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REVISION, PHYLOGENY AND BIOGEOGRAPHY OF THE GENERA *PARABYRSOPOLIS* OHAUS AND *VIRIDIMICUS*, NEW GENUS (COLEOPTERA: SCARABAEIDAE: RUTELINAE)

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ABSTRACT

The North American genus *Parabyrsopolis* is redefined, and a sister genus, *Viridimicus*, is established to accommodate those species from southern Mexico to Guatemala previously placed in *Cotalpa* or *Parabyrsopolis*. *Parabyrsopolis* is now monotypic, and four new species (of six) in the genus *Viridimicus* are described from Mexico: *V. cyanochlorus*, *V. impunctatus*, *V. ratcliffei*, and *V. unitus*. A key to the species of *Viridimicus*, as well as keys to the tribes of Rutelinae, subtribes of Rutelini, and genera of Areodina are presented. Phylogenetic hypotheses (based on cladistic methodology) and biogeographic hypotheses (based on vicariance and dispersal events) for the genera of Areodina and species of *Viridimicus* are presented.

RESUMEN

En este trabajo se redefine el género norteamericano *Parabyrsopolis* y se describe a *Viridimicus* para agrupar a las especies del Sureste de México y Guatemala que con anterioridad estaban incluídas en *Cotalpa* o en *Parabyrsopolis*. *Parabyrsopolis* queda ahora como un género monotípico, mientras que *Viridimicus* agrupa a seis especies, cuatro de ellas nuevas que aquí se describen de México: *V. cyanochlorus*, *V. impunctatus*, *V. ratcliffei*, y *V. unitus*. Se presenta una clave para separar las tribus de Rutelinae, las subtribus de Rutelini, los géneros de Areodina y las especies de *Viridimicus*. Se propone una hipótesis sobre la filogenía (utilizando métodos cladísticos) de los géneros de Areodina y las especies de *Viridimicus* reconocidos. Asi como hipótesis biogeográficás basadas en eventos de vicariancia y dispersión de los Areodina y el genero *Viridimicus*.

The nomenclatural legacy of the genus *Parabyrsopolis* has been beset with complications and disorder since its establishment in 1915 by Ohaus. The reasons for this stemmed from two sources: (1) the lack of a systematic study of the genera *Byrsopolis*, *Cotalpa*, *Parabyrsopolis*, and *Paracotalpa* [all regarded as subgenera of *Cotalpa* by Ohaus (1915)] and (2) the nearly concurrent creation of *Parabyrsopolis* (Ohaus 1915, July) and *Parareoda* (Casey 1915, November) for conspecific taxa. The confusion was amplified due to the rarity of specimens. Historically, members of putative species in the genus *Parabyrsopolis* have been variously placed by systematists. Leng (1920) used *Parareoda* although *Parabyrsopolis* had priority. Blackwelder (1944) amalgamated *Byrsopolis*, *Parabyrsopolis*, and *Ciocotalpa* under *Cotalpa*; in doing so, he did not even recognize the name *Parareoda*. Arnett (1968) recognized the genus *Parabysopolis* (*sic*), as well as *Byrsopolis* and *Parareoda* as synonyms of *Paracotalpa*. Nomencla-

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tural instability is exemplified in collections where the same groups of species are called *Parareoda, Byrsopolis, Cotalpa, Paracotalpa, Parabyrsopolis,* or *Parabysopolis* (*sic*). To resolve these systematic and nomenclatural problems, a broader, more inclusive study was necessary. Through examination of the areodine taxa, it became apparent that *Parabyrsopolis sensu* the user community was a hodge-podge of two groups; hence, *Viridimicus* is here established to accommodate the unnamed assemblage in the Areodina.

Evolutionary relationships of the Areodina and the genus *Viridimicus* are presented in terms of a phylogenetic reconstruction using cladistic methods. A biogeographic analysis using both vicariance and dispersal paradigms is provided for the species of *Viridimicus.*

METHODS AND DEFINITION OF TAXONOMIC CHARACTERS

Examination of 582 specimens, including all type material, from 40 institutions and private collections formed the foundation for this study. The collection acronyms used are those of Arnett and Samuelson (1986). Field work was conducted in southern Arizona and in Chiapas, Mexico. Collecting techniques involved examination of vegetation in favorable forested areas, collecting at light traps (mercury vapor and blacklight), and inspection of rotting logs for immature stages. Live specimens of *Parabyrsopolis* were maintained in the laboratory in attempt to ascertain feeding habits and other natural history information.

Descriptions and keys were constructed using characters and character states that expressed a low level of variability. Several characters historically used in the definition of *Parabyrsopolis* proved to vary considerably. These characters are discussed, but were not used to separate species. The following characters were found to be taxonomically and/or phylogenetically useful:

Measurements: Length was measured from the apex of the clypeus to the apex of the elytra. Two width measurements were taken: (1) across the humeri and (2) greatest width across the elytra.

Punctures: Punctures are defined as large (easily seen without magnification; .17 mm and larger), moderately large (.17–.085 mm), moderate (.085–.034 mm), and small (.034 mm and smaller). Millimeter increments were assessed by using an ocular micrometer.

Puncture density: Punctures are considered dense if they are nearly confluent to less than two puncture diameters apart, moderate if punctures are between 2–6 puncture diameters apart, and sparse if the punctures are separated by more than six puncture diameters.

Color: Unless noted, color is interpreted as viewed by the naked eye. Under magnification and illumination, epicuticular colors (especially metallics) become more diffuse, revealing the darker cuticular layers.

Interocular width: This is defined as the number of transverse eye diameters spanning the interocular gap (vertex).

Head profile: The relative declivity of the clypeus with respect to the frons (in lateral view) is a useful character in *Viridimicus* (Figs. 21–25).

Apex of third anterior tarsomere: In ventral view, this may either be emarginate with a short, stout seta within the emargination (thus being bilobed, see Fig. 19) or entire (Fig. 20).

Clypeal shape: Although this character has been used by several authors for species separation (Bates 1888; Ohaus 1915, 1934; Casey 1915; Morón 1976),
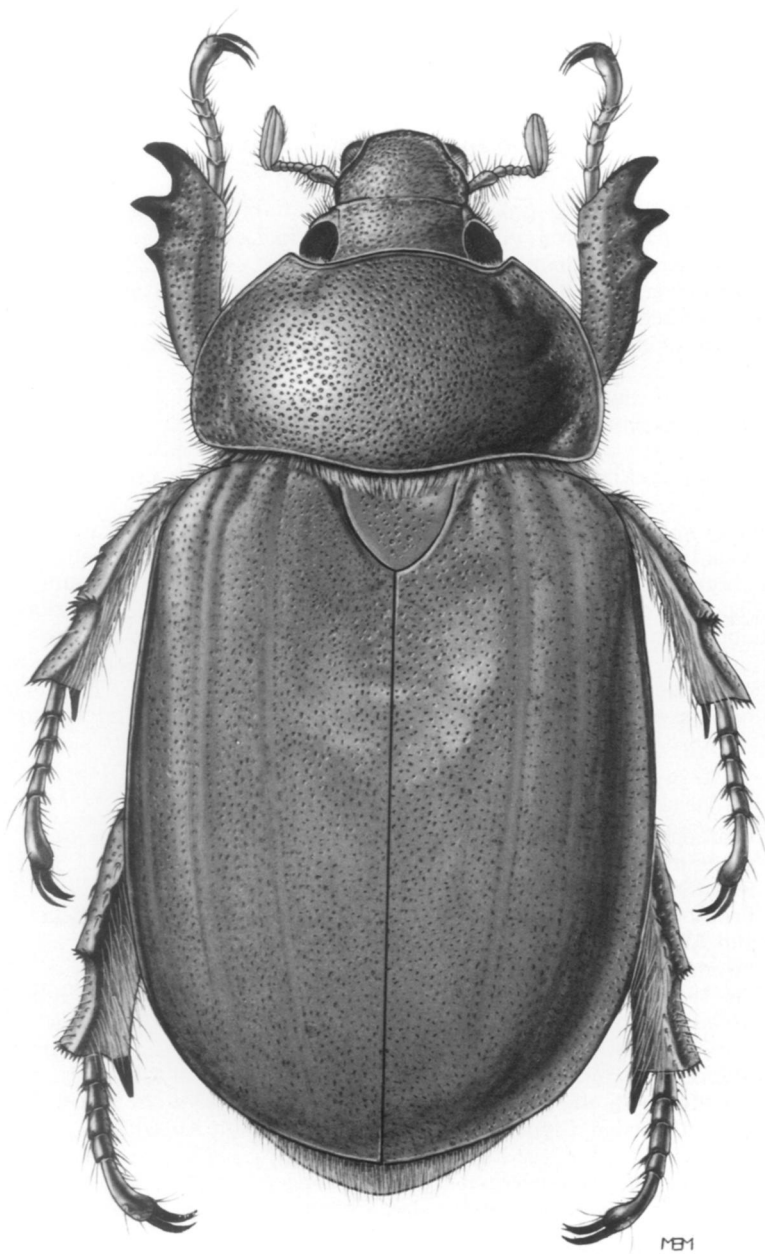
Fig. 1.   *Parabyrsopolis chihuahuae* (Bates), dorsal habitus.

this character is inconsistent in *Parabyrsopolis.* In this monotypic genus, clypeal shape varies from apically truncate, to rounded, to weakly sinuate (Fig. 17).

Genitalia: The parameres are not diagnostic at the specific level because of similarity.

<div align="center">

KEY TO THE TRIBES OF RUTELINAE
(modified from Ohaus 1934)
</div>

1. Labrum horizontally produced with respect to clypeus (Fig. 2), distinctly separated from clypeus by a suture (in *Lagochile* and *Chasmodia,* labrum indistinctly fused to clypeus) 2
1'. Labrum vertically produced with respect to clypeus (Fig. 3) and more or less fused to clypeus 3
2. Margin of elytra with membranous border. Antenna 9-segmented .. .. Anomalini
2'. Margin of elytra without membranous border. Antenna 10-segmented [exceptions: *Parachrysina* (Areodina), *Eremophagous* (Pelidnotina), *Pseudogeniates richterianus* female (Pelidnotina)] .... Rutelini
3. Mentum and labrum each with median apical tooth (or projection) (Fig. 4) 5
3'. Mentum lacking apical tooth or projection, labrum with or without apical tooth (or projection) (Figs. 5, 6) 4
4. Labrum with median apical projection, apex overhanging mentum (Fig. 5) [exception: *Prodoretus* (Adorrhinyptiina)] .... Adoretini
4'. Labrum and mentum both entire, lacking median apical projection (Fig. 6) .... Spodochlamini
5. Foretarsi enlarged in males only or in males and females .... Geniatini
5'. Foretarsi not enlarged in males or females .... *Anoplognathini*

<div align="center">

KEY TO THE SUBTRIBES OF RUTELINI
(modified from Ohaus 1934)
</div>

1. Frontoclypeal suture complete, separating frons from clypeus [obsolete medially in *Paracotalpa deserta* (Areodina)] 2
1'. Frontoclypeal suture obsolete medially or lacking 5
2. Frontoclypeal suture usually straight or slightly bowed. New World and Africa 3
2'. Frontoclypeal suture raised laterally, produced posteriorly in middle. Indochina .... Didrepanophorina
3. Mandibles externally broadly rounded, without a well-developed, preapical tooth .... Areodina
3'. Mandibles externally with a well-developed, preapical tooth 4
4. Antenna with club twice as long as stem. Mandible without teeth on cutting edge. Clypeus with apex pointed. South America .... Acrobolina
4'. Antenna with club subequal to or a little longer than stem. Mandible with 2 or 3 teeth on cutting edge. Clypeus with apex truncate or subparabolic. Mexico and Central America .... Heterosternina
5. Pronotum with basal bead complete (obsolete in *Pelidnota polita*) 6
5'. Pronotum with basal bead medially effaced or completely lacking 7
6. Claws simple on all legs .... Pelidnotina

6'. Larger claw cleft on all legs .... Lasiocalina
7. Frontoclypeal suture obsolete medially, elevated laterally .... Parastasiina
7'. Frontoclypeal suture lacking or nearly obsolete, laterally elevated
    or not 8
8. Clypeus constricted basally, apex trilobed and reflexed .. Desmonychina
8'. Clypeus with sides parallel, anterior angles rounded, apex subtrian-
    gular or parabolic 9
9. Apex of metatibia without spinules on ventrolateral edge (Fig. 7)
    .... Rutelina
9'. Apex of metatibia with spinules on ventrolateral edge (Fig. 8) 10
10. Mandibles of males greatly enlarged, sickle-shaped. Asia ....
    .... Fruhstorferiina
10'. Mandibles of both sexes similar, not enlarged. South America and
    Central America .... Antichirina

KEY TO THE GENERA OF AREODINA

1. Apex of metatibia with more than 10 spinules. Mandibles entirely
   rounded, not sickle-shaped. North America to South America 2
1'. Apex of metatibia with fewer than 10 spinules. Mandibles sickle-
    shaped. Africa .... Xenoproctis
2. Antenna 10-segmented 3
2'. Antenna 8- or 9-segmented .... Parachrysina
3. Mesosternum with keel extending anteriorly beyond mesocoxae 4
3'. Mesosternum without keel extending beyond mesocoxae 5
4. Clypeus in ventral view extending past labrum; weakly trilobed api-
   cally in male, rounded apically in female .... Oplognathus
4'. Clypeus in ventral view not extending past labrum, rounded apically
    in male and female .... Areoda
5. Antenna with club twice as long as segments 2–7 combined .... Byrsopolis
5'. Antenna with club shorter than or subequal to segments 2–7 com-
    bined 6
6. Terminal segment of maxillary palpus as long or longer than antennal
   club .... Pseudocotalpa
6'. Terminal segment of maxillary palpus shorter than antennal club
    (nearly as long as antennal club in Cotalpa subcribrata) 7
7. Apex of mentum sinuate or bininuate or emarginate (Figs. 9–11) 8
7'. Apex of mentum notched (Fig. 12) 9
8. Pronotum glabrous. Clypeus subrectangular, angles narrowly round-
   ed. Large claw of at least metatarsus cleft in males; all claws simple
   in females .... Cotalpa
8'. Pronotum setose (at least in places). Clypeus semicircular (widest at
    base), angles broadly rounded (P. deserta with subrectangular clyp-
    eus). Claws of both sexes simple .... Paracotalpa
9. Clypeus semicircular (widest at middle, Figs. 13, 14). Males metallic
   green, females metallic green, dark brown, or black. Parameres in
   males rounded apically (Fig. 15). Mexico City, Mexico, to Guatemala
   .... Viridimicus, new genus
9'. Clypeus with lateral margin sinuate, converging to truncate or round-
    ed apex (Fig. 17). Males and females reddish-brown, brown, or black.
    Parameres in males subquadrate apically (Fig. 16). Southern Arizona
    to Mexico City, Mexico .... Parabyrsopolis

GENUS *PARABYRSOPOLIS* OHAUS
(Figs. 1, 16, 17, 26, 27; maps 1, 2, 4)

Cotalpa (Parabyrsopolis) Ohaus 1915:256 (July). Type species *Cotalpa (Parabyrsopolis) batesi* Ohaus 1915:257; replacement name for *Byrsopolis lanigera* Bates 1888.

*Parareoda* Casey 1915:99 (November). Type species *Parareoda rufobrunnea* Casey 1915:100.

