fossil Anomalini

Several fossil Anomalini from the Mesozoic era to the Holocene epoch are known in the genera *Anomala*, *Anomalites* Fritsch, and species with doubtful association with *Anomala* (Schwert and Ashworth 1985, Krell 2000). Krell (2000) recorded 18 species of Miocene and Oligocene *Anomala* from China, Germany, and the United States (Colorado) and one species of *Anomalites* from the Tertiary of France. Schwert and Ashworth (1985) cited one species of *Anomala*, *A. undulata* Melsheimer (or near) from Holocene deposits from southern Minnesota.

### Recognition and Classification of Anomalini

Adult anomalines are characterized as follows: elytra with membranous border at lateral margin (Figs. 45 and 46); terminal spiracle not positioned in pleural suture (Figs. 45 and 46); antennae generally nine-segmented; protibiae bidentate (Figs. 17 and 18; rarely unidentate or tridentate); inner protibial spur subapical (Fig. 18; spur lacking in *Leptohoplia* and *Mazahuapertha* [e.g., Fig. 17]).

Anomaline larvae are distinguished from other scarabaeoid larvae as follows: stipes with dorsal row of four to seven acute, recurved stridulatory teeth and a truncate process; lacinia with two apical unci (subequal in size); epipharynx with two to four heli; plegmata well-developed and proplegmata absent; antenna with one elliptical dorso-sensory spot; raster with two monostichous palidia (Ritcher 1966). Based on larvae, Ritcher (1966) noted that members of the tribe Anomalini are remarkably uniform.

A number of homonyms have been created throughout taxonomic history for the genus *Anomala*. A recent ruling of the International Commission on Zoological Nomenclature (1989) suppressed the hymenopteran *Anomala* von Block, 1799 (the senior homonym) and placed *Anomala* Samouelle, 1819 (a junior homonym) on the Official List of Generic Names in Zoology. This action stabilizes the scarab name *Anomala* Samouelle and gives it nomenclatural priority over *Anomala* von Block.

Because of the lack of phylogenetic evidence, the classification of anomaline scarabs remains a subject of debate. According to some researchers, anomalines are classified as a group within the Rutelinae (or Rutelidae) (e.g., Machatschke 1957, 1972–1974, Morón et al. 1997), and according to others, they are classified as a subfamily within the Scarabaeidae (e.g., Potts 1974). In this paper, we follow the classification that places the group as a tribe within the subfamily Rutelinae and family Scarabaeidae (Jameson 2002). The only catalog and overview of world anomaline genera (Machatschke 1957, 1972–1974) follows this classification.

This research was initiated to provide a foundation for systematics research on the Anomalini (see also Paucar-Cabrera and Jameson 2003). Our synopsis of the New World genera consolidates literature on the group, provides character states for identification, and calls attention to taxonomic problems in the group. Revision and phylogenetic analyses of all genera in the tribe Anomalini is beyond the scope of this study and will require a lifetime of research. Where appropriate, we identify genera that we believe are not monophyletic (specifically *Anomala*, *Stigoderma*, *Epectinaspis*, *Callistethus*, *Leptohoplia*). Statements such as these are based on comparative morphology, preliminary phylogenetic analyses based on morphological characters (M.L.J., unpublished data), and preliminary molecular phylogenetic analyses of scarabaeoid beetles based on 350 exemplar taxa (Hawks et al. unpublished data). We consider the genus *Phyllopertha* (which is represented in the New World by *P. latitarsis* Nonfried) to be *incertae sedis* because type specimens cannot be located to confirm the taxon. Future revisionary and phylogenetics research on the Anomalini will help to resolve these problems.

### Materials and Methods

Body measurements, puncture density, puncture size, and density of setae are based on the following standards. Body length was measured from the apex of

the head to the apex of the elytra. Body width was measured at mid-elytra. Puncture density was considered "dense" if punctures were nearly confluent to less than two puncture diameters apart, "moderately dense" if punctures were from two to six puncture diameters apart, and "sparse" if punctures were separated by more than six puncture diameters. Puncture size was defined as "small" if punctures were 0.02 mm or smaller; "moderate" if 0.02–0.07 mm, "moderately large" if 0.07–0.12 mm, and "large" if 0.12 mm or larger. Setae were defined as "moderately dense" if the surface was visible but with many setae, and "sparse" if there were few setae. The interocular width measures the number of transverse eye diameters that fit between the eyes.

Specimens of the new genus and new species are deposited at UNSM (University of Nebraska State Museum, Lincoln, NE), ZMHB (Museum für Naturkunde der Humboldt-Universität, Berlin, Germany), INBC (Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica), CMNC (Canadian Museum of Nature, Ottawa, Canada), and CASC (California Academy of Sciences, San Francisco, CA).

The phylogenetic species concept (Wheeler and Platnick 2000) was applied in this work: "A species is the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states."

We provide a list of generic synonyms that have application to New World Anomalini. This is not an exhaustive list of synonyms; many other names would need to be added if this treatment included Old World anomalines. For genera, we follow the classification of Machatschke (1972–1974) and Potts (1974), with additions from Morón and Nogueira (1999). For subtribes, we follow the classification of Machatschke (1972–1974), with the additions of Potts (1974) and Morón and Howden (2001).

#### *Anomalorhina* Jameson, Paucar-Cabrera, and Solís, New Genus

(Figs. 1a–1d, 2–16)

**Type Species.** *Anomala turrialbana* Ohaus, 1928: 393, here designated.

**Description.** Scarabaeidae: Rutelinae: Anomalini. *Form* (Figs. 1a–1d, 2–4): Elongate oval, apices of elytra broadly rounded, pygidium exposed beyond elytra. Length 10.0–14.0 mm; width 5.5–7.0 mm. *Head* (Figs. 5 and 6): Frons with or without one tubercle on each side of lateral margin (extending posteriorly from near frontoclypeal suture to near base of frons); surface punctate to shagreened; punctures minute or large. Clypeus with surface of disc flat; apex rounded, or quadrate (dorsal view), subtriangular or subquadrate (frontal view), abruptly or moderately reflexed. Frontoclypeal suture obsolete medially, poorly defined at margin. Eye canthus not cariniform. Interocular width equals 3.0–5.5 transverse eye diameters. Antenna nine-segmented; club subequal in length to segments 1–6. Labrum quadrate at middle, sides rounded, not

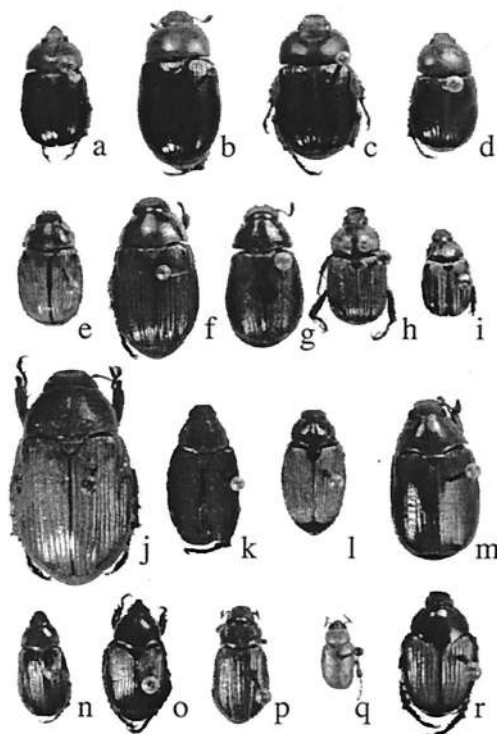
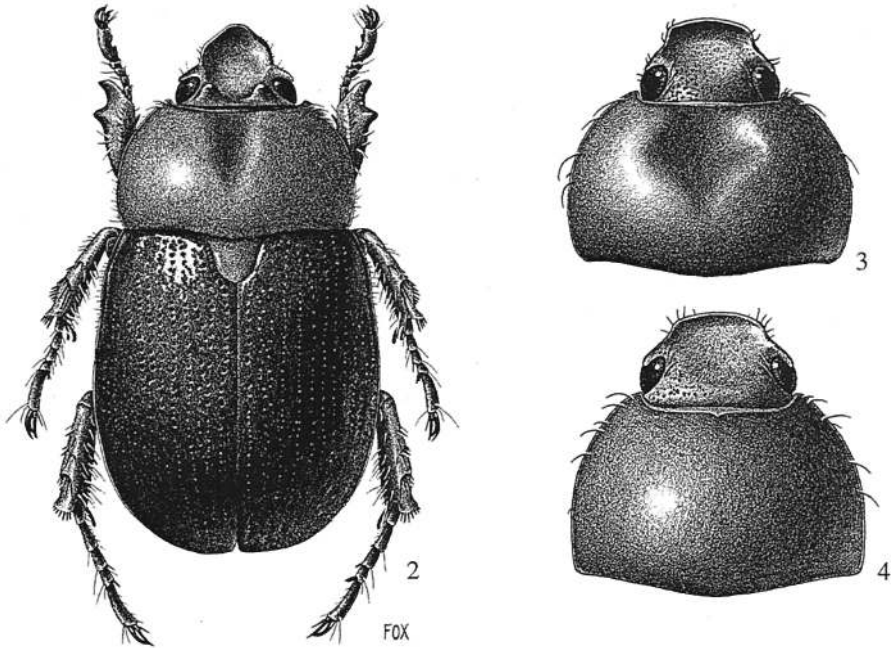