DESCRIPTION. *Form:* Broadly ovate, robust, convex, sides subparallel or narrowly divergent posteriorly to a rounded elytral apex. Length 23.0–32.0 mm; width across humeri 10.5–15.0 mm; greatest width 13.0–16.5 mm. *Head:* Clypeus subequal in length to frons; shape laterally sinuate, converging anteriorly to truncate or rounded apex. Antennal club 3-segmented; subequal to segments 2–7. Labrum weakly sinuate apically. Mandibles broadly rounded externally. Mentum notched apically. *Pronotum:* Widest at middle, margins broadly rounded, beaded. Surface variably punctate. *Elytra:* Surface with variably punctate, feebly defined striae. Suture apically spinose or not, right-angled or slightly divergent. *Venter:* Sternites densely setose. *Legs:* Foretibia tridentate, teeth becoming larger anteriorly. At least larger claw of protarsus in male weakly cleft; all claws of female simple. Apex of fourth protarsomere not expanded. *Parameres:* Symmetrical, simple subquadrate.

DIAGNOSIS. *Parabyrsopolis* is distinguished from other Areodina by the following combination of characters: (1) clypeus sinuate laterally, converging apically toward a truncate or rounded apex (Fig. 17), (2) mentum notched apically, (3) parameres subquadrate apically, and (4) the absence of strong metallic green coloration. Males are separated from females by the presence of one enlarged, split claw on the protarsus and usually on the meso- and metatarsi as well. Generally, males are smaller than females, and possess concave sternites (in lateral view) rather than convex or flattened sternites as in females.

DISTRIBUTION. The single species in this genus occurs from the southern montane region of Arizona in the United States to the Transverse Volcanic Belt (Map 1, 2) near Mexico City, Mexico. Individuals are found in pine/oak forests at elevations from 1,400 m to 2,700 m.

REMARKS. Ohaus (July 1915) described *Parabyrsopolis* as a subgenus of *Cotalpa* while, in the same year, Casey (November 1915) described the genus *Parareoda*. Since that time, *Parabyrsopolis* has been placed in the genus *Cotalpa* (by Blackwelder 1944), *Paracotalpa* (Arnett 1968), and *Byrsopolis* (previous usage by Bates 1888).

The product of Ohaus' study of the Rutelinae was the *Genera Insectorum* (1934). Due to this work's long delay in publication, Ohaus began publishing many of his taxa in journals, long before the book became available. In 1915, Ohaus published his work on *Cotalpa* and *Byrsopolis*. Because he viewed the classification of these two genera as "eroded" by the publication of many new taxa, he placed *Byrsopolis*, as well as two new taxa *Paracotalpa* and *Parabyrsopolis*, as subgenera of *Cotalpa*. In so doing, he moved *Byrsopolis lanigera* Bates to *Parabyrsopolis* and designated it as the type species of the subgenus. The matter was then complicated taxonomically by the creation of a secondary homonym: *Cotalpa (Cotalpa) lanigera* (Linnaeus) and *Cotalpa (Parabyrsopolis) lanigera* (Bates). Because of this, Ohaus designated *Cotalpa (Parabyrsopolis) batesi* as a replacement name for *Cotalpa (Parabyrsopolis) lanigera* (Bates). Evidently, he also transferred *Byrsopolis nigroaenea* Ohaus 1912 to the subgenus *Parabyrsopolis*. Again, because of possible secondary homonymy with *Cotalpa (Cotalpa) nigroaenea* Bates, he coined the replacement name *Cotalpa*
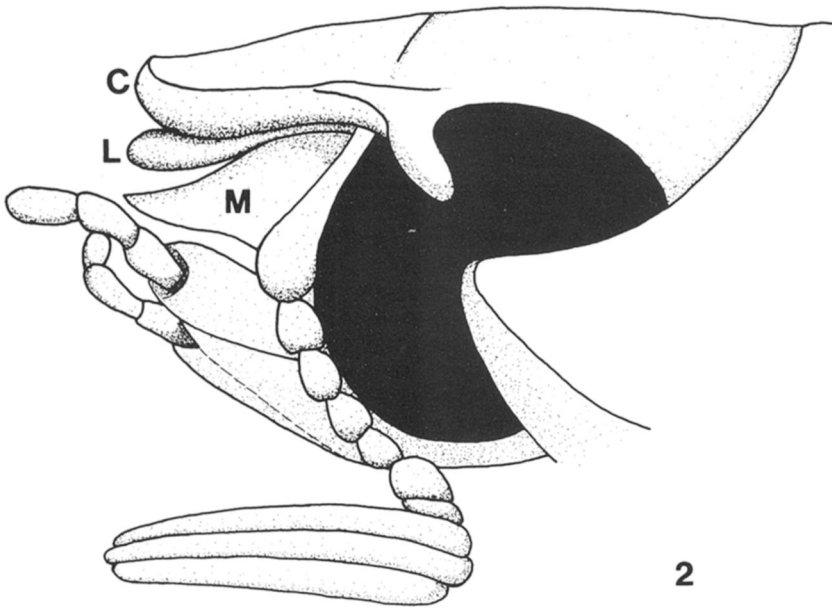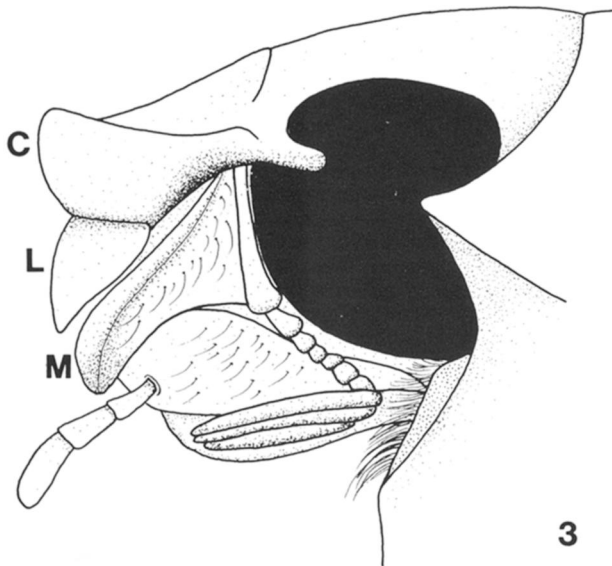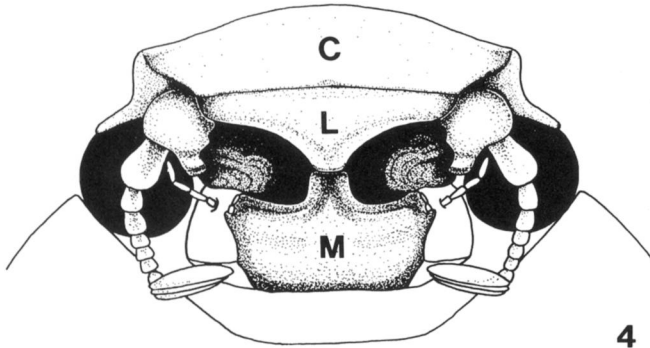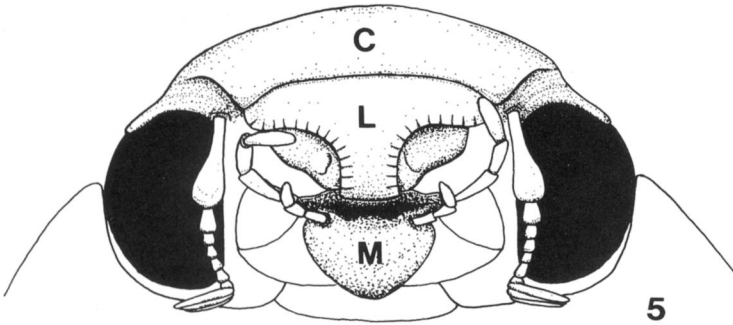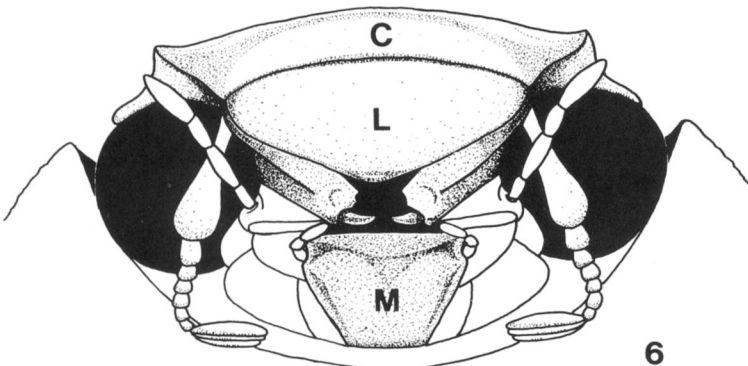
Fig. 2, 3.   Head, lateral view. C, clypeus; L, labrum; M, mandible. 2, labrum horizontally produced with respect to clypeus. 3, labrum vertically produced with respect to the clypeus (maxillary palpus hidden behind mandible).
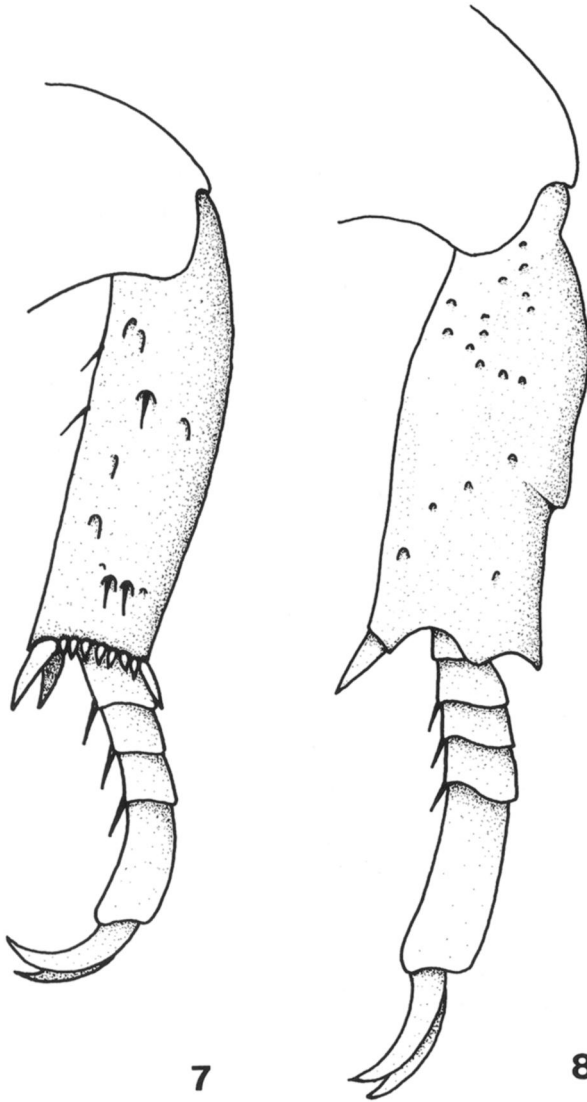
Figs. 4–6.   Head, frontal view. C, clypeus; L, labrum; M, mentum. 4, labrum and mentum both with median, apical tooth or projection. 5, labrum with median, apical tooth or projection, mentum lacking projection (Adoretini). 6, labrum and mentum both lacking median apical tooth (Spodochlamyini).

Figs. 7, 8.   Apex of the metatibia, ventrolateral view. 7, apex with spines (Antichirina and Fruhstorferiina). 8, apex without spines (Rutelina).

(*Parabyrsopolis*) *fuscoaenea* Ohaus. He did so, however, only on specimen labels. The name *P. fuscoaenea* was not formally found in the literature until the publication of Ohaus' section on the Euchirinae, Phaenomerinae, and Rutelinae in the *Coleopterorum Catalogous* (1918:11). The name *P. fuscoaenea* (Ohaus) has since been cited with the erroneous date of publication of 1912 (*the published date of Byrsopolis nigroaenea Ohaus*).

Parabyrsopolis chihuahuae (Bates)
(Figs. 1, 16, 17, 26, 27; maps 1, 2)

Byrsopolis chihuahuae Bates 1888:290. Holotype female at BMNH. Type locality: Mexico, Chihuahua, Pinos Altos.

Byrsopolis lanigera Bates 1888:290. Name preoccupied after transfer to *Cotalpa* (Ohaus 1915); see *Cotalpa* (*Parabyrsopolis*) *batesi*. Holotype female at BMNH. Type locality: Mexico. **New synonymy.**

Byrsopolis arizonae Ohaus 1912:313. Lectotype female, labeled "Arizona," "♀," "type," "Det. F. Ohaus 1912 *Parabyrsopolis arizonae* Ohaus," "88904," "Zool. Mus. Berlin," here designated. Paralectotype male, labeled "Arizona," "Det. F. Ohaus 1912 *Parabyrsopolis arizonae* Ohaus," "88904," "type," "Zool. Mus. Berlin," here designated. An additional paralectotype labeled, "Arizona," "♀," "Typus!" "*Parabyrsopolis arizonae* Ohaus," "Zool. Mus. Berlin," here designated; all at ZMHB with my labels. **New synonymy.**

Cotalpa (*Parabyrsopolis*) *batesi* Ohaus 1915:257. Replacement name for *Byrsopolis lanigera* Bates. Ohaus designated a holotype for this replacement name, but this has no type status under the code. **New synonymy.**

Byrsopolis fuscoaenea Ohaus 1918:11. Not 1912:312 (see discussion under generic description); replacement name for *Byrsopolis nigroaenea* Ohaus (1912). Lectotype male, labeled "La Cumbra, Talpa Jalisco Dr. B. [= Buller]," "Typus!" "*Parabyrsopolis nigroaenea* Ohs.," "Zool. Mus. Berlin," here designated. Allolectotype female, labeled as male, also here designated. Paralectotype female, labeled "Tlaltizapan?" "Mexico J. Flohr G.," "♀," "Ohaus determin 1912 *Byrsopolis nigroaenea* Ohs. ?" "88905," "Zool. Mus. Berlin," "Tlat," here designated; this specimen is removed from *P. fuscoaenea* and designated as a paratype of *Viridimicus ratcliffei* n. sp. All housed at ZMHB. **New synonymy.**

Parareoda rufobrunnea Casey 1915:100. Holotype female at USNM, labeled "Huachuca Mts July 1905 Ariz," "*Parareoda rufobrunnea* Csy," "Casey bequest 1925," "type USNM 48553." **New synonymy.**

Parabyrsopolis villadealendensis Morón 1976:19. Holotype male at Instituto de Biología, Universidad Nacional Autónoma de México (UNAM). Type locality: Mexico, State of Mexico, Villa de Allende, San José. **New synonymy.**

DESCRIPTION (male and female). Length 23.1–31.5 mm; width across humeri 10.9–14.4 mm; greatest width 13.0–16.4 mm. *Color:* Brown, reddish-brown, castaneous, or piceous; opaque to shiny, occasionally with weak, metallic green reflections. *Head:* Densely, confluently punctate to rugopunctate; punctures small and large mixed, with lateral punctures setigerous or not, less densely punctate at base of frons; setae tawny, short, sparse. Frontoclypeal suture feebly impressed to obsolete, straight to feebly sinuate. Clypeus weakly declivous with respect to frons; sides diverging slightly from base to subparallel, sinuate laterally, converging to truncate, rounded, or feebly sinuate apex; apex weakly to broadly reflexed, ventrally punctate, setigerous or not; setae short to moderate, rufous, sparse to moderately dense. Interocular width 3.5–4.0 transverse eye diameters. Labrum apically weakly to moderately sinuate. Mandibles exposed in dorsal view, feebly to moderately concave. Mentum notched anteromedially. *Pronotum:* Disc with nearly obsolete, medial longitudinal groove; surface moderately densely to densely punctate; punctures small and moderately large mixed, some confluent. Laterally, surface moderately dense to densely punctate, confluent to rugopunctate in places; punctures sparse when small or moderately large, dense when moderate in size. *Elytra:* Surface with moderately to very feebly impressed striae about evenly spaced; one next to suture,

one or two in center of disc, one or two just mesad of humerus, one or two just laterad to humerus, one or two near margin (occasionally obsolete); punctures shallow, small to moderately large, moderately dense. Intervals moderately densely to densely punctate; punctures small and large mixed, some transversely rugose; margins laterally and apically without setigerous punctures (although ventral surface may have apical setae); sutural angle of a single elytron with or without spine, right-angled or rounded. *Pygidium:* Moderately to moderately densely punctate; punctures moderate and small, mixed, setigerous; setae tawny to yellow-orange, short to moderate in length. *Legs:* Males with larger pro- and mesotarsal claws cleft and about twice width of smaller claws; metatarsal claws subequal in width, cleft or simple (rarely); females with all claws simple, neither claw enlarged. *Venter:* Densely pilose; setae long, tawny to rufous. Abdominal sternites less densely pilose. *Parameres* (Figs. 16 a, b): Symmetrical, simple, apex subquadrate.

DISTRIBUTION. *Parabyrsopolis chihuahuae* occurs in the Huachuca and Patagonia Mountains of Arizona in the United States (elevation 1,486–1,882 m) (Maps 1, 2). In Mexico, it occupies the Sierra Madre Occidental and the westernmost extension of the Transverse Volcanic Belt (Map 2). It has been recorded at the following elevations: Aguascalientes (about 2,000 m), Chihuahua (1,951–2,103 m), Durango (2,286–2,591 m), Jalisco (2,469–2,499 m), Michoacan (1,650–2,700 m), and Sonora (1,660 m).

Locality records (Map 1): 383 specimens examined from the following collections and institutions: AMNH, ANSP, ASUT, BMNH, CASC, CNCI, ICCM, LACM, MCZC, OSUC, SDMIC, SEMC, UNAM, UNSM, USNM, ZMHB, R. Cunningham, H. & A. Howden, D. LaRue, S. McCleve, M. Morón, B.C. Ratcliffe, J. Ryan, K. Smith, T. Taylor, W. Warner, R. Young.

UNITED STATES. **Arizona** (195): *Cochise County* [Huachuca Mountains (186)]: Ash Canyon, Carr Canyon, Copper Canyon, Miller Canyon, Oslar, Palmerly, Parker Canyon, Sunnyside, no data; *Santa Cruz County* [Patagonia Mountains] (6): Bear Canyon, Harshaw Creek, Hidden Springs Canyon; no data (3).

MEXICO (188). **Aguascalientes** (3): Calvillo (11 mi. E). **Chihuahua** (17): Matachic (2 mi. W), La Polvosa, Perdernales (Hwy 16, 2.5 mi. E, 1 mi. S), Sierra Alta Tarahumara (Hwy 127, 277 mi. SW La Junta, 0.5 mi. N), between Yepachic and Tomachic Canyons. **Durango** (19): Coyotes, El Salto (6 mi. NE; 25 mi. E; 3 mi. E), Durango (30 mi. W), Revolcaderos. **Jalisco** (101): Mazamitla (3 mi. WSW), Nevado de Colima (103°46′W, 19°58′N), Tacalitlan, Talpa (La Cumbra). **Mexico** (15): Villa de Allende (San José), Valle de Bravo. **Michoacan** (9): Hidalgo (11 mi. W), Los Laureles, Mazamitla, San Cayetano, Sierra de Tlalpujahua (Region montagneuse de environs de Toluca). **Sinoloa** (9): El Palmito (8 mi. W; 9 mi. W), Potrerillos (2 mi. SW, Hwy 40). **Sonora** (9): Nacori Chico Rancho Arroyo el Concono (80 km NE); *no data* (6).

Temporal distribution: June (6), July (130), August (204), September (16), October (1).

REMARKS. *Parabyrsopolis chihuahuae* is the sole member of its genus, and is extremely polymorphic. Clypeal form (Fig. 17), a character widely used in the Rutelinae for separation of taxa, is especially variable. In this genus, the clypeus may be truncate, rounded, or even slightly sinuate apically, and reflexed or not. Additionally, the claws (distinctly cleft to only weakly cleft); color (brown, black, or reddish-brown, with or without weak metallic reflections); apex of the elytral suture (spinose or not, right-angled or rounded); and punctation of the head, pronotum, and elytra also vary to some degree. With such a wide array of differing character states, many species have been described for this single taxon. For example, *Parabyrsopolis fuscoaenea* was named by
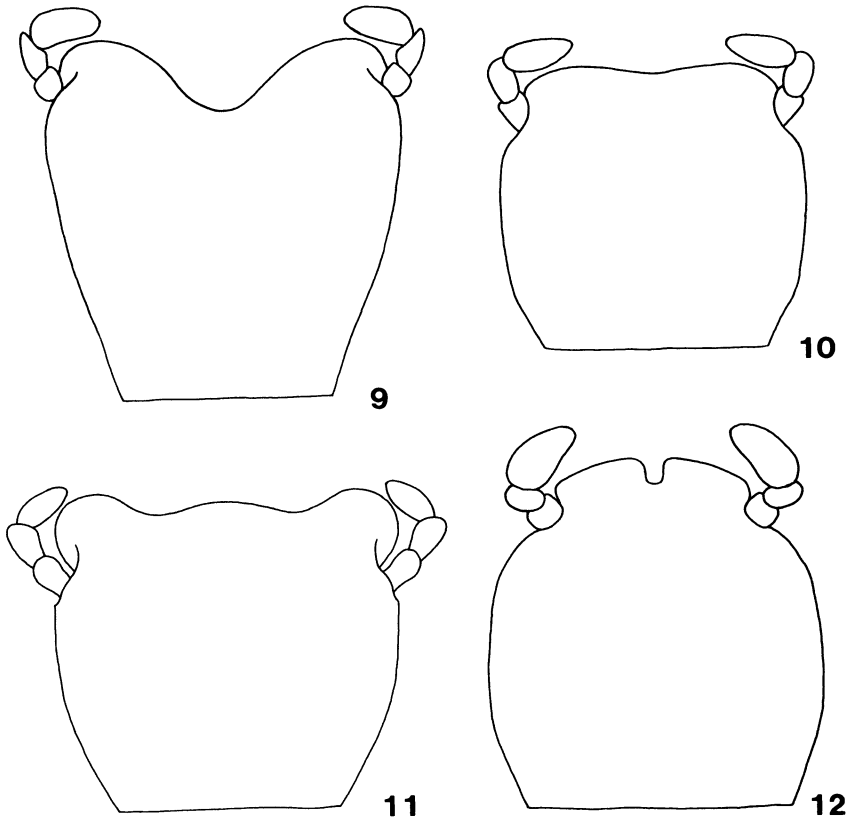
Figs. 9–12.   Apex of mentum. 9, deeply sinuate. 10, weakly sinuate. 11, bisinuate. 12, notched.

Ohaus (1918) to describe a dark morphotype of *P. chihuahuae.* Color polymorphism, such as in *Parabyrsopolis chihuahuae,* has been observed and studied in *Tribolium castaneum* Herbst (Roseland *et al.* 1987) and tiger beetles of the genus *Cicindela* (Schultz 1986). These studies concluded that color morphotypes are due to enzymatic differences dictated by genes. The black to reddish-brown color observed in *P. chihuahuae* can be brought about by minor genetic changes that affect discrete steps in the pathways of sclerotization and melanization (Tom Scholtz, pers. comm., 1988) and are not differences that would be indicative of species separation.

As suggested by Hardy (1971) and Morón (1976), *P. arizonae* (Ohaus) and *P. rufobrunnea* (Casey) are sympatric and conspecific, both named for reddish-brown morphotypes with parabolic clypeal apices (as was determined by studying the type series). *Parabyrsopolis batesi* (Ohaus) and *P. villadealendensis* Morón were named for morphotypes with truncate clypeal apices and slight color variations.

One sample of 84 *Parabyrsopolis* from a single night of collecting at a single locality, exhibited all of the variations of the clypeus in the supposed six species

of *Parabyrsopolis* (Fig. 17). Within this sample, no character states clustered to suggest species groups.

From north to south, following the Sierra Madre Occidental, a clinal variation of character states is observed. Northern individuals (those in southern Arizona) are usually reddish-brown, the clypeus is normally rounded apically, the body is less robust, and the populations are more homogeneous, perhaps due to isolation of this population in the Huachuca Mountain region. Individuals from the southern part of the range (Jalisco, Mexico) tend to be a darker brown, the elytra tend to have less defined striae, the body is more robust, and they have a more variable clypeal form (parabolic, truncate, or even weakly sinuate apically). Individuals between these two extremes in range display all degrees of variation, with no distinguishable groups. This is a progressive, uniform variation, not stepped or delineated by any geographic barriers that would warrant subspecific designation.

Byrsopolis lanigera and *B. chihuahuae* were both described by Bates (1888) and removed to the subgenus *Parabyrsopolis* by Ohaus (1915, 1918). Because these two taxa were the first to be described from the genus *Parabyrsopolis*, they have priority over the remaining conspecific taxa. As first reviser, I select *P. chihuahuae* as the name for the taxon rather than *P. lanigera*. This obviates complications and confusions due to past usage of the specific epithet *lanigera* in both *Cotalpa* and *Parabyrsopolis*.

Parabyrsopolis chihuahuae can be collected at lights and will fly during rain. These beetles have been observed flying from dusk until approximately 10:00 p.m. They usually approach the light trap flying very close to the ground and land low on the back-drop sheet.

Ecological data indicate that vegetation where *P. chihuahuae* is collected is primarily *Pinus-Quercus* (pine-oak) forest with other characteristic vegetation being *Crategus* and *Pyrus* (Rosaceae), *Arbutus* (Ericaceae; madrone), *Platanus* (Platanaceae; sycamore), and *Liquidambar* (Hamamelidaceae).

Adults from the Huachuca Mountains were collected at lights and maintained in the laboratory. Fresh leaves of *Arbutus* sp. and *Quercus* sp., as well as decaying wood of *Quercus*, were provided, but no feeding or egg laying were observed.

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Viridimicus Jameson, **new genus**
(Figs. 13–15, 18–26, 28–33; maps 1, 2, 4)

</div>

TYPE SPECIES. *Cotalpa aurescens* Bates 1888:289, here designated.

DESCRIPTION. *Form:* Broadly ovate, convex, sides subparallel or weakly divergent posteriorly, apex of elytra rounded. Length 19.0–27.5 mm; width across humeri 10.0–14.5 mm; greatest width 11.0–17.0 mm. *Color:* Male dorsally metallic brassy green, dark metallic green, or metallic blue-green. Female with head dorsally castaneous or piceous (occasionally with weak metallic green reflections); pronotum, elytra, and pygidium castaneous, piceous (occasionally with weak metallic green reflections) or metallic green; shiny to opaque. *Head:* Frons and clypeus convex to flat in profile. Clypeus subequal in length to frons, semicircular (diverging slightly from base and widest at middle), apex weakly to broadly reflexed and ventrally punctate, setigerous or not. Interocular width 2.0–5.0 transverse eye diameters. Antennal club 3-segmented, subequal in length to segments 2–7. Labrum truncate, rounded, or weakly sinuate apically. Mandibles broadly rounded externally, flat to concave, hidden or exposed. Mentum with apex notched anteromedially. *Pronotum:* Widest at middle. Lateral margins broadly rounded; beaded, bead obsolete antero- and basomedially. Surface variously punctate. *Elytra:* Surface with poorly defined, punctate striae reaching neither apex nor base. Suture apically without
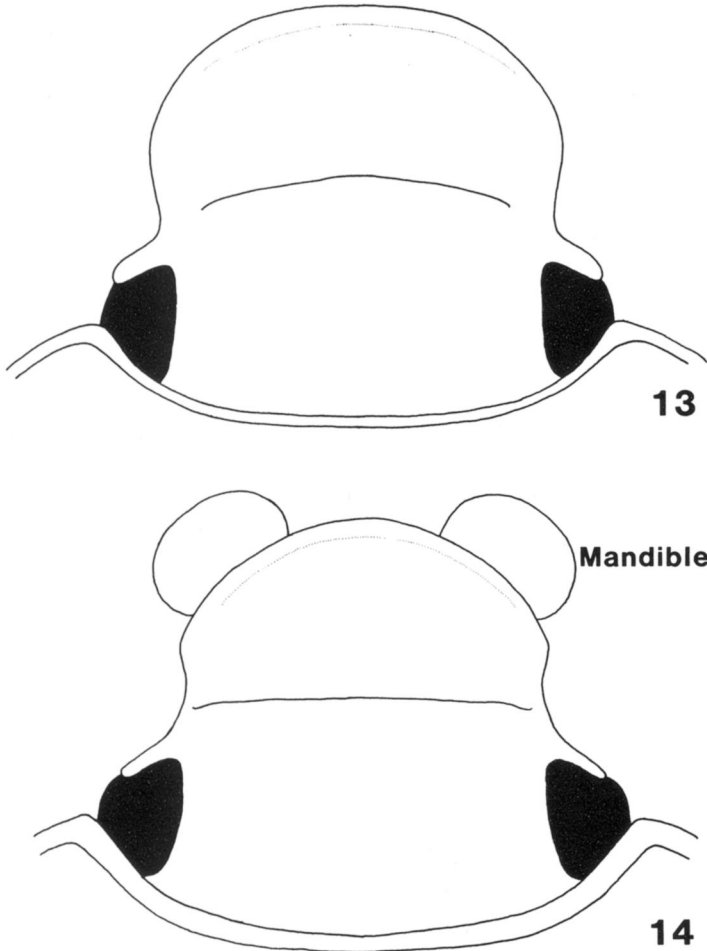
Figs. 13, 14.   *Viridimicus* spp. head, dorsal view showing semicircular clypeus (clypeus widest at middle). 13, mandibles hidden (*V. aurescens, V. cyanochlorus, V. unitus, V. nigroaeneus, V. impunctatus*). 14, mandibles broadly exposed (*V. ratcliffei*).

spine, right-angled or weakly divergent. Margin basally and apically sparsely setigerous. *Pygidium:* Surface setigerously punctate to rugopunctate, punctures moderate to densely punctate. *Venter:* Thoracic sternites and femora densely clothed with long, light-colored pilosity; abdominal sternites less densely pilose. *Legs:* Protibia tridentate, teeth becoming larger apically. Foretarsus in male (dorsal view) with large claw 2–4 times wider than small claw; at least one set of claws in male slightly cleft; pro- and mesotibial claws of female simple, metatibial claw cleft; third protarsomere emarginate with a short, stout seta within emargination (bilobed) or entire. Apex of fourth tarsomere expanded (greater than width of two spines). *Parameres* (Figs. 15 a, b): Symmetrical, simple, apex rounded.