Fig. 1. (a–r) New World genera of Anomalini represented by exemplar species: (a) *Anomalorhina turrialbana* (male), (b) *Anomalorhina turrialbana* (female), (c) *Anomalorhina osaensis* (male), (d) *Anomalorhina osaensis* (female), (e) *Anomala orientalis*, (f) *Callistethus marginalis*, (g) *Chelilabia piniphaga*, (h) *Epectinaspis mexicana*, (i) *Mazahuapertha tolucaana*, (j) *Nayarita viridinota*, (k) *Rugopertha sericeomicans*, (l) *Strigoderma arboreicola*, (m) *Yaaxkumukia ephemera*, (n) *Anomalacra clypealis*, (o) *Callirhinus metalllescens*, (p) *Dilophochila bolacooides*, (q) *Leptoploia testaceipennis*, (r) *Popillia japonica*. A pdf file of this image is available at <http://www.museum.unl.edu/research/entomology/Guide/Rutelinae/Anomalini/Anomalinipdf.htm>.

visible or weakly visible in dorsal view. Mandible rounded externally, dorsal surface flat, inner apex bifid (teeth short, acute), molar region with 8–12 lamellae, scissorial region brush-like (lacking teeth). Maxilla (Fig. 7) with six acute teeth, two basal-most teeth fused at middle; external apex with 10–16 long setae; palpus 4-segmented, terminal segment subequal in length to segments 1–3 combined. Mentum with surface weakly convex or flat; apex weakly bisinuate; length subequal to greatest width or 1.25 times wider; terminal segment of palpus subequal to segments 1–2 combined. *Pronotum* (Figs. 3 and 4): Widest at middle; apical margin membranous; basal margin weakly protuberant posteriorly at middle. Disc in male with moderately depressed fovea from apex to near middle. Marginal bead present apically, laterally, and at basal angle; apical bead produced posteriorly at middle, V-shaped (female) (Fig. 4). Surface shagreened and

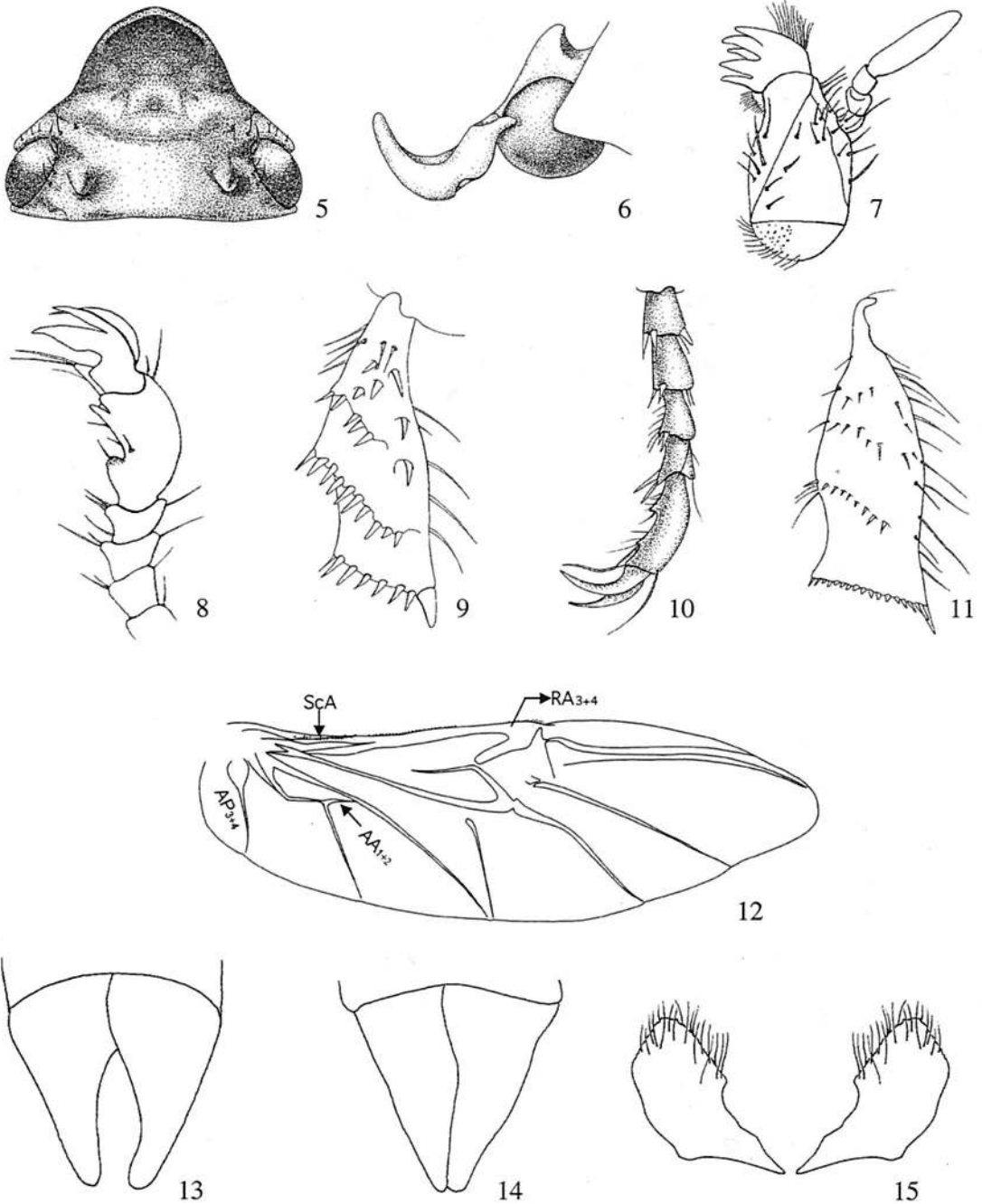


Figs. 2-4. *Anomalorhina turrialbana* (male) dorsal habitus (Fig. 2). Head, and pronotum of *Anomalorhina osaensis* male (Fig. 3) and female (Fig. 4).

with minute or moderately large punctures; punctures sparse to moderately dense; punctures with or without setae laterally. *Scutellum*: Parabolic, slightly wider than long; base declivous at elytral base. Surface variably punctate. *Mesepimeron*: Base weakly exposed beyond base of elytra. *Elytra*: Surface with longitudinal, punctate striae; punctures small and moderately large, ocellate or not. *Epipleuron* from base to metacoxa rounded; beaded from base to near apex, membranous from metacoxa to apex. *Propygidium*: Concealed by elytra. *Pygidium*: Width about twice length at middle. Shape subtriangular in caudal view, weakly convex in lateral view. Surface punctate, some punctures setose; setae moderately long, tawny or reddish. Apex and lateral margins beaded. *Venter*: Prosternum shield-like, not produced ventrally, not produced to trochanter, setose; setae dense at middle, moderately long. Mesometasternal region with narrow projection (subequal to width of mesotibial spur) produced to mid-mesocoxa, apex quadrate in lateral view. Apical abdominal sternite broadly sinuate at apex with poorly defined setose punctures; setae moderately long, tawny. *Legs*: Profemur without rounded, dilated apex. Protibia with two teeth and subapical spur, spur subequal to length of protarsomere 2; base without weak protibial notch. Protarsomere five subequal in length to protarsomeres 2-4, with or without well-developed, rounded, internomedial protuberance (Fig. 8). Unguitractor plate of protarsus produced beyond apex of protarsomere 5, laterally flattened, bisetose. Protarsal claw with modified claw split; ventral ramus two times wider than dorsal ramus in males, ventral ramus subequal in width to dorsal ramus in females. Mesotibia

(Fig. 9) widest at middle, weakly expanded at apex; external margin with one weak, oblique carina in basal one-third or one-fourth (with six to seven spines) and with one moderately developed, oblique carina at middle (with 11 to 12 spines); apex with 7-10 spines and two inner spurs; spurs produced to near apex of mesotarsomere 1. Meso- and metatarsomere five with weak internomedial protuberance (Fig. 10). Mesotarsus with claws split; ventral ramus subequal in width or 1.5 times wider than dorsal ramus. Unguitractor plate of meso- and metatarsi produced beyond apex of tarsomere 5, laterally flattened, bisetose. Metatrochanter with apex not produced beyond posterior border of femur. Metatibia (Fig. 11) widest at apical one-third, weakly expanded at apex, external margin carinate and with spines, spines of female more elongate than those of male; apex with 20-35 spines and two inner spurs; spurs produced to subapex of metatarsomere 1. Metatarsus with claws simple. *Hind Wing* (Fig. 12): Apex of  $AA_1 + 2$  weakly united with  $CuA$ .  $AP_3 + 4$  at base bulbous, setose.  $ScA$  with reduced membrane and single row of pegs. Region anterior to  $RA_3 + 4$  lacking setae except near fold. *Parameres* (Figs. 13 and 14): Symmetrical. *Gonocoxites* (Fig. 15): Poorly sclerotized, setose at apex; setae moderately dense, tawny, short and moderate in length.

**Diagnosis.** Members of the genus *Anomalorhina* differ from other genera in the tribe Anomalini by the following characteristics: clypeus with apex abruptly reflexed (male) or moderately reflexed (female; Figs. 2-6); pronotum with apical marginal bead produced posteriorly at middle and V-shaped in female (Figs. 4); pronotal disc of male with moderately depressed fovea



Figs. 5–15. Characters of *Anomalorhina* species. Head of *A. turrialbana* dorsal (Fig. 5) and lateral view (Fig. 6); maxilla of *A. turrialbana* (Fig. 7); foretarsus (male) of *A. turrialbana* (Fig. 8); mesotibia (Fig. 9) and metatarsus (Fig. 10) of *A. osaensis* (male); metatibia (male) of *A. turrialbana* (Fig. 11); hindwing of *A. turrialbana* (Fig. 12); parameres of *A. turrialbana* (Fig. 13) and *A. osaensis* (Fig. 14); and gonocoxites of *A. turrialbana* (Fig. 15).

from apex to middle of pronotum (Figs. 2 and 3); frontoclypeal suture obsolete medially, poorly defined at margin; male protasomere five with rounded internomedial protuberance (Fig. 8). Although not a generic character, males of *A. turrialbana* are easily

separated from other Anomalini by the two tubercles at the base of the frons (Figs. 2, 5, and 6).