DIAGNOSIS. *Viridimicus* is distinguished from related genera by the following combination of characters: (1) clypeus semicircular, diverging slightly from the
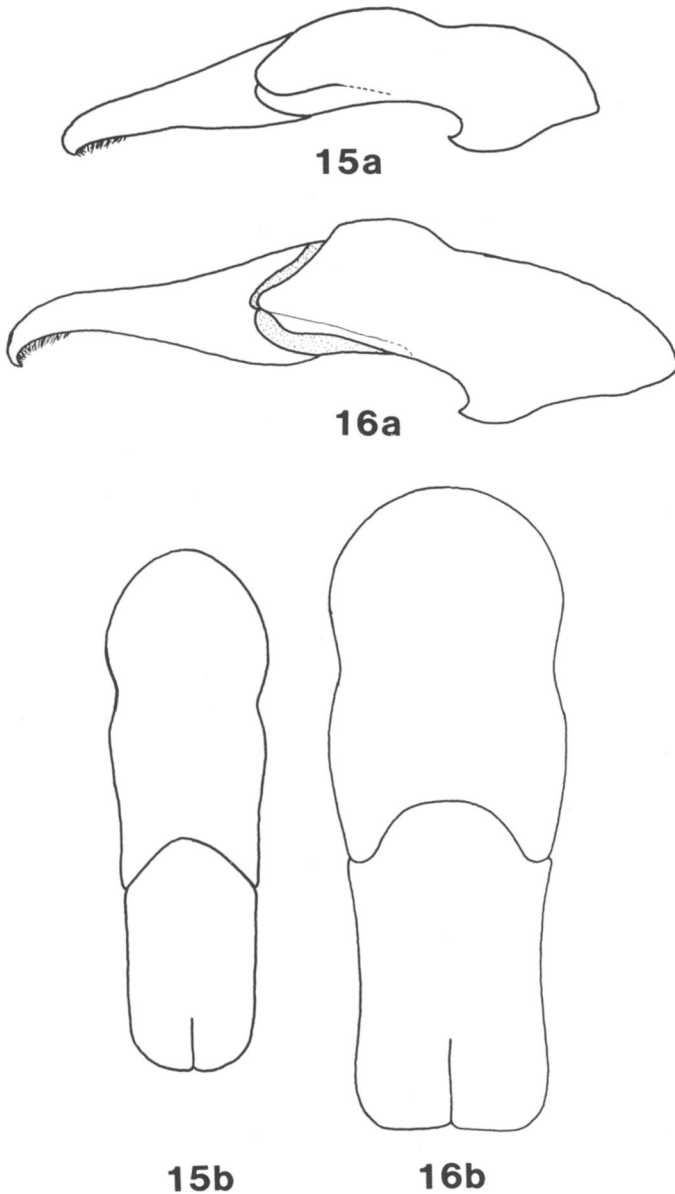
Figs. 15, 16.   Parameres: a. lateral view; b. dorsal view. 15, *Viridimicus* sp. (rounded apically). 16, *Parabyrsopolis* sp. (subquadrate apically).

base and widest at middle (Figs. 13, 14), (2) mentum notched apically (Fig. 12), (3) apex of the parameres rounded (Fig. 15), and (4) metallic green coloration of the male.

DISTRIBUTION. *Viridimicus* occurs from the Transverse Volcanic Belt in

Mexico from near Mexico City, Mexico, to northern Guatemala (Maps 1, 2, 4). Individuals are found in pine-oak forests at elevations from 1,700 to 2,300 m.

REMARKS. *Viridimicus* is established to accommodate those species in Mexico south of the Transverse Volcanic Belt previously referred to as *Cotalpa* and *Parabyrsopolis*.

This genus is most closely allied to *Parabyrsopolis* as evidenced by the notched apex of the mentum. However, beyond this synplesiomorphy, more characters separate the two genera (apex of the parameres, general color dimorphism between sexes, form of the clypeus, and expanded apex of the anterior tarsomeres in males) than bind the two together as one genus. *Viridimicus* differs from *Cotalpa* in the notched mental apex and clypeal form (semicircular rather than subrectangular).

The apices of the parameres do not differ in form between species in the genus. However, this character may be used to separate *Parabyrsopolis* (apex quadrate) from *Viridimicus* (apex rounded).

The type species of the genus, *V. aurescens,* was originally described by Bates (1888) in the genus *Byrsopolis* and has previously been placed in *Cotalpa* (Blackwelder 1944) and *Parabyrsopolis* (Ohaus 1918, 1934; Machatschke 1972).

ETYMOLOGY. This genus is named for the green (*viridi-*) and shiny (*-micus*) dorsum present in all males. The generic name is considered masculine in gender.

KEY TO THE SPECIES OF *VIRIDIMICUS*

1. Protarsus with inner claw enlarged and apically toothed. Abdomen ventrally flat or concave. Males 2
1'. Protarsus with inner claw not enlarged or apically toothed. Abdomen ventrally swollen or convex. Females (known for only three species) 7
2. Protarsus with third tarsomere ventrally emarginate, stout seta arising from emargination (bilobed) (Fig. 19) 3
2'. Protarsus with third tarsomere ventrally entire, not emarginate (bilobed) (Fig. 20) .... *V. cyanochlorus* Jameson, n. sp.
3. Mandibles narrowly exposed or hidden (Fig. 13), concave. Clypeus and frons in lateral view appearing convex; clypeus declivous with respect to frons. (Figs. 21–24) 4
3'. Mandibles broadly exposed (Fig. 14), flat (not concave). Clypeus and frons in lateral view appearing flat (Fig. 25), not convex .... *V. ratcliffei* Jameson, n. sp.
4. Pronotum laterally with punctures moderate to moderately large, neither confluent nor rugopunctate. Color of pronotum dark metallic green to brassy green (under illumination and magnification) 5
4'. Pronotum laterally with punctures large, confluent to rugopunctate. Color of pronotum reddish-brown with brassy green reflections (under illumination and magnification) .... *V. unitus* Jameson, n. sp.
5. Disc of pronotum sparsely punctate, punctures small .... *V. impunctatus* Jameson, n. sp.
5'. Disc of pronotum moderately densely punctate, punctures moderately large (dense) and small (sparse) 6
6. Disc of pygidium finely, confluently punctate. Discal regions of clyp-
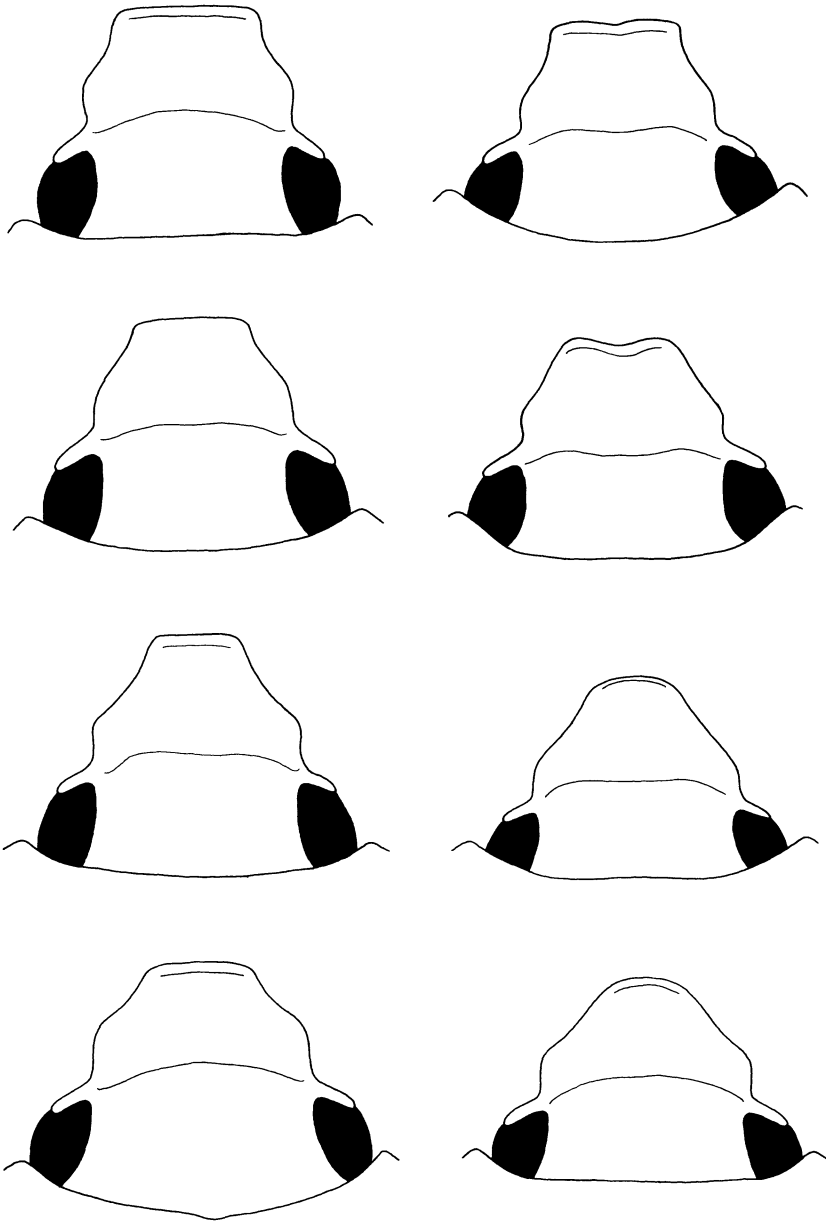
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Fig. 17.   Head, dorsal view, *Parabrysopolis chihuahuae,* showing variability of clypeus in one sample (all from one locality and one night). [Line near apex of clypeus denotes reflexion of clypeal apex.]

eus and frons with large punctures generally separated by one punc-
ture diameter .... *V. nigroaeneus* (Bates)
6'. Disc of pygidium moderately densely punctate, not confluent. Discal
region of head confluently punctate .... *V. aurescens* (Bates)
7. Mandibles narrowly exposed or hidden (Fig. 13), concave. Clypeus
and frons in lateral view appearing convex; clypeus declivous with
respect to frons 8
7'. Mandibles broadly exposed (Fig. 14), flat, not concave. Clypeus and
frons in lateral view appearing flat, not convex ....
.... *V. ratcliffei* Jameson, n. sp.
8. Disc of pronotum sparsely punctate, punctures small. Color of pro-
notum shiny dark green, color of head opaque black ....
.... *V. impunctatus* Jameson, n. sp.
8'. Disc of pronotum moderately densely punctate, punctures moder-
ately large. Color of pronotum and head piceous to brown with weak
metallic green reflections .... *V. aurescens* (Bates)

Viridimicus aurescens (Bates), **new combination**
(Figs. 19, 21, 28, 29; maps 1, 2)

Cotalpa aurescens Bates 1888:289. Holotype male at BMNH. Type locality:
Chiapas state, Mexico.

DESCRIPTION. Male. Length 19.4–23.8 mm; width across humeri 9.9–11.8 mm; great-
est width 11.2–14.1 mm. *Head:* Frons dark metallic green; clypeus piceous with or
without slight violaceous and/or green reflections. Surface densely, confluently punctate,
less dense at base of frons; punctures small to moderately large, mixed, setigerous laterally;
setae tawny, short to moderate in length. Frontoclypeal suture biarcuate to nearly straight.
Clypeus declivous with respect to frons (Fig. 21); sides divergent from base then broadly
rounded (widest at middle); apex semicircular, broadly to moderately reflexed, setiger-
ously punctate on the ventral side of the reflexed apex; setae moderately long, moderately
dense, rufous. Interocular width 2.0–3.0 transverse eye diameters. Mandibles hidden in
dorsal view. *Pronotum:* Color metallic brassy green to dark green. Surface moderately
densely punctate; punctures small (sparse) to moderately large (dense). *Elytra:* Color
(with magnification and illumination) piceous with metallic green relfections (metallic
green to unaided eye). Surface with weakly impressed, punctate striae; one next to suture,
one or two in center of disc, two just mesad of humerus, two just laterad of humerus,
two near margin (occasionally obsolete); punctures small to moderate in size. Intervals
broad, moderately densely punctate; punctures small to moderate, some transverse,
sparsely setigerous on margins and at apex; setae tawny, moderate in length. *Pygidium:*
Color as in elytra. Surface moderately to densely punctate; punctures small, setigerous;
setae testaceous, moderately long to long. *Legs:* Pro- and mesotarsi each with one claw
enlarged, cleft, 3 times as wide as smaller claw. Metatarsus with large claw 1.5–2.0 times
width of smaller claw; distinctly cleft. Protarsus with third tarsomere bilobed, stout seta
between lobes (Fig. 19). *Venter:* Densely clothed with long, testaceous pile. Abdominal
sternites less densely pilose.
Female. Length 23.7–27.4 mm; width across humeri 14.0–14.5 mm; greatest width
13.9–16.6 mm. As male except for the following features: Color piceous to brown with
weak metallic green reflections (only with illumination and magnification). Pronotum
with punctures small (very sparse) to large, mixed, becoming more densely laterally.
Metatarsi only with larger claw cleft apically.

DIAGNOSIS. This species is separated from its congeners by the confluently
punctate discal regions of the head (frons and clypeus) and the moderately to
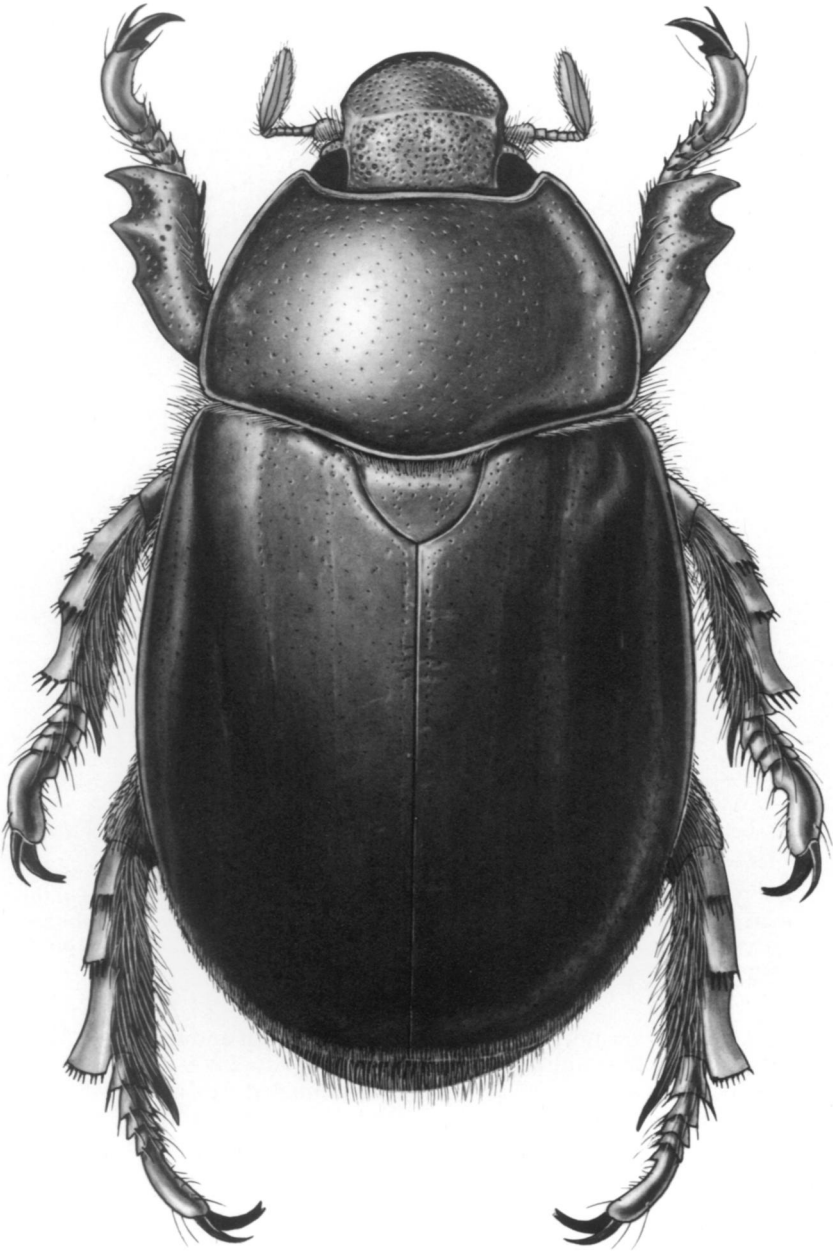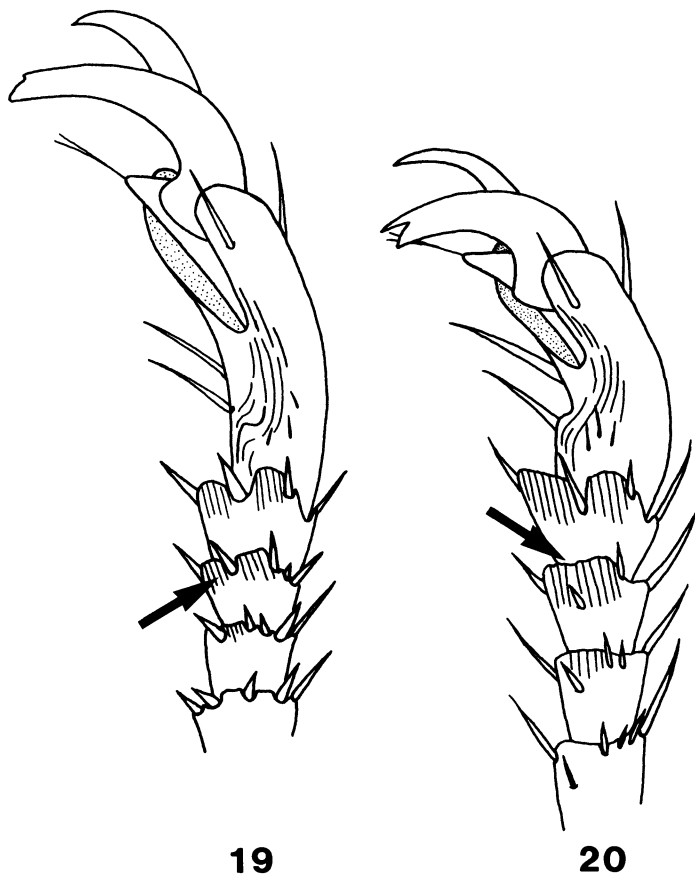densely (but not confluently) punctate pygidial disc.