**Distribution** (Fig. 16). Costa Rica and Nicaragua.

**Etymology.** We name this genus for its overall anomaline-like body form and the clypeal apex that is



Fig. 16. Distribution of *Anomalorhina* species in Costa Rica and Nicaragua.

abruptly reflexed (from the Latin “-rhina” meaning “nose,” in reference to the clypeus that is loosely analogous to a nose). The Latin root “anomalo-” means “weird” and also applies to the unusual form of the clypeal apex of the genus, particularly the male specimens of *A. turrialbana* (the type species). The name is considered feminine in gender.

Key to the Species of *Anomalorhina*

- 1. Pronotal disc with depressed fovea from apex to one-half or two-thirds length of pronotum. Abdominal sternites weakly concave (male) . . . . . 2
- 1'. Pronotal disc evenly rounded (without fovea). Abdominal sternites weakly convex (female) . . . . . 3
- 2. Base of frons with two tubercles (Figs. 2, 5, and 6). Clypeus abruptly reflexed with apex acute in frontal view (Figs. 5 and 6) . . . . . *Anomalorhina turrialbana* (Ohaus)
- 2'. Base of frons without tubercles (Figs. 3 and 4). Clypeus broadly reflexed with apex quadrate in frontal view (Figs. 3 and 4) . . . . . *Anomalorhina osaensis* Jameson, Paucar-Cabrera, and Solís, n. sp.
- 3. Elytral interval between stria one and two near base twice width of interval between elytral suture and stria 1. Frons with disc slightly concave. Head and pronotum rufous; elytron black or reddish-brown. . . . . *Anomalorhina turrialbana* (Ohaus)
- 3'. Elytral interval between stria one and two near base equal in width to interval between elytral suture and stria 1. Frons with disc slightly convex. Head and pronotum castaneous; elytron castaneous. . . . . *Anomalorhina osaensis* Jameson, Paucar-Cabrera, and Solís, n. sp.

*Anomalorhina turrialbana* (Ohaus),  
New Combination  
(Figs. 1a–1b, 2, 5–8, 11–13, 15, 16)

**Synonymy.** *Anomala turrialbana* Ohaus, 1928:393.  
**Type Material.** Holotype female at ZMHB labeled (a) “Turrialba, Costa Rica, Heyne, Berlin-Wilm, X, 900 m” (typeface and handwritten), (b) ♀ (typeface), (c) “type” (typeface, red label), (d) “*Anomala turrialbana* Ohs.” (handwritten, red label), (e) “*Anomalorhina turrialbana* (Ohaus), det. Jameson, Paucar-Cabrera, Solís” (typeface and handwritten), and (f) mouthparts card-mounted.

**Redescription.** *Males* ( $n = 3$ ). *Form* (Figs. 1a and 2): Length 10.4–13.1 mm; width 5.8–7.4 mm. *Color:* Head, pronotum, and scutellum shiny reddish-brown; pygidium, legs, and venter shiny testaceous; elytra shiny black or reddish-brown. *Head* (Figs. 5 and 6): Frons with surface moderately concave, tuberculate, punctate, and shagreened; one tubercle mesad of each lateral margin, tubercle extending posteriorly from near frontoclypeal suture to near base of frons, produced dorsally about length of maxillary palpus (lateral view, Fig. 6); punctures small, moderately dense at base; disc shagreened. Clypeus with surface of disc moderately concave; sides subparallel or weakly convergent from base, constricted to abruptly recurved, subtriangular apex (frontal view); apex in frontal view flat, broadly reflexed (about perpendicular to frons in lateral view). Interocular width equals 3.7 transverse eye diameters. Mentum with surface weakly convex, length 1.25 times greatest width. *Pronotum* (Fig. 2): Disc with moderately depressed fovea from apex to two-thirds length of pronotum. Marginal bead present apically (slightly thickened at middle), laterally, and at basal angle. Surface shagreened with minute (mid-disc) to small (lateral margin) punctures; punctures sparse (minute) to moderately dense (small). Lateral margin with minute, setose punctures; setae short to moderately long, tawny. *Scutellum:* Surface with small, sparse punctures. *Elytra:* Surface with longitudinal, punctate striae; punctures small and moderately large, ocellate, moderately dense; six striae on disc, five laterad of humerus. Interval between stria one and two broad near base (twice width of interval 1) and with randomly placed, ocellate punctures from base to apex; remaining intervals narrow, punctate; punctures small, moderately dense, simple. *Pygidium:* Surface with moderately large, dense punctures, some setose (at apex); setae moderately long, tawny. Apex and margins beaded. *Venter:* Mesometasternal projection produced to mid-mesocoxa, apex quadrate or rounded in lateral view. Abdominal sternites 2–4 and apical sternite subequal in length, sternite 5  $\approx$  2 times length of sternite 4. *Legs:* Mesotibia widest at middle, weakly expanded at apex; external margin with weak, oblique carina in basal one-fourth (composed of 6–8 spines) and moderately developed, oblique carina at middle (composed of 11–12 spines); apex with eight spines and two inner spurs; spurs produced to near apex of mesotarsomere I. Mesotarsus with modified claw split, ventral ramus subequal in width to dorsal ramus.

Metatibia (Fig. 11) widest at apical one-third, weakly expanded at apex, external margin with weak, oblique carina at apical one-third (composed of 9–14 spines; spines progressively longer toward external margin); apex with 22–24 spines and two inner spurs. *Parameres*: (Fig. 13). Apices divergent.

*Females* ( $n = 4$ ). *Form* (Fig. 1b): Similar to males except for the following characteristics: Length 12.5–13.8 mm; width 6.8–7.6 mm. *Color*: Elytra dark reddish-brown or black. *Head*: Frons with surface weakly concave (base) and flat (disc and apex), punctate; punctures minute and moderately large mixed, moderately dense (base) to rugopunctate (disc), confluent at margin. Clypeus with surface flat, rugopunctate (punctures moderately large), sides weakly convergent toward apex; apex quadrate, sides rounded, moderately reflexed. Interocular width equals 3.2 transverse eye diameters. *Pronotum*: Apical margin with bead weakly produced posteriorly at middle. Surface with minute (mid-disc) to moderately large (lateral margin) punctures; punctures sparse (minute) to moderately dense (moderately large). *Venter*: Abdominal sternites 2–4 subequal in length, sternite 5  $\approx$  1.6 times length of sternite 4, apical sternite three-fourths length of sternite 4. Apical abdominal sternite with small, setose punctures; setae moderately long, tawny. *Legs*: Protarsomere five with weak internomedial protuberance. Protarsal claw with modified claw split, ventral ramus subequal in width to dorsal ramus. Mesotibia with carina in basal one-fourth composed of 6–7 spines. Metatibia at external margin with moderately developed, oblique carina at apical one-third; apex with 27–32 spines.

**Diagnosis.** *A. turrialbana* is separated from *A. osaensis* by the presence of tubercles on the frons of the male (Figs. 2, 5, and 6; lacking in *A. osaensis*), the interval between stria one and two that is broad near the elytral base (narrow in *A. osaensis*), elytral color black or reddish-brown (castaneous in *A. osaensis*), mentum weakly convex (greatly convex in *A. osaensis*), metatibial apex of females with 28–32 spines (22–24 in females of *A. osaensis*), and form of the male parameres (apices divergent as in Fig. 13; apices convergent in *A. osaensis* as in Fig. 14).

**Distribution.** Northcentral Costa Rica and southern Nicaragua (Fig. 16).

**Material Examined.** Seven specimens (three males, four females).

**Locality Data.** COSTA RICA (6). Alajuela (4): San Ramón (Río San Lorencito, 800m), UCR-Reserva Forestal Ml. Alberto Brenes (10° 13' N 84° 35' W, 800 m), Upala (Bijagua, Albergue Heliconias, 700m). Cartago (2): Turrialba. NICARAGUA (1). Río San Juan (1): Casa de Mareña (10° 59' 41" N 84° 16' 38" W).

**Temporal Data.** April (1), May (3), June (1), October (1).

**Remarks.** Ohaus (1928) described *A. turrialbana* based on a single female specimen. He stated that the species is "isolated among the American anomalines" based on "the somewhat peculiar body form and coloring" and the "form of the labrum and hind tibiae." Lacking male representatives of the genus, it is easy to

see why Ohaus placed the species in the genus *Anomala*; females closely resemble other female *Anomala* species.

**Natural History.** According to label data, some specimens of this species were attracted to benzyl acetate traps that were placed high in the forest canopy.

***Anomalorhina osaensis* Jameson, Paucar-Cabrera, and Solís, New Species**

(Figs. 1c-d, 3-4, 9-10, 14, 16)

**Type Material.** Holotype, allotype, and one paratype. *Holotype male* at INBC labeled (a) "Rancho Quemado, Pen. Osa, Prov. Punt, COSTA RICA, F. Quesada, Mar 1991, L-S-292500, 511000" (printed), (b) "COSTA RICA [bar code], INBIO CRI000 577351" (printed), (c) our holotype label. Male genitalia, mouthparts, and hind wing card-mounted. *Allotype female* at INBC labeled (a) "Rancho Quemado, 200 m, Peninsula de Osa, Prov. Puntarenas. Costa Rica F. Quesada y G. Varela, May 1992, L-S 292500, 511000" (printed), (b) "COSTA RICA [bar code], INBIO CRI000 870195" (printed), (c) our allotype label. *Paratype female* at UNSM labeled (a) "Rancho Quemado, 200 m, Peninsula de Osa, Prov. Puntarenas. Costa Rica D. Brenes, Abr 1992, L-S 292500, 511000" (printed), (b) "197" (handwritten, red ink), (c) "COSTA RICA [bar code], INBIO CRI000 494524" (printed), (d) our paratype label.