Fig. 18.   *Viridimicus nigroaeneus,* dorsal habitus.

19   **20**

Figs. 19, 20. *Viridimicus* spp. Anterior tarsomeres, ventral view. 19, apex of third tarsomere emarginate with a short, stout seta within the emargination (thus being bilobed) (*V. aurescens, V. unitus, V. nigroaeneus, V. ratcliffei, V. impunctatus*). 20. Apex of third tarsomere entire (*V. cyanochlorus*).

DISTRIBUTION. Occurs in the Chiapas Central Massif and the Sierra Madre de Chiapas (Map 2) at altitudes ranging from 1,850 to 2,300 m.

Locality records (Map 1): 183 specimens examined (sex ratio 3.75M: 1F) from the following institutions and collections: CNCI, UCMC, UNSM, R. Cunningham, H. & A. Howden, D. LaRue, M. Morón, B. C. Ratcliffe, A. Reifschneider, T. Taylor, D. Thomas, W. Warner.

MEXICO (136). **Chiapas** (136): Angel Albino Corzo (El Triunfo), San Cristóbal (8 mi. SE; 4 mi. E; 8 mi. NE; 10 mi. E), Teopisca (10 mi. SE).

GUATEMALA (47). **Chimaltenango** (8): San Jose Chirijuyu. **El Quiche** (35): Chichicastenango, Chopol, Chuguexa (mpio. Santo Tomas Chichicastenango). **Quetzaltenango** (2): Zunil. **Solola** (2): Xajaxac.

Temporal distribution: May (93), June (53), July (22), August (18).

REMARKS. This species was first described in the genus *Cotalpa* by Bates

(1888) and was moved to *Parabyrsopolis* by Ohaus (1918, 1934), back to *Cotalpa* (Blackwelder 1944), and then again to *Parabyrsopolis* by Machatschke (1972). *Viridimicus aurescens* is the most commonly collected species of this genus and also the most widely distributed. A brassy green morphotype of this species occurs in Guatemala (two males and three females were examined). Females of this morphotype are more brown or castaneous (rather than piceous as in most female *V. aurescens*). Other than slight variations in color, there are no significant differences among individuals. This species has been collected from malaise traps as well as light traps. Natural history information is lacking.

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Viridimicus cyanochlorus Jameson, **new species**
(Figs. 20, 22, 30; maps 1, 2)

</div>

TYPE MATERIAL. Holotype labeled, "Mexico. Oaxaca, 5,800', 22.2 mi. S. Juchatengo, VII-21-22-1966," "George E. Ball, D.R. Whitehead collectors," "*Cotalpa* (*Byrsopolis*) *nigroaenea* Bates, Det. H.F. Howden 67." Deposited at CNCI. Paratype labeled, "Km. 180–212, Puerto Escondido Hwy., Oax., Mex. Sept. 6–9, 1968, G. Pollard." Deposited in the Howden collection (Ottawa).

DESCRIPTION. Holotype male. Length 23.4 mm; width across humeri 11.5 mm; greatest width 12.3 mm. *Head:* Frons (with illumination and magnification) metallic dark green with dark blue reflections; clypeus dark metallic green (color of head metallic blue-green to unaided eye). Surface of head moderately densely punctate; punctures moderate to small, mixed. Disc of frons and clypeus with larger punctures randomly placed, separated by approximately one puncture diameter, surface (especially of clypeus) alutaceous between punctures. Frontoclypeal suture slightly impressed, suture bent posteriorly at each lateral edge. Frons and clypeus in profile evenly convex (Fig. 22). Clypeus with sides diverging slightly from base, then broadly rounded to broadly oval apex; apex moderately reflexed; ventral side of reflexed apex punctate, punctures moderately large, very sparsely setigerous (more so laterally); setae short, rufous. Interocular width equals 5.0 transverse eye diameters. Labrum truncate apically. Mandibles hidden in dorsal view. *Pronotum:* Color metallic dark green with dark blue reflections (metallic blue-green to unaided eye). Surface moderately densely punctate, punctures small (sparse) to moderate (dense), mixed; marginal bead metallic blue-green under illumination and magnification. *Elytra:* Color (under magnification and illumination) piceous with metallic dark blue reflections (very dark metallic blue to unaided eye). Surface with striae feebly impressed, nearly obsolete; sutural stria a row of punctures only, center of disc with one impressed stria, two feeble striae mesad of humerus, one short stria posterior to humerus. Intervals moderately densely punctate, punctures small to moderate mixed, sparsely setigerous apically; setae short, rufous. *Pygidium:* Color metallic dark green (to unaided eye and with illumination and magnification). Disc with surface finely densely rugopunctate, becoming increasingly rugopunctate to rugulose towards margins; punctures small, setigerous; setae tawny, moderate in density, short on disc, becoming longer near apical margins. *Legs:* Pro- and mesotibial claws enlarged, one of each pair slightly cleft; larger claw 4 times wider (in dorsal view) than smaller claw. Metatibial claws simple, each of equal width. Protarsus with third tarsomere entire, not emarginate apcially with short, stout seta in emargination (Fig. 20). *Venter:* Densely clothed with moderate to moderately long tawny pile; sternites 1–6 less densely pilose.

Paratype male. Length 21.7 mm; width across humeri 10.7 mm; greatest width 13.5 mm. Differs from holotype in the following respects: *Head:* Color metallic dark green without dark blue reflections (with or without magnification and illumination). In profile, frons weakly concave, clypeus convex. Interocular width 4.5 transverse eye diameters. *Pronotum:* Color metallic green without dark blue reflections. Disc with punctures small (dense) and moderate in size (moderately dense), moderate-sized punctures becoming more dense apically and laterally. Marginal bead bronze with green reflections. *Elytra:* Color (with illumination and magnification) dark metallic blue-green (dark metallic green

to unaided eye). Intervals near humerus with some transverse rugosity; punctures setig-
erous near apex; setae moderately dense, short, rufous.
    Female unknown.

    DIAGNOSIS. *Viridimicus cyanochlorus* is readily distinguished from others
in the genus because the apex of the third protarsomere is *not* ventrally bilobed
(Fig. 20); instead, it is entire.
    DISTRIBUTION (Map 1). Occurs in the southern Sierra Madre in Oaxaca,
Mexico (Map 2).
    REMARKS. The holotype of this species was collected in an area George E.
Ball (pers. comm., 1988) called a "sylvan paradise," a place where many steep-
sided ravines converge in west-facing montane rain forest. In 1966, this region
was densely forested; since then, the area has been cleared for corn, papaya,
and banana. Females and the natural history are unknown for this species.
    ETYMOLOGY. This species is named for the color of the holotype specimen
which is distinctly blue- (*cyano-*) green (*-chloros*).

Viridimicus impunctatus Jameson, new species
(Figs. 19, 23; maps 1, 2)

    TYPE MATERIAL. Holotype labeled, "MEXICO: Guerrero, Sierra Madre del
Sur, 28 km NNE El Paraiso, 2220 m, 14 July 1982, John E. Rawlins." Allotype
and paratypes (4 males) labeled as holotype. Holotype and 3 paratypes de-
posited at CMNH. Allotype and 1 paratype deposited at UNSM.

    DESCRIPTION. Holotype male. Length 21.4 mm; width across humeri 11.0 mm; great-
est width 12.3 mm. *Head:* Color of frons and clypeus dark metallic green. Surface
moderately densely punctate; punctures mixed, moderate to small, sparsely setigerous
laterally; setae rufous, short to moderate. Discal region of clypeus with large punctures
randomly placed, nearly confluent apically, basally and laterally some separated by one
puncture distance. Punctures of frons larger laterally and apically; basal punctures small;
small group of about 15 punctures at center base. Frontoclypeal suture medially obsolete,
slightly biarcuate. Clypeus declivous with respect to frons (Fig. 23), sides diverging slightly
from base, then broadly rounded to semiovate apex; apex moderately reflexed, ventral
side of reflexed apex sparsely punctate, not setigerous; punctures small. Interocular width
5.5 transverse eye diameters. Labrum truncate apically. Mandibles hidden in dorsal
view. *Pronotum:* Color metallic dark green (with or without magnification and illumi-
nation). Surface sparsely punctate, punctures small (micropunctate), larger but obscure
at margin. *Elytra:* Color (under illumination and magnification) black, shiny. Surface
with weakly impressed, nearly obsolete striae; two in center of disc, one (poorly defined)
posterior of humerus. Intervals moderately densely punctate, punctures small, sparsely
setigerous laterally (at middle) and apically; setae short, tawny. *Pygidium:* Color as
pronotum. Surface moderately densely punctate; punctures small and moderate mixed,
becoming larger laterally, confluent basolaterally, setigerous laterally; setate moderately
long to long, tawny. *Legs:* Pro- and mesotarsi each with one claw enlarged, feebly cleft,
4 times width of smaller claw. Metatarsus with large claw 2 times width of smaller claw,
distinctly cleft. Protarsus with third tarsomere emarginate, stout seta within emargination
(Fig. 19). *Venter:* Densely clothed with long, tawny pile. Abdominal sternites less densely
clothed.
    Allotype female. Length 22.6 mm; width across humeri 11.8 mm; greatest width 13.7
mm. Differs from holotype in the following respects: *Head:* Color black, opaque. Frons
moderately densely punctate; punctures moderate to small, more shallow than punctures
of male. Clypeus confluently punctate; punctures small and moderate, mixed. Interocular
width 7.0 transverse eye diameters. *Pronotum:* Punctures laterally moderate in size.
Pygidium: Punctures at base confluent. *Legs:* Protarsus with claws of equal size and
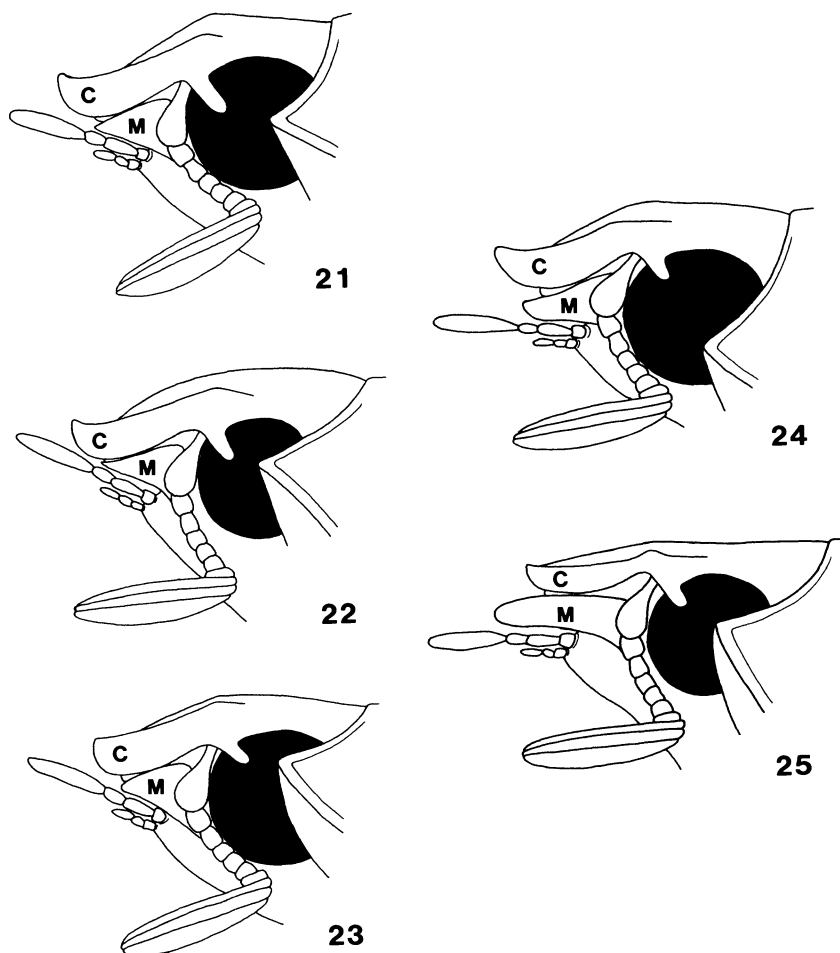
Figs. 21–25. *Viridimicus* spp. Head, lateral view (profile) showing relative declivity of clypeus with respect to frons; 21–24, clypeus declivous with respect to the frons. 21, *V. aurescens.* 22, *V. cyanochlorus.* 23, *V. nigroaeneus* and *V. impunctatus.* 24. *V. unitus.* 25. *V. ratcliffei,* clypeus and frons horizontal (also note forward projecting mandible).

width, not cleft. Mesotarsus with claws of equal size and width, one claw cleft. Metatarsi absent.