**Holotype, Male.** *Form* (Fig. 1c and 3): Length 12.9 mm; width 6.8 mm. *Color*: Head shiny reddish-brown; pronotum shiny dark brown; elytra shiny castaneous; legs, venter testaceous. *Head* (Fig. 3): Frons with surface weakly convex, lacking tubercles, punctate; punctures small (moderately dense at base and sides, dense on disc) and moderate in size (adjacent to eye, sparse, setose); setae reddish, short and moderately long. Clypeus with surface of disc flat, punctate; sides weakly convergent from base; apex in dorsal view abruptly recurved, broadly rounded; apex in frontal view subquadrate, broadly reflexed; punctures mixed small and moderately large, dense on disc to moderately dense at sides and near apex. Interocular width equals 3.2 transverse eye diameters. Mentum with surface of disc greatly convex; apex bisinuate, length subequal to greatest width. *Pronotum* (Fig. 3): Disc with moderately depressed fovea from apex to middle (one-half length) of pronotum. Marginal bead present apically (slightly thickened at middle), laterally, and at basal angle. Surface shagreened and with minute (mid-disc) to small (lateral margin) punctures; punctures sparse (minute) to moderately dense (small); some punctures setose laterally; setae moderately long, reddish. *Scutellum*: Surface with moderately large, sparse punctures. *Elytra*: Surface with longitudinal, punctate striae; punctures small and moderately large, ocellate, moderately dense; six striae on disc, five laterad of humerus (stria five incomplete). Interval between stria one and two narrow near base (subequal in width to interval 1) and with randomly placed, ocellate punctures from base to middle, and



punctures in a line from middle to apex; remaining intervals narrow, punctate; punctures small, moderately dense, simple. *Pygidium*: Width about twice length at middle. Surface with crescent-shaped punctures; punctures moderate and moderately large, moderately dense (base and sides) to dense (disc), setose at apex and margin; setae moderately long, tawny. Apex and lateral margins beaded. *Venter*: Mesometasternum with apex rounded in lateral view. Abdominal sternites 2-4 and apical sternite subequal in length, sternite 5 ≈1.5 times length of sternite 4. *Legs*: Mesotibia (Fig. 9) widest at middle, weakly expanded at apex; external margin with weak, oblique carina in basal one-third (composed of six spines) and moderately developed, oblique carina at middle (composed of 11 spines); apex with seven spines and two inner spurs; spurs produced to near apex of mesotarsomere 1. Mesotarsus with claws split; ventral ramus ≈1.5 times width of dorsal ramus. Metatibia widest at apical one-third, weakly expanded at apex, external margin with weak, oblique carina at apical one-third (composed of 11 spines; spines progressively longer toward external margin); apex with 20 spines and two inner spurs; spurs produced to near apex of metatarsomere 1. Metatarsus with claws simple (Fig. 10). *Parameres*: (Fig. 14). Apices convergent.

**Allotype.** *Female.* *Form* (Fig. 1d): Length 13.9 mm; width 6.7 mm. Allotype differs from the holotype in the following respects: *Head*: Frons with surface weakly convex, punctate; punctures minute and moderately large, mixed, moderately dense (base) to rugopunctate (disc), confluent at lateral margin, some setose; setae moderately long, reddish. Clypeus with surface flat, rugopunctate on disc (punctures moderately large) to densely punctate on sides (punctures moderately large), sides weakly convergent toward apex; apex quadrate, sides rounded, moderately reflexed. Interocular width equals 5.4 transverse eye diameters. *Pronotum* (Fig. 4): Apical margin with bead produced posteriorly at middle, V-shaped (Fig. 4). Surface with minute (mid-disc) to moderately large (lateral margin) punctures; punctures sparse (minute) to moderately dense (moderately large), some setose at lateral margin; setae moderately long, reddish. *Elytra*: Interval between stria one and two with randomly placed punctures from base to middle, linear punctures from middle to apex. *Venter*: Abdominal sternites 2-4 subequal in length, sternite 5 ≈1.6 times length of sternite 4, apical sternite three-fourths length of sternite 4. Apical sternite with small, setose punctures; setae moderately long, tawny. *Legs*: Protarsomere five with weak internomedial protuberance. Protarsal claw with modified claw split; ventral ramus subequal in width to dorsal ramus. Mesotibia with carina in basal one-third composed of six spines; apex with eight spines. Metatibia at external margin with moderately developed, oblique carina at apical one-third composed of 13 spines; apex with 24 spines.

**Paratype.** *Female.* Length 10.7 mm; width 5.7 mm. Paratype differs from the allotype in the following respects: Metatibial apex with 22 spines.

**Diagnosis.** *Anomalorhina osaensis* differs from *A. turrialbana* by the following characteristics: elytra castaneous rather than black or reddish-brown; interval between stria one and two narrow near base (width of interval 1), with punctures randomly placed from base to middle, and punctures in a vertical line from middle to apex (interval broad and with randomly placed punctures in *A. turrialbana*); frons weakly convex and lacking tubercles in males; mentum with disc greatly convex and length subequal to greatest width (flat with length ≈1.25 times longer than greatest width in *A. turrialbana*); metatibia of female with 22-24 spines at the apex (28-32 in *A. turrialbana*); and form of the male parameres (apices convergent as in Fig. 14; apices divergent in *A. turrialbana* as in Fig. 13).

**Distribution.** Osa Peninsula, southern Costa Rica (Fig. 16).

**Material Examined.** Three specimens (one male, two females).

**Locality Data.** COSTA RICA (3). Puntarenas (3): Rancho Quemado (Osa Península, 200 m).

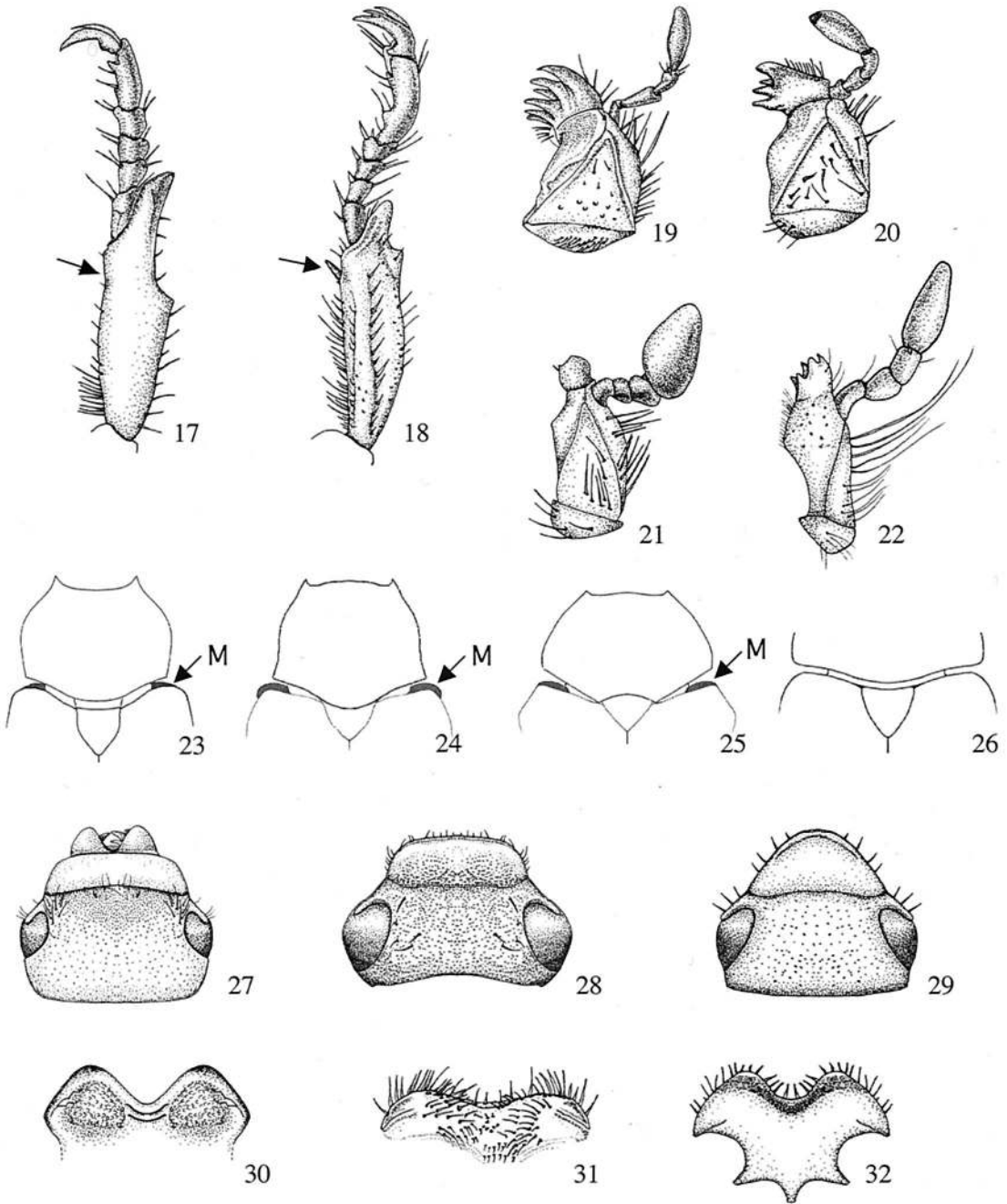
**Temporal Data.** March (1), April (1), May (1).

**Etymology.** The specific epithet, "osaensis," refers to the Osa Peninsula of Costa Rica where all of the type specimens were collected.

**Key to the New World Genera of Anomalini**

(*Phyllopertha latitarsis* Nonfried is *incertae sedis* and is omitted from the key)

- 1. Protibial spur absent (Fig. 17). Maxilla reduced, with two or fewer teeth (Figs. 21 and 22) . . . . . 2
- 1'. Protibial spur present (Fig. 18). Maxilla not reduced, with >2 teeth (Figs. 19 and 20) . . . . . 3
- 2(1). Mesepimeron not visible in dorsal view (e.g., Fig. 26). Clypeus with lateral margins at base straight (forming a right angle with frontoclypeal suture). Maxilla with last segment of palpus two times wider than width of third segment (Fig. 21). Dorsal color testaceous. . . . . *Leptohoplia* Saylor
- 2'. Mesepimeron visible in dorsal view (e.g., Figs. 23-25). Clypeus with lateral margins at base oblique (forming an acute angle with frontoclypeal suture). Maxilla with last segment of palpus subequal in width to third segment (Fig. 22). Dorsal color of head, pronotum, and pygidium castaneous with greenish reflections, elytron testaceous with castaneous, longitudinal markings. . . . . *Mazahupertha* Morón and Nogueira
- 3(1'). Labrum projecting anteriorly beyond



Figs. 17–32. Characters of anomalines. Prothoracic legs with arrows indicating absence or presence of apical spur in *Leptohoplia testaceipennis* (Fig. 17) and *Anomala chrysanthe* (Fig. 18); maxilla of *Anomala chrysanthe* (Fig. 19), *Dilophochila bolacoides* (Fig. 20), *Leptohoplia testaceipennis* (Fig. 21), and *Mazahuaertha toluca* (Fig. 22); form of pronotum and mesepimeron with arrows and “M” indicating exposed mesepimeron in *Epectinaspis* (Fig. 23), *Strigoderma* (Fig. 24), *Popillia* (Fig. 25), and *Yaaxkumukia* (Fig. 26); form of head in *Chelilabia* (Fig. 27), *Anomala* (Fig. 28), and *Anomalacra* (Fig. 29); and labrum (ventral view) in *Chelilabia* (Fig. 30), *Anomala* (Fig. 31), and *Dilophochila* (Fig. 32).

apex of clypeus (Fig. 27). Apex of labrum deeply emarginate (Figs. 27 and 30). . . . . *Chelilabia* Morón and Nogueira

3'. Labrum hidden or partially hidden, only apex exposed beyond apex of clypeus (Figs. 28 and 29). Apex of quad-

- rate, rounded, sinuate (Fig. 31), or emarginate (Fig. 32) . . . . . 4
- 4(3'). Anterior border of clypeus emarginate, lobed either side of emargination (Fig. 33). . . . . *Dilophochila* Bates
- 4'. Anterior border of clypeus quadrate (Fig. 28), rounded, parabolic (Fig. 29), or produced anteriorly (Figs. 34–37) . . . . . 5
- 5(4'). Frontoclypeal suture incomplete (obsolete at middle, poorly defined at margin; Fig. 36). Sides of clypeus elevated at base of canthus (Fig. 37). Males with pronotal disc with depression (Figs. 2 and 3). Females with apical margin of pronotum with bead produced posteriorly at middle (V-shaped) (Fig. 4). . . . . *Anomalorhina* Jameson, Paucar-Cabrera, and Solís n. gen.
- 5'. Frontoclypeal suture complete (Figs. 28 and 29). Sides of clypeus weakly elevated or flat at base of canthus (Figs. 28 and 29). Males with pronotal disc evenly rounded (without fovea). Females with apical margin of pronotum with bead not produced posteriorly. . . . . 6
- 6(5'). Clypeus abruptly reflexed and snout-like, apex abruptly constricted (Figs. 34 and 35). . . . . *Callirhinus* Blanchard
- 6'. Clypeus not abruptly reflexed and snout-like, apex quadrate, rounded, or parabolic (e.g., Figs. 27–29). . . . . 7
- 7(6'). Mesepimeron partially visible anterior to base of elytron in dorsal view (Figs. 23–25). . . . . 8
- 7'. Mesepimeron concealed by base of elytron in dorsal view (Fig. 26) . . . . . 11
- 8(7). Base of pronotum tri-emarginate (Fig. 25). Mesometasternum produced anteriorly beyond base of mesocoxae (Fig. 38). . . . . *Popillia* Dejean
- 8'. Base of pronotum rounded posteriorly (e.g., Figs. 23, 24, and 26). Mesometasternum not produced anteriorly beyond base of mesocoxae (Figs. 39 and 40) . . . . . 9
- 9(11'). Pronotal surface finely rugopunctate. Elytral surface finely rugopunctate, lacking punctate striae or raised longitudinal ridges. . . . . *Rugopertha* Machatschke
- 9'. Pronotal surface punctate. Elytral surface with punctate striae, raised longitudinal ridges, or entirely smooth. . . . . 10
- 10(9'). Mesosternal intercoxal region subequal in width to base of mesofemur (Fig. 41). Mesepimeron subrectangular, well-exposed (Fig. 24). Clypeus of male narrowly reflexed at apex. Dorsal surface of elytron flat. . . . . *Strigoderma* Burmeister
- 10. Mesosternal intercoxal region less than one-fourth width of base of meso-

- femur (Fig. 40). Mesepimeron subtriangular, partially exposed (Fig. 23). Clypeus of male broadly reflexed at apex. Dorsal surface of elytron evenly rounded. . . . . *Epectinaspis* Blanchard
- 11(7'). Clypeus parabolic (Fig. 29). . . . . *Anomalacra* Casey
- 11'. Clypeus rounded or quadrate (e.g., Fig. 28). . . . . 12
- 12(11'). Mesosternal intercoxal region subequal in width to base of mesofemur or one-half width of base of mesofemur (Fig. 42). Mesometasternum produced anteriorly beyond base of mesocoxae (Fig. 42). . . . . 13
- 12'. Mesosternal intercoxal region less than one-fourth width base of mesofemur (Fig. 39). Mesometasternum not produced anteriorly beyond base of mesocoxae (Fig. 39). . . . . *Anomala* Samouelle
- 13(12'). Height of clypeal apex in frontal view approximately one-half length of clypeus in dorsal view (Fig. 43). Maxilla with five teeth. . . . . *Nayarita* Morón and Nogueira
- 13'. Height of clypeal apex in frontal view approximately one-third to one-fourth the length of clypeus in dorsal view (Fig. 44). Maxilla with six teeth. . . . . 14
- 14(13'). Last abdominal spiracle tuberculiform in male (Fig. 45). Pronotum with apical margin not beaded. . . . . *Yaaxkumukia* Morón and Nogueira
- 14'. Last abdominal spiracle simple, not tuberculiform in male or female (Fig. 46). Pronotum with apical margin beaded. . . . . *Callistethus* Blanchard