Paratypes (4 males). Length 21.4–23.7 mm; width across humeri 10.6–12.2 mm; greatest width 12.2–13.9 mm. Paratypes differ from holotype in the following respects: *Head:* Frontoclypeal suture obscured or not medially. Interocular width 5.5–7.0 transverse eye diameters. *Pronotum:* Punctures laterally small to moderate, obscured or not. *Elytra:* Color (under magnification and illumination) black and shining, with or without metallic green reflections. Surface with two or three striae in center of disc, none or one (poorly defined) posterior of humerus. *Pygidium:* Moderately densely or densely punctate; punctures confluent laterally or only basolaterally.
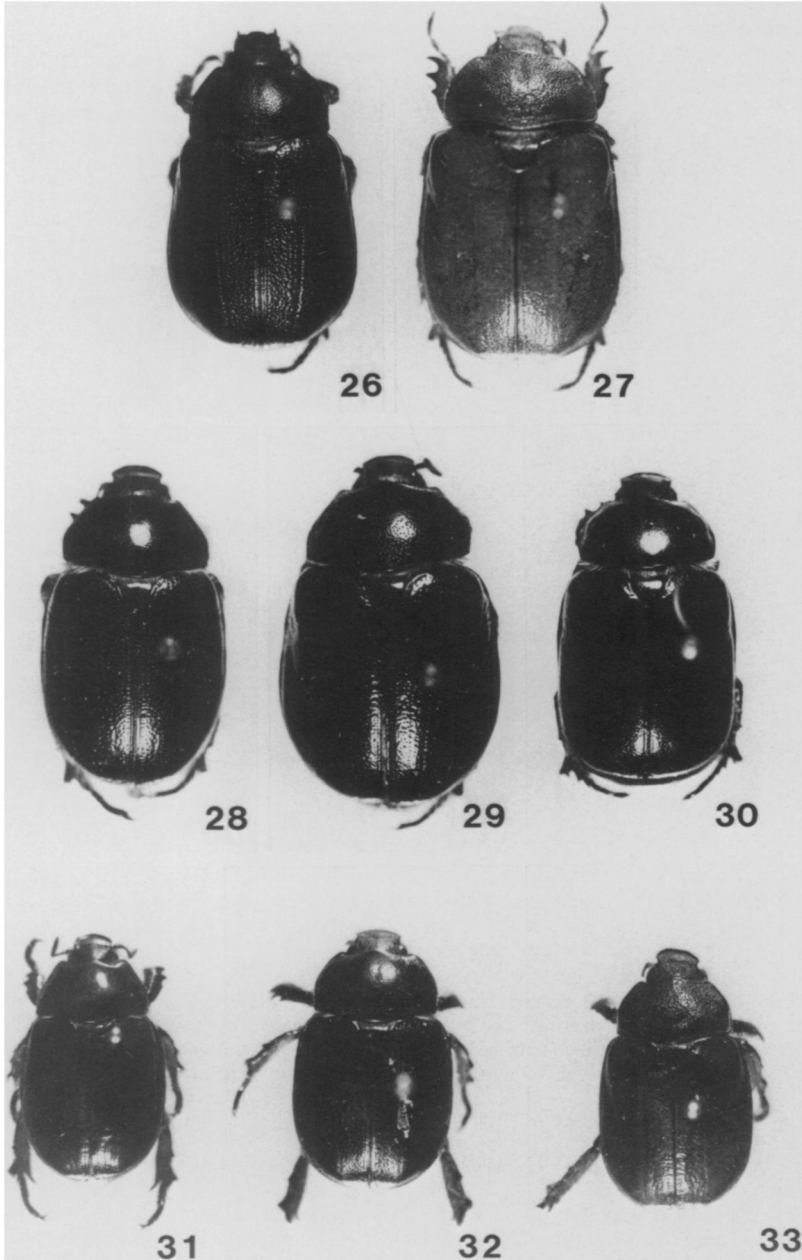
Figs. 26–33. Dorsal views of *Parabyrsopolis* sp. and *Viridimicus* spp. 26, 27, *P. chihuahuae* (both males). 28, *V. aurescens* (male). 29, *V. aurescens* (female). 30, *V. cyanochlorus* (holotype male). 31, *V. nigroaeneus* (paralectotype male). 32, *V. ratcliffei* (holotype male). 33, *V. unitus* (holotype male).

DIAGNOSIS. *Viridimicus impunctatus* can be separated from others in the genus due to the sparsely micropunctate pronotum, the metallic coloration of the female, the large interocular width (5.5–7.0 in males, approximately 7.0 in females), and the punctures of the discal regions of the head not confluent.

DISTRIBUTION (Map 1). Occurs in the northern extent of the Sierra Madre del Sur in Guerrero, Mexico (Map 2).

REMARKS. This species was collected by John E. Rawlins in the Rio Balsas region which has yielded many new species of plants and animals (Rawlins, pers. comm., 1989). The site where the insect was collected was wet montane forest covered with dense vegetation. Due to the elevation (2,220 m), steep terrain, and south facing slope, the locality is wet throughout the year. The beetles were collected from vegetation during the day.

Viridimicus nigroaeneus (Bates), new combination
(Figs. 18, 23, 31; maps 1, 2)

Cotalpa nigroaenea Bates 1888:289. Lectotype male at BMNH with my lectotype label; 3 paralectotypes also at BMNH, all males. Type locality: Cerro Zunil, Guatemala.

DESCRIPTION. Male. Length 19.8–20.3 mm; width across humeri 9.7–10.4 mm; greatest width 10.6–11.6 mm. *Head:* Color metallic dark green (with or without illumination and magnification). Surface moderately densely punctate; punctures moderately large to small, mixed, becoming larger laterally. Discal regions of frons and clypeus with larger punctures randomly placed, generally separated by their own diameters, setigerous laterally; setae rufous, short to moderate in length. Frontoclypeal suture slightly raised, biarcuate. Clypeus declivous with respect to frons (Fig. 23), sides subparallel, diverging only slightly from base, then broadly rounded to semicircular apex; apex moderately reflexed, ventral side of reflexed apex setigerously punctate; setae moderate to moderately long, moderately dense, rufous. Interocular width 3.0–4.0 transverse eye diameters. Labrum truncate apically. Mandibles hidden in dorsal view. *Pronotum:* Color metallic dark green (to unaided eye), metallic green to brown with green reflections (with illumination and magnification). Surface moderately densely punctate; punctures small (very sparse) to moderate (dense) on disc, moderate to moderately large laterally. *Elytra:* Color (with magnification and illumination) brown to piceous, with blue and/or green reflections (black with dark metallic green reflections to unaided eye). Surface with loosely defined punctate striae; one next to suture, one on disc, one just mesad of humerus; punctures small to moderate in size. Intervals broad, moderately densely punctate; punctures small to moderate, those on sides (at middle of elytra) and apex setigerous; setae rufous, short to moderate in length. *Pygidium:* Color as pronotum. Surface of disc finely, densely rugopunctate to confluently punctate, becoming rugulose laterally; punctures small, setigerous; setae moderately long to long, rufous. *Legs:* Pro- and mesotarsi each with one claw enlarged and indistinctly cleft, 4 times as wide (in dorsal view) as smaller claw. Metatarsus with larger claw about 1.5 times size of smaller claw, cleft poorly defined. Protarsus with third tarsomere emarginate with stout seta between emargination (Fig. 19). *Venter:* Densely pilose; pile long, rufous. Abdominal sternites less densely pilose. Female unknown.

DIAGNOSIS. *Viridimicus nigroaeneus* is distinguished by large punctures on discal regions of clypeus and frons separated by approximately their own diameters and by the confluently punctate to rugopunctate pygidial disc.

DISTRIBUTION. Occurs on the Pacific slopes in Guatemala (southern extension of the Sierra Madre de Chiapas, Map 2), 12 km southeast of Quezaltenango (91°29′W, 14°43′N) (Selander and Vaurie 1962). The elevation of this area is approximately 2,000 m.

Locality records (Map 1): 4 specimens examined (all males from the original type series) from BMNH. GUATEMALA (4). **Quetzaltenango** (4): Zunil.

Temporal distribution: Unknown. (See remarks for possible dates collected.)

REMARKS. This species was described by Bates (1888) in the genus *Cotalpa*. Since its description, it has shifted between *Cotalpa* and *Parabyrsopolis*. Ohaus (1918, 1934) removed it to *Parabyrsopolis*, Blackwelder (1944) moved it back to *Cotalpa*, and Machatschke (1972) moved it back again to *Parabyrsopolis*.

This species is known only from the type series of four specimens. The collector of these specimens, G. C. Champion, published an itinerary of his travels in Central America (Champion 1907). In this brief schedule, he lists two entries in 1880 for Cerro Zunil (the type locality), during which time he may have collected the specimens: "Aug. 20–Sept. 9. Finca of Las Nubes, on the Pacific slope of the Cerro Zunil, above Mazatenango (4050 ft.). Coffee plantations, with dense forest above," and "Nov. 19–Dec. 14. Las Nubes (Cerro Zunil)." It has been over one hundred years since these specimens were collected. The habitat has, in all probability, been severely altered.

Natural history and females are unknown.

Viridimicus ratcliffei Jameson, **new species**
(Figs. 14, 19, 25, 32; maps 1, 2)

TYPE MATERIAL. Holotype labeled, "7 mi. E. Teziutlan Puebla, Mexico, 7-20-1955." Allotype labeled as holotype. Both deposited at UNSM. Paratype labeled, "Tlaltizapan? [Veracruz]" "Mexico, J. Flohr G.," "Tlat," "Zool. Mus. Berlin," "88905," "Ohaus determin 1912, *Byrsopolis nigroaenea* Ohs. ? ♀" and "*Parabyrsopolis nigroaenea* (Ohaus) (= *fuscoaenea* (Ohaus)), paralectotype, M. E. Jameson 1988." Deposited at ZMBH.

DESCRIPTION. Holotype male. Length 21.3 mm; width across humeri 11.0 mm; greatest width 12.2 mm. *Head:* Frons dark metallic green; clypeus metallic violet-brown. Surface densely, confluently punctate; punctures small and moderately large, mixed, setigerous laterally; setae rufous, short to moderate in length. Frontoclypeal suture weakly impressed, only slightly raised (as seen in profile). Clypeus not declivous with respect to frons (Fig. 25), appearing more or less flat in profile; sides diverging from base then converging abruptly to semicircular apex; apex weakly reflexed, ventral side of reflexed apex setigerously punctate; setae moderate in length, moderate in density, straw-colored. Interocular width 4.0 transverse eye diameters. Labrum weakly sinuate apically. Mandibles exposed, flat in dorsal view (Fig. 14). *Pronotum:* Color (with illumination and magnification) castaneous with metallic green reflections (dark metallic green to unaided eye). Surface moderately densely punctate; punctures moderate to moderately large, becoming larger laterally, coalescing at center of lateral margin (areas of internal muscle attachment). *Elytra:* Color as in pronotum. Surface with striae weak; one next to suture, one on disc, two just mesad of humerus; punctures small to moderate. Intervals moderately densely punctate; punctures small to moderate in size, margins with some intervals transverse, sparsely setigerous at apex; setae short, tawny. *Pygidium:* Color as in pronotum and elytra. Surface moderately punctate; punctures small, setigerous; setae moderately dense, tawny, moderately long. *Legs:* Protibia with one claw enlarged, cleft; in dorsal view, larger claw 2 times as wide as smaller claw. Mesotarsus with one claw enlarged and cleft; larger claw twice as wide as smaller claw. Protarsus with third tarsomere apically emarginate, stout seta in emargination (Fig. 19). Metatarsi missing. *Venter:* Densely clothed with long, tawny pile. Sternites 1–6 less densely pilose.

Allotype female. Length 24.8 mm; width across humeri 12.8 mm; greatest width 15.0 mm. Differing from holotype in the following respects: *Head:* Color castaneous, opaque. Clypeus very weakly convex in profile. *Pronotum:* Color (with illumination and magnification) castaneous with slight metallic green reflections (piceous to unaided eye).

Elytra: Color as in pronotum. Surface with punctate striae; one next to suture, one on disc, one just mesad of humerus. First interval broad, moderately densely punctate; second interval about half as wide as first, moderately densely punctate; third interval broad, sparsely punctate, punctures small. Apex of elytra without setae. *Legs:* Pro- and mesotibial claws simple, equal in width. Metatibia with one claw slightly cleft, both claws of equal width.

Paratype female. Length 24.3 mm; width across humeri 12.2 mm; greatest width 14.4 mm. Differing from allotype in the following respects: *Elytra:* Surface with punctate striae; 1 next to suture, 1 in center of disc, 2 just mesad of humerus. First interval broad, moderately densely punctate, punctures small; second interval half width of first, moderately punctate, punctures small; third interval sparsely punctate, punctures small; fourth interval broad, moderately punctate, punctures small. *Pygidium:* Surface of disc with feebly impressed longitudinal groove.

DIAGNOSIS. The broadly exposed, flat (not concave) mandibles (Fig. 14), the head which appears flat in profile (Fig. 25), and the sparsely punctate (punctures not confluent) pygidium serve to easily distinguish this species.

DISTRIBUTION (Map 1). Occurs in the southernmost extension of the Sierra Madre Oriental where it meets the Transverse Volcanic Belt (Map 2) at an elevation of approximately 1,900 m.

REMARKS. The female paratype of this species was a part of the type series of *Parabyrsopolis fuscoaenea* Ohaus (1918), who described the noticeable differences in this specimen as being due to only partial sclerotization and/or melanization or local variation. The validity of this specimen's locality data is questionable. A temporary label (handwritten in pencil) reads, "Tlat" which was translated to the permanent label as Tlaltizapan (with a question mark). *If* this is the correct locality, it was collected in Morelos, 30 km SSE of Cuernavaca (99°07′W, 18°41′N, 915 m).

Life history information of this species is lacking.

ETYMOLOGY. I am pleased to name this species in honor of my mentor and friend, Brett Ratcliffe, who drew this specimen to my attention and who has contributed much to the study of Neotropical Scarabaeidae.

Viridimicus unitus Jameson, **new species**
(Figs. 19, 24, 33)

TYPE MATERIAL. Holotype male labeled, "Mexico," "Ohaus determin *Parabyrsopolis aurescens* Bts ♂? or n. sp." Deposited at BMNH.