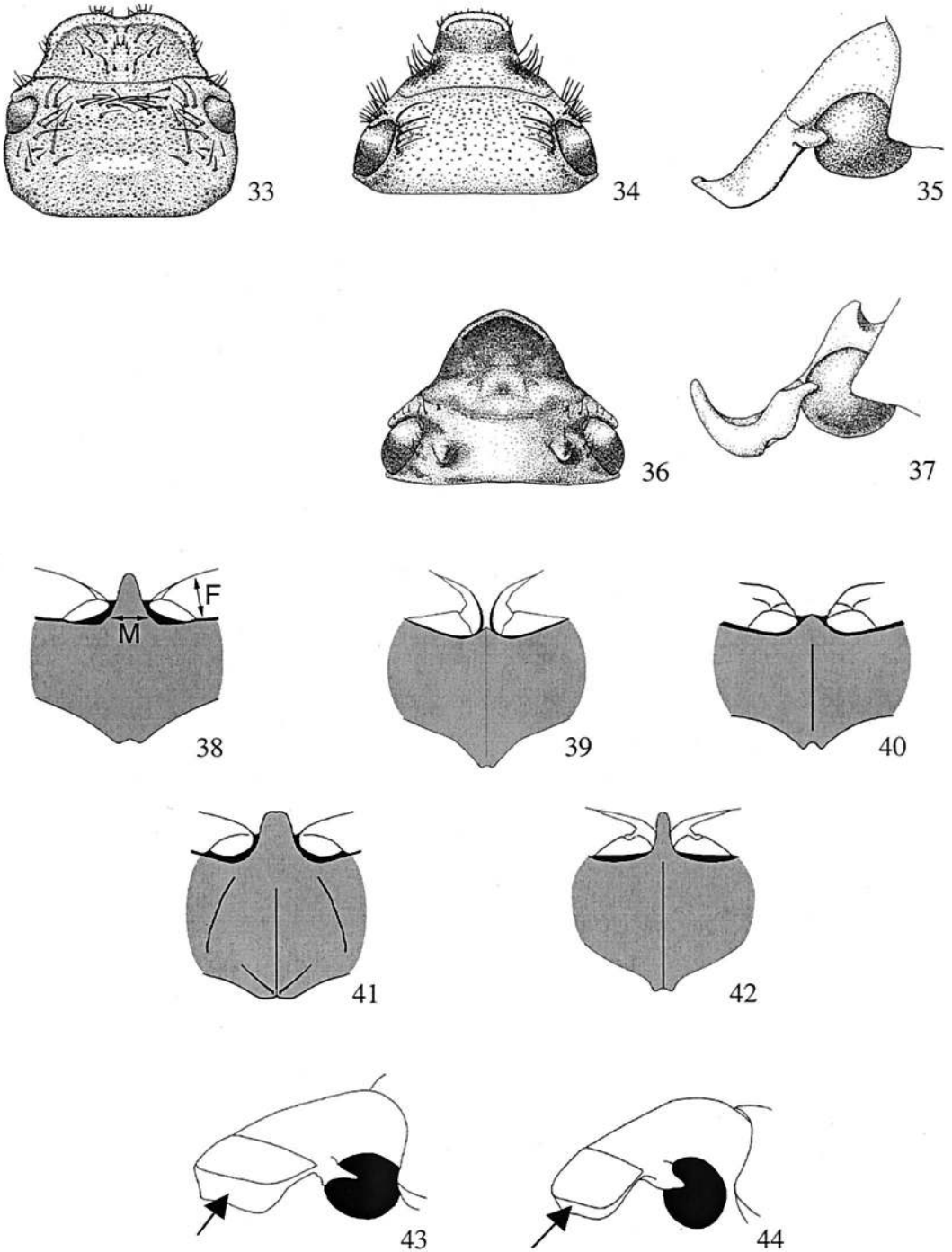
Overview of New World Anomaliini Genera

Subtribe Anomaliina Mulsant, 1842

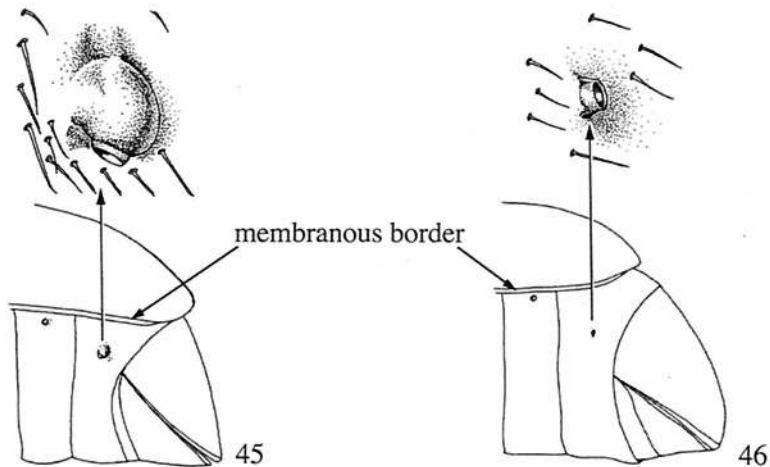
*Anomala* Samouelle, 1819

- Phyllopertha* Stephens, 1830
- Pachystethus* Blanchard, 1851
- Blitopertha* Reitter, 1903
- Exomala* Reitter, 1903
- Anomalepta* Casey, 1915
- Anomalopus* Casey, 1915
- Hemispilota* Casey, 1915
- Oliganomala* Casey, 1915
- Paranomala* Casey, 1915
- Rhombonalia* Casey, 1915
- Anomalopides* Strand, 1928

The genus *Anomala* (e.g., Fig. 1e) contains a heterogeneous assemblage of species and is in serious need of taxonomic study. Worldwide, the genus includes ≈1,000 species: 180 species are recorded in the New World (Machatschke 1972–1974); 48 species are recorded in the Nearctic realm (Smith 2002); 75 species are recorded in Mexico (Morón et al. 1997); and Bates (1886–1890) cited 106 species from Central America. A worldwide revision of the genus has never been conducted. Based on a preliminary examination



Figs. 33–44. Characters of anomalines. Form of head in *Dilophochila* (Fig. 33), *Callirhinus* (Fig. 34: dorsal view; Fig. 35: lateral view), *Anomalorhina* (Fig. 36: dorsal view; Fig. 37: lateral view); form of mesosternum in *Popillia* (Fig. 38), *Anomala* (Fig. 39), *Epectinaspis* (Fig. 40), *Strigoderma* (Fig. 41), and *Callistethus* (Fig. 42); and head, frontolateral view with arrows indicating height of clypeal apex in *Nayarita* (Fig. 43) and *Yaaxkumukia* (Fig. 44).



Figs. 45 and 46. Lateral view of abdomen showing form of terminal spiracle (enlarged) in *Yaaxkumukia* (Fig. 45) and *Callistethus* (Fig. 46).

of the phylogeny of the Anomalini (M.L.J., unpublished data), the genus is paraphyletic, and many species are more appropriately placed in other genera. In his discussion of the taxonomy of the genus *Anomala*, Potts (1974) stated that it "... is obvious that a number of the proposed groupings were without true value from their inception, merely following in the mold of an early-day taxonomy that regarded any large genus as unmanageable until infinitely divided, no matter how precariously." Species-level taxonomic treatments for *Anomala* include Bates (1886–1890; Mexico and Central America, 110 species, lacking key), Arrow (1917; India, 180 species, with key), Paulian (1959; French Indochina, 78 species, with key), and Potts (1977; United States and Canada, 35 species, with key). Adults are diurnal or nocturnal and feed on foliage and flowers (including the florets of grasses). Adults of many species are readily attracted to lights at night. Body length ranges from 5 to 30 mm. In the Nearctic region,  $\approx 20\%$  of the larvae of *Anomala* are described (Ritcher 1966). In the New World, however, probably  $<5\%$  of the larvae of *Anomala* are known and described. Larvae are important recyclers and are found in logs, compost, and under dried cow dung. Some species of larvae are pests of small grain products (corn, wheat, oats, etc.). In Mexico, Central America, and northern South America, larvae are referred to as "gallina ciega" or "joboto," a group of agriculturally important larvae.

The oriental beetle, *Anomala orientalis* (Waterhouse), was accidentally introduced from Japan and became established in the United States before 1920 (Ritcher 1966, Capinera 2002). It is distributed throughout the eastern United States and is of considerable economic importance as a turfgrass pest. Controversy and confusion have surrounded the generic placement of *A. orientalis*. This species was described in the genus *Phyllopertha* and has been transferred in and out of the genera or subgenera *Anomala*, *Exomala* Reitter, and *Blihoppertha* Reitter. This insta-

bility is caused by a poor taxonomic foundation in the group as well as differing generic concepts among taxonomists. Based primarily on the form of the male copulatory apparatus, Baraud (1991) elevated *Exomala* from a subgenus of *Blihoppertha* to generic rank. Since the time of Baraud's publication, the species has been referred to as *Anomala orientalis* (e.g., Zhang et al. 1994, Cowles and Villani 1996, Koppenhofer et al. 1999) as well as *Exomala orientalis* (e.g., Leal et al. 1994, Alm et al. 1999, Facundo et al. 1999, Choo et al. 2002). Before Baraud's publication, most literature referred to the species as *Anomala orientalis* (e.g., Dunbar and Beard 1975, Baker 1986, Staines 1986, Wang et al. 1987, Bai et al. 1991). According to Piatella and Sabatinelli (1994), the taxonomic position of *Exomala* (as a genus, subgenus, or synonym) is questionable because of a lack of modern systematic foundation of the Anomalini, and *Exomala* is probably polyphyletic. Based on the fact that *Exomala* is poorly characterized and poorly circumscribed and because it may be within the scope of the genus *Anomala*, we conservatively consider the taxon a synonym of *Anomala*. Thus, rather than *E. orientalis*, we use the combination *A. orientalis*.

#### *Anomalorhina* Jameson, Paucar-Cabrera, and Solís, This Paper

This genus includes two species: *A. turrialbana* (Figs. 1a, 1b, and 2) from Costa Rica and Nicaragua and *A. osaensis* (Figs. 1c, 1d, 3, and 4) from the Osa Peninsula in southern Costa Rica. Members of the genus *Anomalorhina* are recognized by the pronotal disc of males with moderately depressed fovea from apex to middle of pronotum (Figs. 2 and 3), clypeal apex abruptly reflexed (males) or moderately reflexed (females) (Figs. 5 and 6), pronotum with apical marginal bead produced posteriorly at middle and V-shaped in females (Fig. 4), frontoclypeal suture

obsolete medially, and poorly defined at the margin. Males of *A. turrialbana* have two tubercles at the base of the frons (Figs. 2, 5, and 6). Body length ranges from 10 to 14 mm. Adults were attracted to benzyl acetate traps that were placed high in the forest canopy. Specimens were recorded from 200 to 800 m. Larvae are not known.

### *Callistethus* Blanchard, 1851

*Spilota* Burmeister, 1844

Based on the classification of Machataschke (1957, 1972–1974), the genus *Callistethus* (e.g., Fig. 1f) is comprised of  $\approx 130$  species, and  $\approx 60$  of these are distributed in the New World. *Callistethus marginatus* (Fabricius) (often considered as *Anomala marginata*) is the only species that is distributed in the United States. Seven species of *Callistethus* are recorded in Mexico (Morón et al. 1997, Morón and Nogueira 2002). Monophyly and validity of the genus, especially of New World species, is debatable. Some authors who have worked on New World anomaline taxa consider *Callistethus* to be a synonym of *Anomala* (Bates 1886–1890, Blackwelder 1944, Potts 1974). This may be symptomatic of the probable paraphyly of the genus *Callistethus* (some species that are currently placed in the genus *Callistethus* are more appropriately placed in *Anomala*). Morón and Nogueira (2002) consider the taxon valid and noted some species of *Anomala* that are more appropriately placed in the genus *Callistethus*, but they delayed transferring the species until a more thorough study of New World anomalines is conducted. Until a phylogenetic study of world Anomalini is conducted, the question of paraphyly in the *Callistethus* (as well as *Anomala*) cannot be reasonably assessed. As described here, members of the genus *Callistethus* are recognized by a mesometasternal process that is produced beyond the apex of the mesocoxae (often produced to the procoxae [Fig. 42]), concealed mesepimeron (e.g., Fig. 26), lack of a tuberculate terminal spiracle in the male (tubercle present in *Yaaxkumukia* [Fig. 45]), clypeus not reflexed, and maxilla with six teeth. These character states uphold the genus as we define it. Body length ranges from 11 to 23 mm. Adults of some species are readily attracted to lights at night, while others are diurnal and are found on flowers and foliage. The larva of *C. marginatus* is described (Ritcher 1966).