DESCRIPTION. Holotype male. Length 21.3 mm; width across humeri 10.8 mm; greatest width 12.3 mm. *Head:* Color (with illumination and magnification) reddish-brown with slight metallic brassy-green reflections on lateral part of frons (dull violet-green to unaided eye). Surface entirely rugopunctate; punctures mixed moderate and large, setigerous laterally; setae tawny, moderately long. Frontoclypeal suture weakly biarcuate. Clypeus declivous with respect to frons (Fig. 24); sides diverging from base for one-fourth length, then broadly rounded to subtruncate apex; apex broadly reflexed, ventral side of reflexed apex setigerously punctate; setae rufous, moderately dense, moderately long. Interocular width 3.5 transverse eye diameters. Labrum truncate apically. Mandibles barely visible in dorsal view. *Pronotum:* Color (with illumination and magnification) reddish-brown with brassy-green reflections. Surface of disc moderately densely punctate; punctures small (sparse) and large (dense), mixed, some confluent; margin confluently punctate to coarsely rugopunctate. *Elytra:* Color (with magnification and illumination) as in pronotum. Surface with four poorly defined striae: one next to suture (nearly obsolete), one on disc, two just mesad of humeri; strial punctures moderate in size. First interval broad, moderately densely punctate, punctures moderate in size, irregularly spaced; second interval with a few transverse rugae medially; third interval
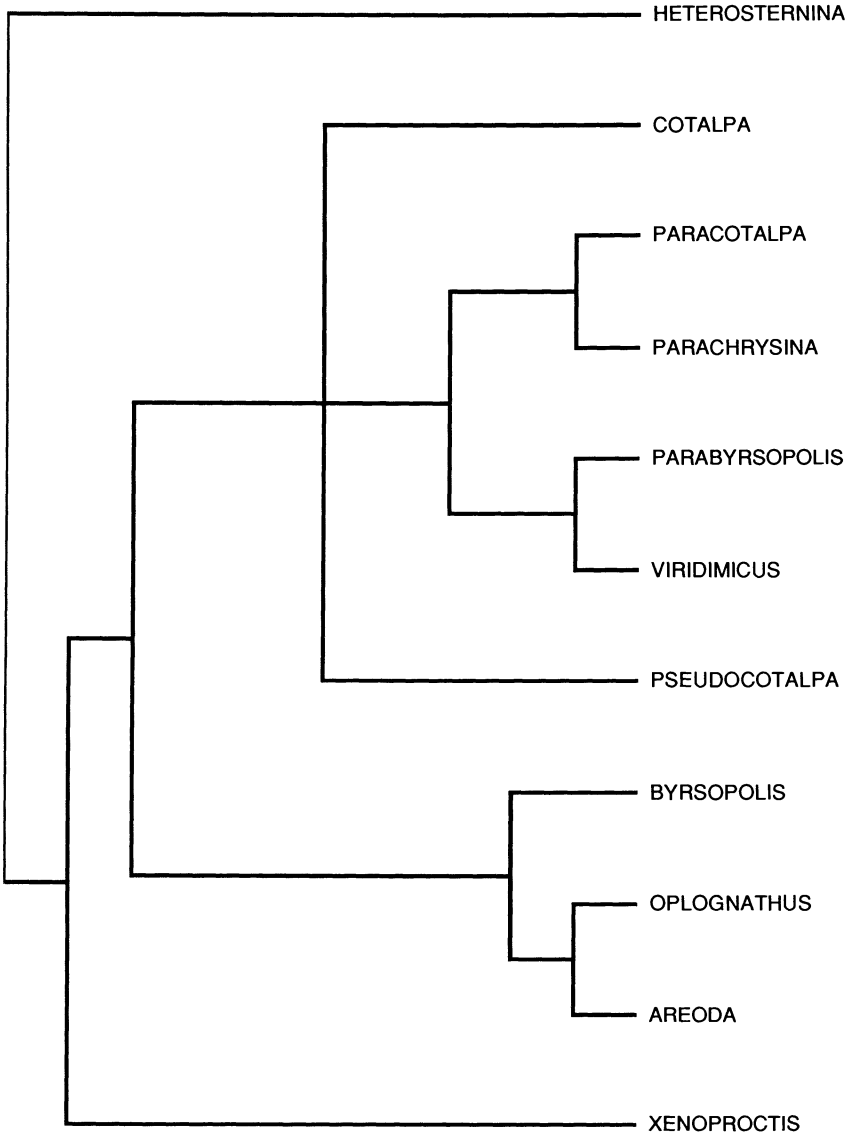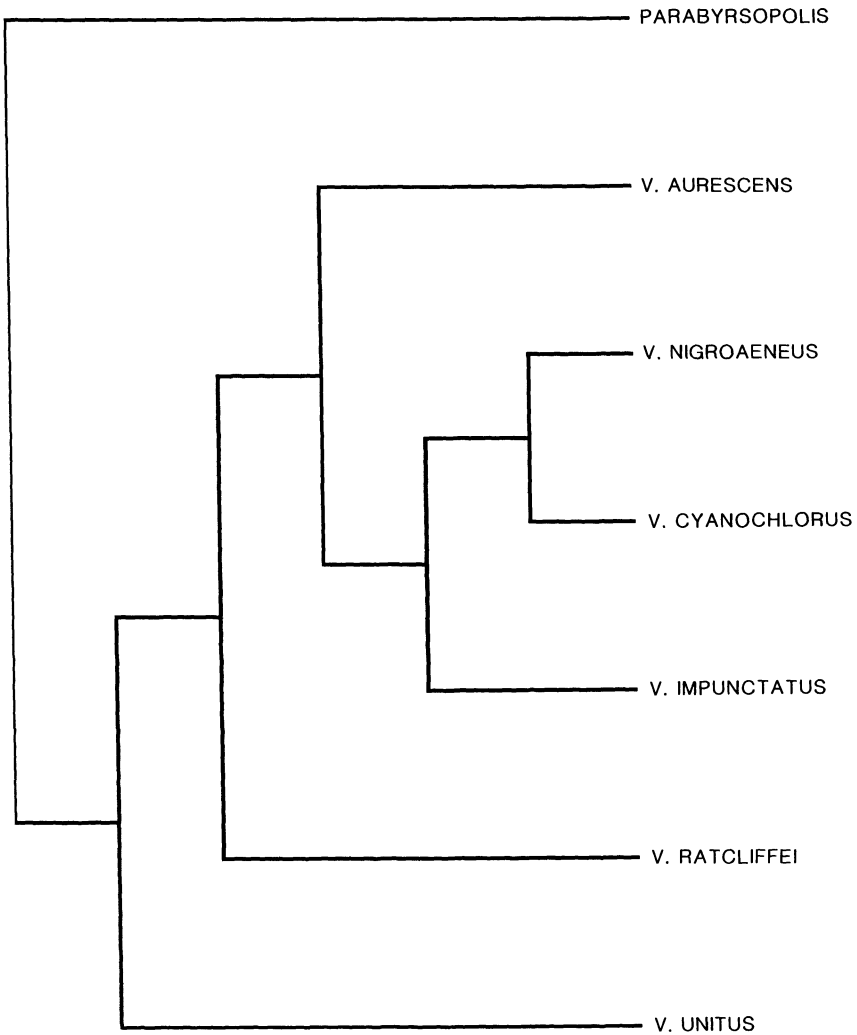
HETEROSTERNINA

COTALPA

PARACOTALPA

PARACHRYSINA

PARABYRSOPOLIS

VIRIDIMICUS

PSEUDOCOTALPA

BYRSOPOLIS

OPLOGNATHUS

AREODA

XENOPROCTIS

34

Fig. 34.   Cladogram for genera of Areodina using Heterosternina as the out-group.

35

Fig. 35.   Cladogram for *Viridimicus* spp. using *Parabyrsopolis* as the out-group.

moderately to moderately densely punctate, punctures small. Apex of elytra with narrow margin of setigerous punctures; setae tawny, short. *Pygidium:* Color as in elytra. Surface of disc densely punctate, becoming densely rugopunctate laterally, punctures small and moderate, mixed, setigerous; setae moderately dense, tawny, moderately long. *Legs:* Pro- and mesotarsi each with larger claw 2.5 times as wide (in dorsal view) as smaller claw, feebly cleft. Mesotarsus with larger claw cleft and twice as wide as smaller claw. Metatarsal

Map 1.   Distribution of *Parabyrsopolis chihuahuae* and *Viridimicus* spp.

claws missing. Protarsus with third tarsomere bilobed with stout seta between lobes. *Venter:* Densely pilose; pile long, tawny. Abdominal sternites less densely pilose.

Female unknown.

DIAGNOSIS. The rugopunctate head, brassy-green color, confluently punctate lateral regions of the pronotum, and rugopunctate lateral margins of the pygidium distinguish this species.

DISTRIBUTION. Known only from an unknown locality in Mexico.

REMARKS. Although this species is known only from a single male, it is unique among *Viridimicus* for its strongly rugopunctate head and sides of the pronotum.

Females and life history are unknown for this species.

ETYMOLOGY. This species is named from the Latin *unitus* which means to join together, as it has character states reminiscent of both *Parabyrsopolis* (general rugosity, large punctation, and brown base color of the cuticle) and *Viridimicus* (semicircular clypeal apex, rounded parameres, green luster to the epicuticle).

BIOGEOGRAPHY OF THE AREODINA

Though a good deal is too strange to be believed, nothing is too strange to have happened.

—Thomas Hardy

Evolutionary reconstruction of the Areodina is impeded by the usual obstacle in paleoentomology—the lack of fossil evidence. Because of this, biogeographical analyses must rely upon data from continental drift, distributions of modern taxa, and the distribution of well-fossilized plants and animals. We

must also consider that the geological phenomena that we witness today (positions of the continents, oceans, mountains, etc.) took shape in the time frame of millions of years. The Earth and its lithosphere are dynamic. As a result of these geologic changes, the evolution and dispersal of fauna and flora are dynamic as well, constantly changing as a result of climate, orography, vegetation, and even the "progress" of man.

Relative to Earth history and the establishment of physical features, barriers, and corridors, the dispersal of a taxon can evolve very rapidly. For example, the extinct Gomphotheridae (Mammalia) began a long sojourn from Africa some 30 million years ago and arrived in South America approximately 2 million years ago (Darlington 1957). Their feet tread on thousands of miles of land and crossed many geographic barriers, but, in the end, led them in the direction of favorable climate and habitat. This well-substantiated movement spanned four continents and lasted approximately 28 million years. As a modern analog of long-distance migration, the Africanized honeybee (*Apis mellifera scutellata* Lepeletier) has dispersed 300 to 500 km per year from Rio Clara in southern Brazil to central Mexico (Camazine and Morse 1988) in only *30 years* and has crossed a wide range of vegetational and climatic zones. Although long-distance dispersal may not be viewed as parsimonious, reliable fossil records, as well as modern-day analogs, document its occurrence throughout the history of the Earth and its biota.

The Modern Areodina

The extant Areodina is comprised of ten genera: *Areoda, Oplognathus* (*not Hoplognathus* as is commonly cited), and *Byrsopolis* from South America; *Cotalpa, Paracotalpa, Pseudocotalpa, Parabyrsopolis, Viridimicus,* and *Parachrysina* from North America; and *Xenoproctis* from Africa (the *only* genus of Rutelini in Africa) (Map 4). The subtribe is represented by three genera and 15 species in South America, six genera and 24 species in North America, and one genus with three species in Africa.

The disjunct distribution of the subtribe between the Western Hemisphere and Africa, as well as the disjunction between northern Central America and northern South America, has led me to consider the group as polyphyletic, but phylogenetic analyses have upheld monophyly, and the variation in character states is not outside the range displayed by many other subtribes in the Rutelini. These disjunctions have also caused me to critically view many biogeographical hypotheses ranging from Holarctic and Nearctic patterns to Gondwanan and Laurasian models.

Asian and American Affinities

The Rutelini is represented by 11 subtribes and approximately 80 genera (Machatschke 1972) that occur in Africa, southeast Asia, and the Western Hemisphere (Map 3). Within the Rutelini, two subtribes, the Parastasiina and the Pelidnotina, occur in both Asia and North America. The Pelidnotina is a wide-ranging group with taxa in southeastern Asia, the United States, Mexico, Central America, and South America (Machatschke 1972). The Parastasiina are predominantly Asian with two species in the United States. Distributional affinities between Asia and the Western Hemisphere, such as in the Rutelini, while common, remain poorly studied.

In Coleoptera, this distributional pattern is manifested in many taxa, such as the tribe Dorcaschematini (Cerambycidae) (Matthews 1980), in the closely

related melolonthine (Scarabaeidae) genera *Phyllophaga, Cnemarachis, Cle-mora, Holotrichia, Brahmina,* and *Microtrichia* (Morón 1986), and in the Pe-nichrolucaninae (Lucanidae) (Ratcliffe 1984). Extant plant taxa, such as *Mi-trastemon, Magnolia, Engelhardtia, Clethra, Turpinia,* and a dozen other plant genera also display this distributional pattern (Rzedowski 1986).

Mammals that originated in Asia have become a major part of the fauna in the Western Hemisphere. These include the jaguar, tapir, musk ox, deer, bear, moose, mountain sheep, caribou, mammoths, lemmings, and several others (Kurtén and Anderson 1980; Schultz 1960). This faunal exchange also occurred from North America to Asia as, for instance, Camelidae and Equiidae.

Affinities between Asia and North America exist as far back as the Late Cretaceous and are supported by reliable fossil evidence, such as tyranno-saurids, protoceratopids, ceratopids, pachyrhinosaurids, and dromaeosaurids (Charig 1983). Fossil plants of the Upper Cretaceous also demonstrate this link (Charig 1983).

## The Ancestral Areodina of the Western Hemisphere

These past and present distributions of plants and animals substantiate a previous land connection with a suitable climate between Asia and the Western Hemisphere that is explained by the geologic history of the region.

From the Late Cretaceous to the Early Oligocene (Map 5), North America was split into two continents by the Mid-Continental Seaway (Charig 1983; Noonan 1986). One continent, Euramerica, lay in the eastern half of North America, and a second continent, Asiamerica, lay in the western half.

In the northern portions of Asiamerica, favorable climate and vegetation, as well as dry land (perhaps intermittent), existed from the Cretaceous until the Late Cenozoic (Charig 1973; McKenna 1983). This corridor allowed for the interchange and dispersal of adaptively capable organisms from both Asia and North America (McKenna 1973). The dispersal, genetic interchange, cli-mate, and vegetation within this region created what Matthews (1980) referred to as an "evolutionary center."

Within Asiamerica, the ancestral Rutelini began to radiate, expanding south-wards on either side of the corridor and probably extending their range in the Western Hemisphere as far south as northern Central America [the most south-ern extent of the North American continent at this time (Map 5)]. However, in the Cenozoic, as the lithosphere near Beringia began to move closer to the rotational pole, temperatures declined and daylength decreased (McKenna 1983). By the Mid-Eocene, survival of tropical and subtropical biotas was improbable, and these organisms were forced southward to either side of Beringia (Matthews 1980), perhaps as far as 45°N latitude (Matthews 1978). Lineages became fragmented and the interchange of tropical and subtropical Asiamerican taxa was diminished (Noonan 1986). The lineages of Rutelini and Areodina became effectively separated between Asia and North America.

In the Late Tertiary, the climatic vicissitudes of North America placed pressures on ancestral areodines, promoting evolutionary diversification or causing extinction. For some ancestral areodines, and orographic features in Mexico and the United States fragmented suprageneric lineages, thus causing differentiation of genera. Periodic glacial episodes, the maximum reaching as far south as 40°N latitude (Toledo 1982), also were strong evolutionary forces for the Areodina. Several ancestral taxa probably survived in benign pockets of habitat, expanding their ranges when the climate allowed.
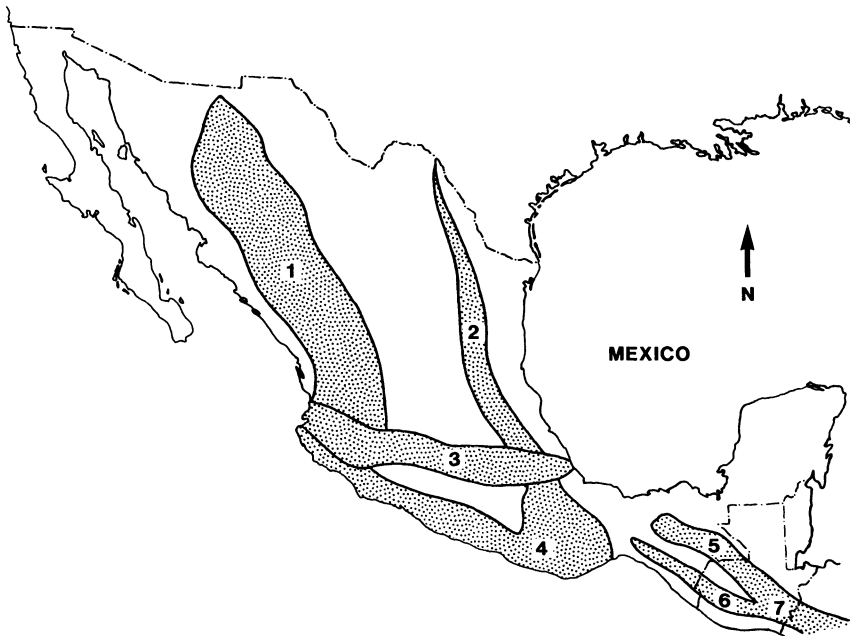
Map 2.   Distribution of the major mountain systems in Mexico (from Rzedowski 1986; Halffter 1987). 1, Sierra Madre Occidental. 2, Sierra Madre Oriental. 3, Transverse Volcanic Belt. 4, Sierra Madre del Sur. 5, Chiapas Central Massif. 6, Sierra Madre de Chiapas. 7, Central American Nucleus.