### *Chelilabia* Morón and Nogueira, 1999

This genus includes only one species, *C. piniphaga* Morón and Nogueira (Fig. 1g), from the states of Mexico and Guerrero in Mexico. Members of the taxon are recognized by the unique form of the labrum and mentum, both of which are deeply emarginate at the apex (Figs. 27 and 30). In addition, the labrum projects beyond the apex of the clypeus (Fig. 27). Body length ranges from 12 to 13 mm. Members of the species are known to feed on the foliage of *Pinus* species (from which the species name is derived). Morón and Nogueira (1999) hypothesized that the

emarginate form of the labrum and mentum enabled feeding on pine needles. Members of the genus *Dilophochila* share the emarginate form of the labrum with the genus *Chelilabia*, but the emargination is more pronounced in *Chelilabia* and the labrum is hidden in *Dilophochila* (Fig. 27 versus Fig. 33). Adults have been collected at lights at night and on the needles of *Pinus pringleii* Shaw during the day (Morón and Nogueira 1999). Larvae are not known.

### *Epectinaspis* Blanchard, 1851

*Epectinaspis* (e.g., Fig. 1h) is a neotropical genus with its species distributed from southern Mexico to northern Venezuela at elevations ranging from 10 to 2,500 m. This genus is comprised of nine species (Paucar-Cabrera 2003), and its species are characterized by a mesepimeron that is partially visible anterior to the base of the elytron (in dorsal view; Fig. 23), a mesometasternum that is not produced anteriorly beyond the base of mesocoxae (Fig. 40), males with apex of clypeus moderately reflexed, maxilla with six teeth, mandible with two small, sharp teeth (second tooth bifid), and anterior angles of pronotum covering posterior one-third of eye. Phylogenetic analyses (Paucar-Cabrera 2003) demonstrated that the genus *Epectinaspis* was paraphyletic, and species were included in two clades: the “*Epectinaspis* clade” (with nine species) and an “undescribed clade” which represented a new genus of Anomalini (with one species of *Epectinaspis* transferred into this new taxon). Phylogenetic analyses showed that *Strigoderma* is the sister group of *Epectinaspis* (Paucar-Cabrera 2003). Morphological character examination revealed that *Strigoderma* species are distinguished from *Epectinaspis* species by the following characteristics: mesepimeron subtriangular and weakly exposed beyond elytra in *Epectinaspis* (Fig. 23), subrectangular and well exposed in *Strigoderma* (Fig. 24); surface of elytra evenly rounded in *Epectinaspis*, flattened in *Strigoderma*; and mesosternal intercoxal region less than one-fourth width of base of mesofemur in *Epectinaspis* (Fig. 40), as opposed to subequal in width to base of mesofemur in *Strigoderma* (Fig. 41). Species of *Epectinaspis* are diurnal and are found on flowers and vegetation. The feeding habits of adults of some species have been documented but remain unknown for most species. Specimens of *Epectinaspis mexicana* (Burmeister) feed on exudates of flowers of *Hibiscus rosa-sinensis* Linnaeus (Malvaceae) (Morón and Nogueira 1999). *Epectinaspis* larvae are unknown; however, Morón et al. (1997) reported that larvae of *E. mexicana* live in the soil, but their food source is unknown.

### *Mazahuaptertha* Morón and Nogueira, 1999

The genus includes only one species, *M. tolucana* (Bates) (Fig. 1i), from the state of Mexico in Mexico. Bates (1886–1890) originally placed the species in the genus *Phyllopertha*. Morón and Nogueira (1999) created the genus *Mazahuaptertha* based on the following

characteristics: absence of a protibial spur (Fig. 17; shared with *Leptohoplia*), form of the mandibles (apex wide and bidentate, molar area reduced), antennal club 1.4 times longer than six preceding segments, mesepimeron weakly exposed anterior to elytral base, and small size ( $\approx 8$  mm). Based on the form of the pronotum, elytral border, and form of the pro- and mesotarsal claws, Morón and Nogueira (1999) stated that the taxon may be related to *Cyriopertha* Reitter and *Cyriopertha* (*Apleopertha*) Semenov, genera that are distributed from Siberia to Turkey. The species is only known from the original type series. Larvae are not known.

#### *Nayarita* Morón and Nogueira, 1999

This genus includes one species, *N. viridinota* Morón and Nogueira (Fig. 1j), from Nayarit state in Mexico. Members of the genus are recognized by the following characteristics: pronotum finely rugopunctate and shining green, elytra testaceous and regularly striate, mesometasternal process weakly produced beyond the apex of the mesocoxae, large size (nearly 17–19 mm), lateral margin of elytron weakly produced, and clypeus in frontal view flattened. Based on many shared characters, the taxon is probably closely related to *Anomala* and *Callistethus* (Morón and Nogueira 1999). The species is known to inhabit subhumid oak forest from 1,000 to 2,240 m elevation (Morón and Nogueira 1999). Adults are attracted to lights at night. Larvae are not known.

#### *Phyllopertha* Stephens, 1830

*Phyllopertha latitarsis* Nonfried was described in Honduras, and it is the only New World representative of this genus. In the Old World, *Phyllopertha* species are distributed from Europe to China and Japan. The genus includes  $\approx 30$  species. *Phyllopertha horticola* Linnaeus is economically important in Europe and causes damage to horticultural plants (Smits et al. 1994). We have searched for the type of *P. latitarsis* in institutions across Europe, but we were unable to locate it. Based on Nonfried's description (Nonfried 1891), the species has the following notable characteristics: color shining reddish-brown and surface glabrous, venter sparsely setose, antenna nine-segmented with an elongated club, elytra with parallel costae and strongly punctate, pygidium shining and finely punctate, tarsi at the middle extremely wide and flat, claws long and not split at the apex, and length  $\approx 14$  mm. It is possible that (1) this species should more appropriately be assigned to another anomaline genus (perhaps *Anomala* or *Strigoderma*), (2) that this species should be assigned to another ruteline genus (not necessarily an anomaline genus), or (3) that this species is a member of the genus *Phyllopertha*. Because Nonfried (1891) also described the recently rediscovered *R. sericeomicans* in the same publication and from the same country (Honduras), we have hopes that a specimen matching the above description and specimens from the type series will surface in the near

future. Lacking type specimens for examination or any specimens identified by Nonfried that bear this species name, we consider the taxon *Incertae sedis*.

#### *Rugopertha* Machatschke, 1957

*Rugopertha sericeomicans* (Nonfried) (Fig. 1k) is the only member of this genus. This taxon was recently rediscovered because of collecting efforts in Honduras. The species is known only from north-central Honduras (Cortes, Olancho, and Yoro states). The species was originally described in the genus *Phyllopertha* by Nonfried (1891), and then it was transferred to the genus *Rugopertha* by Machatschke (1957). The species resembles *Strigoderma* because of its elongate body form and exposed mesepimeron. Because of the finely rugopunctate surface of the elytra, it is most similar to Bader's (1992) *S. costulipennis* group (Bader refers to the elytra surface as "granular"). However, *Rugopertha* is separated from *Strigoderma* because of the surface of the pronotum that is very finely rugopunctate (punctate in *Strigoderma*) and the elytral surface that is finely rugopunctate (elytra with punctate striae, with raised ridges, or entirely smooth in *Strigoderma*). Phylogenetic analysis may demonstrate that *Rugopertha* is a member of the *Strigoderma* clade. Dorsal color of *R. sericeomicans* is shiny green or tan and green. Body length is  $\approx 12$  mm. The species inhabits forest at  $\approx 1,500$  m elevation with dominant tree species of pine, oak, laurel, and liquidambar. Adults are probably diurnal and found on vegetation. Larvae are not known.

#### *Strigoderma* Burmeister, 1844

*Alamona* Casey, 1915

*Strigoderma* Casey, 1915

The genus *Strigoderma* is distributed from Canada to South America and includes  $\approx 40$  species (e.g., Fig. 1l). Thirty species occur from North America to Panama (Bader 1992, Katbeh-Bader 2000). Morón et al. (1997) recorded 18 species in Mexico, and 8 species occur in South America (Machatschke 1972–1974). Bader (1992) revised the species north of Panama, thus providing a foundation for revising the entire genus. Potts (1974) believed that the genus was poorly characterized and should include Asian species. Bader (1992) stated that the genus was probably paraphyletic or polyphyletic, and Paucar-Cabrera (2003) obtained additional character data that demonstrated that the genus is paraphyletic (some species of *Anomala* are more appropriately placed in the genus *Strigoderma*). Additional studies will be necessary to resolve these problems. Based on the current concept, members of the genus are characterized by a mesepimeron that is partially visible anterior to the base of elytra in dorsal view (Fig. 24), well-developed elytral striae, the mesosternal intercoxal region that is subequal in width to base of mesofemur (Fig. 41), and clypeus sub-trapezoidal with a narrowly reflexed apex. *Strigoderma* species are similar to *Epectinaspis*, but are separated by characters of the mesepimeron, meso-

metasternum, and elytra (see *Epectinaspis* section above). Body length ranges from 4 to 15 mm. Species in the genus range from 50 to 2,700 m elevation. Adults are diurnal and nocturnal and are found on a wide variety of flowering plants and foliage. Adults of *S. arboricola* (Fabricius) are encountered on many flowering plants including roses (Bader 1992). This species has been implicated in causing damage to several crops, including peanuts (Miller 1943). Larvae of *S. arboricola* and *S. pygmaea* (Fabricius) are described (Ritcher 1966). Larvae of *S. arboricola* are known to be parasitized by the nematode *Neoplectana glaseri* Steiner (Steinernematidae) (Poinar 1978).

#### *Yaaxkumukia* Morón and Nogueira, 1999

One species, *Y. ephemera* Morón and Nogueira (Fig. 1m), is described from southern Mexico (Chiapas state), western Guatemala (San Marcos and Zacapa states), and western Honduras (Ocotepeque state). Members of the taxon are bright, shiny green; the mesometasternal projection is produced anteriorly to near the procoxae (e.g., Fig. 42); the pronotum is not beaded at the apex or base; and the posterior spiracle is weakly tuberculate in the male (Fig. 45). Body length ranges from 14 to 15 mm. The taxon is probably closely related to *Anomala* and *Callistethus* (Morón and Nogueira 1999) with which it shares many character states. Phylogenetic analysis may demonstrate that *Yaaxkumukia* is a member of either the *Anomala* and/or *Callistethus* clade. The species is found in forests between 1,500 and 2,300 m elevation (Morón-Ríos and Morón 2001). Adults are attracted to lights at night. Larvae are not known.

#### Subtribe *Anisopliina* Burmeister, 1844

##### *Anomalacra* Casey, 1915

*Anomalacra* is a monotypic genus that includes only *A. clypealis* (Schaeffer) (Fig. 1n), and it occurs in Arizona and northern Mexico. Members of the genus are recognized by their parabolic clypeus (Fig. 29), labrum that is entirely hidden beneath the clypeus, and hidden mesepimeron. Body length ranges from 7 to 9 mm. The genus was created by Casey (1915) for *Anomalacra cuneata* Casey from northern Mexico. Howden (1955) later described *Anomalacra werneri* from Arizona. Potts (1974) synonymized *A. cuneata* with *Anomala clypealis* Schaeffer but did not discuss *A. werneri*. *A. werneri* was synonymized with *A. clypealis* by Hardy (1991). Thus, the genus includes only one valid species, *A. clypealis*. Potts (1974) placed the genus *Anomalacra* near the genera *Callirhinus* and *Anisoplia* Fischer (an Old World genus) in the subtribe *Anisopliina* based on the "thinned" form of the clypeus and the "thinned" and reduced labrum. Little is known about the natural history of the species. Adults are attracted to lights at night. Larvae are not described.

#### *Callirhinus* Blanchard, 1851

The polychromatic species *C. metallescens* Blanchard (Fig. 1o) is the sole member of its genus. Its distribution in western Mexico is considered relictual (Morón et al. 1997). The taxon is easily recognizable because of its produced and up-turned clypeal apex (Figs. 34 and 35) and metallic coloration. Members of the species vary greatly in color and include black, green, orange, and yellow (Morón and Hernández-Rodríguez 1996). Body length ranges from 9 to 13 mm. Adults are diurnal and feed on a variety of foliage including *Hibiscus* spp. and sugar cane (Morón and Hernández-Rodríguez 1996) as well as grass and floral parts. Larvae are not known.

#### Subtribe *Dilophochilina* Morón and Howden, 2001

##### *Dilophochila* Bates, 1888

The genus *Dilophochila* (e.g., Fig. 1p) is the only member of the subtribe and includes six species that are distributed in southern Mexico, Guatemala, and Honduras (Morón and Howden 2001). Members of the genus are recognized by their bilobed clypeal apex that is notched in the middle (Fig. 33) and the bilobed labrum that is hidden beneath the clypeus (Fig. 32). Among the Anomalini, the genus is most similar to *Chelilabia*, but it can be separated based on the form of the labrum (produced beyond the apex of clypeus in *Chelilabia* [Fig. 27]; hidden under the clypeus in *Dilophochila* [Fig. 33]). Body length ranges from 8 to 12 mm. Species of *Dilophochila* feed on pine and are collected by beating vegetation during the day (Morón and Howden 2001). They are distributed in high, humid forests from 1,800 to 2,600 m elevation (Morón and Howden 2001). Larvae are not known.

#### Subtribe *Leptohopliina* Potts, 1974

##### *Leptohoplia* Saylor, 1935

The genus currently includes only one species from California: *L. testaceipennis* Saylor (Fig. 1q). We believe that a few species of North American *Anomala* are more appropriately placed in this genus based on a number of shared characters, and our future research will address this. Members of the genus are distinctive for the reduced claws on the hind tarsi (some specimens have only one apparent claw), the thickened clypeal apex (in frontal view), and the nearly obsolete epipleuron (Potts 1974). Body length ranges from 5 to 7 mm. Based on the form of the claws, this taxon was originally placed in the Melolonthinae near the tribe Hopliini (which is characterized by having only one hind claw). Howden and Hardy (1971) hypothesized that the taxon may be closely related to *Anomala* (referred to as *Rhombonalia* Casey in their publication). Based on shared characters with other Anomalini (position of the terminal spiracle, membranous border at lateral margin of elytra, bidentate protibia, and nine-segmented antennal), we agree with placement of the genus in the Anomalini. Two



reductions or symplesiomorphs are noted: inner prothibial spur lacking (Fig. 17; shared with *Mazahua-pertha*) and reduced claws on the hind tarsi. Preliminary molecular phylogenetic analyses by Hawks et al. (2003) also support the genus as a member of the Anomalini. *Leptohoplia testaceipennis* inhabits sand dune areas in California and is a strong burrower. This action may account for wear on legs, tarsi, and claws (Howden and Hardy 1971). Hardy and Andrews (1986) recorded additional information about the natural history of the species. They stated that adult males are active from the late afternoon to evening, during which time they fly a few centimeters above the surface of the dune in search of females. Females are larger and emit pheromones that attract a large number of males. Adults are attracted to lights at night but frequently land near the light and then rapidly take flight again. Adults are preyed on by antlions (*Bradynemurus* spp.; Myrmeleontidae) and sand crickets (*Macrobaenetes* spp.; Rhaphidophoridae). Larvae are not known.

#### Subtribe *Popilliina* Ohaus, 1918

##### *Popillia* Dejean, 1821

Worldwide, the genus *Popillia* includes  $\approx 250$  species. The Japanese beetle, *P. japonica* Newman (Fig. 1r), was accidentally introduced from Asia into New Jersey in the roots of nursery stock in  $\approx 1911$  (Potter and Held 2002). The species has expanded its range from the eastern regions (including Ontario and Quebec, Canada) to as far west as Nebraska in the United States (Ratcliffe 1991). Infestations in southern California from 1961 to 1985 were controlled by chemical eradication (Potter and Held 2002). Destruction attributed to this pest total more than \$450 million each year (Potter and Held 2002). *P. japonica* is the only New World representative of the subtribe *Popilliina*, which is comprised of 14 genera and  $\approx 320$  species that are distributed in the Old World (Machatschke 1972–1974). Adults of *P. japonica* are easily recognized because of their bright, metallic green head and thorax, metallic brown to copper elytra, and white setal patches on either side of the abdomen. Additionally, this is the only New World anomaline with a trimarginate pronotal base (Fig. 25) and produced mesometasternal projection (Fig. 38). Body length for *P. japonica* ranges from 9 to 13 mm. Adults feed on over 275 plant species (Hawley and Metzger 1940) and are severe pests of fruits and vegetables, field and forage crops, tobacco, and ornamental plants (Fleming 1972). Tell-tale damage of *P. japonica* beetles is skeletonized leaves. Beetles are often found in great numbers and often in aggregations. Larvae feed on various plant roots including ornamentals, grasses (including turfgrass), and vegetables. Larvae of *P. japonica* were described by Ritcher (1966).

#### Acknowledgments

We thank Hella Wendt (ZMHB), Bill Warner (Chandler, AZ), François Génier and Henry Howden (CMNC), Yves Bousquet (Canadian National Insect Collection), Roberta

Brett and Keve Ribardo (CASC), Ron Cave (EAP, Zamorano, Honduras; now at Ft. Pierce, FL), Brett Ratcliffe (Brett Ratcliffe collection, Lincoln, NE), Jean Michel Maes (Jean Michel Maes Collection, Leon, Nicaragua), and Robert Turnbow (Robert Turnbow Collection, Fort Rucker, GA) for loans of representative taxa for this research. We thank the United States National Museum for the loan of all "higher scarabs" to the University of Nebraska State Museum for off-site enhancement. Angie Fox (UNSM) is thanked for her excellent habitus illustrations. The manuscript was improved because of comments and contributions by Brett Ratcliffe, Andrew Smith, Federico Ocampo, Matt Paulsen (all UNSM), and Charles Brodel (USDA-APHIS-PPQ, FL). This research was supported by NSF-PEET (DEB-9712447) to B. C. Ratcliffe and M. L. Jameson and NSF-PEET (DEB-0118669) to M. L. Jameson and B. C. Ratcliffe.

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Received for publication 15 August 2002; accepted 30 January 2003.

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