During the Late Tertiary, the Central American Nucleus (Map 2) was not subject to vulcanism (Kohlmann and Halffter 1988), as were many other regions in Mexico. Because of this and the favorable tropical to subtropical climate, this region served as a diversification center for many plants and animals (Raven and Axelrod 1974), including the Areodina. Competition for resources due to compression of the habitat probably promoted intense motivation for southward dispersal. However, the connection between northern Central America and South America was not complete. From the Late Cretaceous to the Oligocene, the Americas were separated by approximately 1,300 km of ocean (Raven and Axelrod 1975). For almost 50 million years, the only access between the areas of northern Central America and northern South America was an arc of volcanic islands. Even in the Miocene, these islands were separated from one another by a distance of 70 to 100 km (Matthews 1980) and served as a *highly filtered* dispersal route. Some biogeographical analyses of Coleoptera (Kohlmann and Halffter 1988; MacVean and Schuster 1981) propose dispersal across the Proto-Antilles archipelago (present in the Mesozoic) or across the islands between North and South America (which were continuous near the Mid-Miocene) before the rise of the Panamanian isthmus in the Pliocene. Sweepstakes dispersal between the two continents before the Pliocene, while possible, was, in my opinion, improbable with regards to the Areodina. Even after the rise of the isthmus (between 3 and 5.7 mya) (Marshall 1988; Raven and Axelrod 1974 respectively), this area served as a *filter* rather than a corridor

due to its primarily, if not entirely, woodland savannah and thorn forest habitat (as indicated by fossil evidence) (Matthews 1980; Webb 1978). However, Pleistocene glacial episodes, 2 to 4 million years after the rise of the isthmus, would have shifted altitudinal vegetation zones allowing for dispersal of montane fauna into South America (Kohlmann and Halffter 1988). Areodine taxa that had been under constraints (such as habitat compression and intense competition) and were adaptively capable, dispersed across the isthmus and into South America.

However, these ancestral areodines became the inhabitants of an unstable South American environment. Cooler temperatures brought by the Humboldt Current created a temperate habitat, and by the Quaternary, South America (as well as Africa) underwent ice age aridity (Raven and Axelrod 1974). The survival of the Areodina was dependent upon restricted areas of relative stability, or refugia. Surviving Areodina became isolated in these refugia in response to the changing climate and fragmentation of habitat (Ratcliffe and Jameson 1989; Haffer 1982; Endler 1982; Mayr and O'Hara 1986). Refuge areas are known for endemic biota; birds, reptiles, primates, and insects. In the Scarabaeidae alone, a number of taxa from the tribes Rutelini, Geniatini, Pentodontini, Agaocephalini, and Phileurini are inhabitants of refugia (Ratcliffe and Jameson 1989). These isolated land relictual habitats, as well as many other tropical regions in the world, are now on the brink of total destruction. Refuge areas are being drastically altered by man (Brown 1976, 1982), and by the end of the 20th century these gene pools may be irretrievably lost.

Among the extant Areodina, no taxa are found in the region between southern Guatemala and Guyana. Although enigmatic, disjunctions between southern Mexico and northern South America *have* been observed in other organisms. Many Pleistocene vertebrates (birds, reptiles, and rodents) of woodland savannahs are entirely absent from Central America and continue their range on either side of the isthmus. Plant taxa, such as *Alchemilla pinnata, Selaginella peruviana,* and *Larrea* sp., also display this distributional gap (Rzedowski 1986).

Some of these taxa may have been able to cross the Panamanian isthmus during glacial episodes when vegetational zones descended as much as 650 m in relation to present altitudinal limits (Kohlmann and Halffter 1988). After glacial retreat, however, the low and arid Nicaraguan Depression (just south of the Central American Nucleus), in combination with recurring savannah-like habitat and drier climate of the isthmus, probably caused extinction or dispersal from the isthmian region. This aridity posed as a substantial barrier for new dispersal and tended to isolate taxa north and south of the isthmus.

Areodina in Africa

In the Mid-Eocene, the cooling northern climate promoted southward movement of tropical biota in Asiamerica and subsequent movement of tropical and subtropical fragmentation of the Rutelini North America and Asia. For those Rutelini and Areodina in Asia, dispersal as far as Africa over intermittent land occurred before the Miocene and uplift of the Himalayas (Riedel 1988). After appreciable uplift of the Himalayas, Rutelini became isolated in regions of southeast Asia to the east and in regions of Asia/Africa to the west. Similar to the Areodina in South America, the taxa in Africa and Asia encountered Late Tertiary and Quaternary droughts (Raven and Axelrod 1974). In Africa during the Miocene, the Benguela Current drastically decreased precipitation (Raven
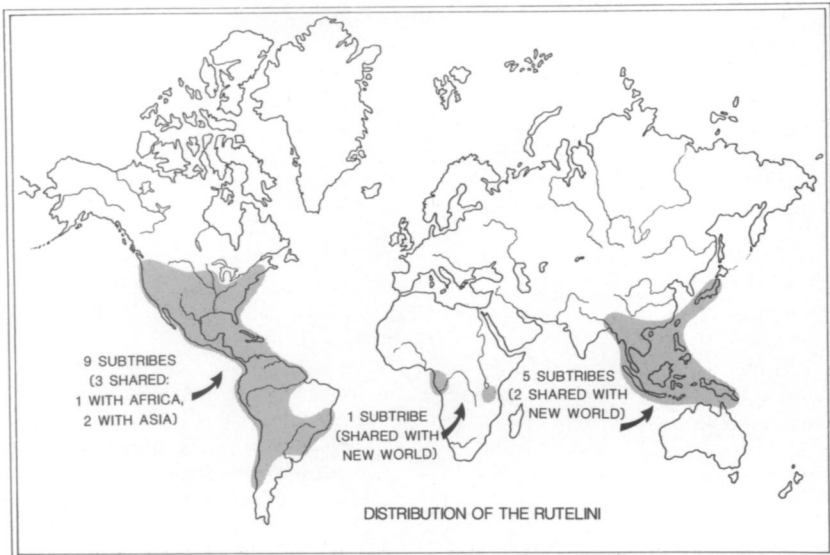
Map 3. Distribution of Rutelini of the world.

and Axelrod 1975). Drought caused desertification as far south as the Congo (Haffer 1982) and extinction of many taxa. The Areodina survived in refugia similar to those taxa in South America. The postulated refuge areas of west-central Africa and east-central Africa (Haffer 1982; Grubb 1982) remain today as the only regions where *Xenoproctis* (the only genus of African Rutelini and Areodina) occurs.

BIOGEOGRAPHY OF *VIRIDIMICUS* AND *PARABYRSOPOLIS*

Mountains can be regarded as islands and centers for differentiation, diversification, and speciation. Speciation in *Parabyrsopolis* and *Viridimicus* are the result of orogenic isolation and endemism as well as vulcanism: The only species of *Parabyrsopolis* occurs north of the Transverse Volcanic Belt in the Sierra Madre Occidental, and to the south occurs *Viridimicus* in the several mountain systems of southern Mexico.

Before the Late Eocene or Early Oligocene and major uplift of the Mexican mountain systems, the lineage that gave rise to *Parabyrsopolis* and *Viridimicus* had retreated southwards from middle North America to more favorable climes in Mexico and northern Central America due to cooling northern temperatures (McKenna 1983). By the end of the Laramidian orogeny in the Miocene (Halffter 1987), the lineage was gradually fragmented by the uplifted Transverse Volcanic Belt (occurring from the Pliocene to recent). As a result, *Parabyrsopolis* became isolated to the north of the Transverse Volcanic Belt, and *Viridimicus* became isolated to the south. This mountain system, which forms a vicariance barrier across central Mexico, acted as an important evolutionary force, promoting allopatric speciation in many Mexican taxa (Kohlmann and Halffter 1988; Halffter 1987).
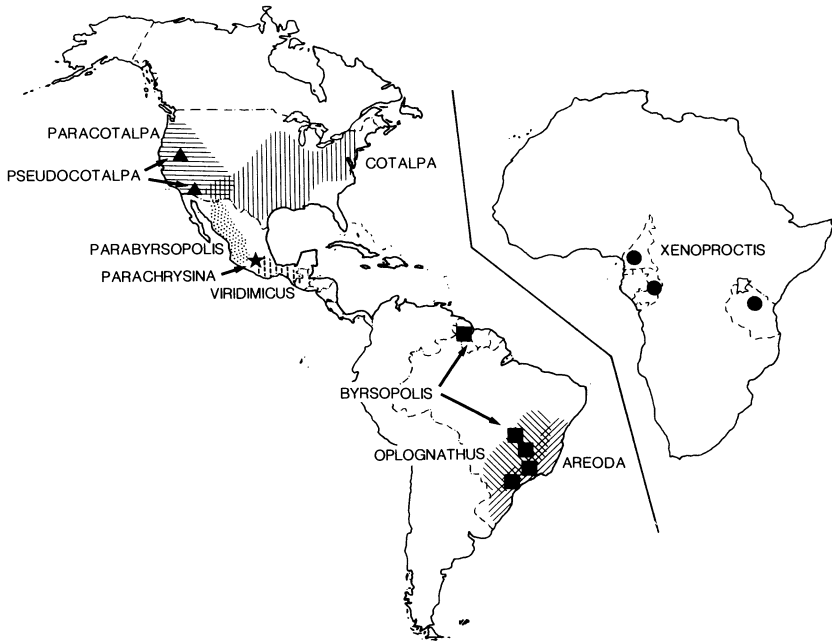
Map 4.   Distribution of genera of Areodina.

Biogeography of *Parabyrsopolis*

Climatic oscillations during the Late Cenozoic (Kohlmann and Halffter 1988; Toledo 1982) caused recurring contraction and expansion of the range of *Parabyrsopolis*. The Sierra Madre Occidental, being a more or less continuous mountain system, served as a dispersal corridor during climatically favorable periods. In times of glacial advance, montane vegetation was pushed to lower elevations and created corridors between mountains (Hall 1985). This allowed the *Parabyrsopolis* lineage to extend its range in concert with that of the pine-oak forest and as far as the Huachuca and Patagonia mountains in Arizona.

Since differentiation of the genus, the continuity of this mountain system and local climate has *prevented* isolation, has allowed for recurrent dispersal and overlap of populations, and has permitted a relatively continuous gene flow. Because of these factors, further speciation has not been favored.

Biogeography of *Viridimicus*

South of the Transverse Volcanic Belt, the same set of geologic events and climatic factors affected the species of *Viridimicus*. Interglacial and interpluvial periods caused constriction of forests, and glacial advances promoted expansion of these same forests (Haffer 1982; Prance 1982). But whereas the mountain system north of the Transverse Volcanic Belt is relatively continuous, mountain ranges to the south are discontinuous. Species of *Viridimicus* became isolated and underwent speciation in montane regions to the south of the Transverse Volcanic Belt: *V. ratcliffei* in the southernmost extent of the Sierra Madre
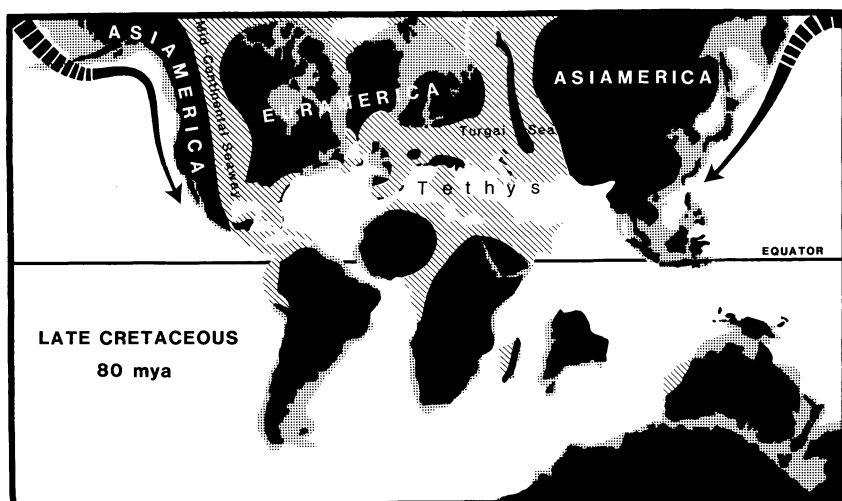
Map 5.   Map showing the world in the Cretaceous, 80 million years ago. Stippled areas around present-day continents depict continental shelves that were above water at this time. Diagonal lines represent epicontinental seas. The Rutelini evolved in the region called "Asiamerica," a continent then joined near the pole that allowed dispersal between the two regions (after Charig 1983).

Oriental, *V. cyanochlorus* and *V. impunctatus* in the Sierra Madre del Sur (separated by the Rio Balsas depression), *V. aurescens* in the Sierra Madre de Chiapas, Chiapas Central Massif, and the Central American Nucleus, and *V. nigroaeneus* in the Central American Nucleus. Halffter (1987) recognized mountains in southern Mexico as particularly important areas of isolation and vicariance, thus lending additional weight to this region being an area of speciation.

The dispersal of *Viridimicus* southwards into Central America was prevented by two factors. First, the isthmus of Panama served as a *filter* bridge for tropical and subtropical organisms after its rise in the Pliocene due to its more arid habitat (Matthews 1980; Webb 1978). Second, the southern limit of pine-oak forest (the habitat for both genera) is the Nicaraguan Depression, just south of the Central American Nucleus. This low, arid region was a barrier for animals as well as plants, such as *Pinus, Acer, Arbutus, Arceuthobium, Carpinus, Fraxinus, Liquidambar, Ostraya,* and *Platanus* (Rzedowski 1986). These plant taxa are important constituents of the habitat for both *Parabyrsopolis* and *Viridimicus.* The southern limit of the genus *Viridimicus* correlates exactly with the southern limit of these plant taxa.

PHYLOGENY

Methods

The postulated phylogenetic relationships for the genera of Areodina and the species of *Viridimicus* (Figs. 34, 35) are based upon cladistic methodology (*i.e.,* Nelson and Platnick 1981). The resultant branching sequences and nested sets are a product of out-group comparison (Watrous and Wheeler 1981), presumed monophyletic lineages, and parsimony. Computer-assisted analyses

Table A.   Polarization of character states for the Areodina using the Heterosternina as the out-group.

No.	Character	Apotypic state	Plesiotypic state
1a	Mandibular apex	Lacking strong preapical tooth	With strong preapical tooth
2a	Mandibular shape	Sickle-shaped	Entirely rounded
3a	Hind femur (male)	Enlarged	Normal
4a	Metatibial apex	10 or fewer spinules	More than 10 spinules
5a	Antennal segmentation	8 or 9	10
6a	Metasternal process	Present	Absent
7a	Antennal club length	Subequal or shorter than stem	Longer than stem
8a	Clypeal shape	Subrectangular, subquadrate	Semitrapezoidal, rounded, parabolic
9a	Apex of mentum	Notched (Fig. 12)	Sinuate, deeply sinuate, weakly emarginate (Figs. 9–11)
10a	Terminal segment of maxillary palpus	Longer than antennal club	Shorter than antennal club
11a	Dorsal surface	Setigerous	Glabrous
12a	Prothoracic process	Absent	Present
13a	Color dimorphism	Present	Absent

were performed using the PAUP computer program (Phylogenetic Analysis Using Parsimony) developed in 1984 by David L. Swofford (Illinois Natural History Survey).

Within this group of beetles, the level of confidence for construction of phylogenetic trees was reduced by the overlap of character states between the out-group and the in-group, as well as the general scarcity of reliable characters at the subtribal level. This is not to say that these organisms do not represent a defined group—only that, in reality, *combinations* of characters and character states define a taxon rather than autapomorphs alone. In many cases, insect taxonomists must rely on more than one character to define a taxon. This state of affairs is, obviously, an obstacle in insect phylogenetic reconstructions.

The polarity of a character (primitive or derived) was determined by out-group comparison. The basic tenet of this method is that the character state occurring in related groups is assumed to be plesiotypic (primitive), and the alternative state is assumed to be apotypic (derived) (Watrous and Wheeler 1981). When polarizations could not be resolved utilizing the out-group, the larger out-group of the Rutelini was used.

Homoplasies, such as reversals, parallelisms, convergences, and trichotomies, were minimized by making use of characters with consistent expressions.

In the following discussions, numbers following text refer to characters in Tables A–D.

Character Analysis: Subtribe Areodina (Tables A, B)

Members of the Heterosternina were chosen as the out-group for the phylogenetic analysis of the Areodina. Characters used are summarized in Tables A, B. These two subtribes are closely related sister lineages (Morón 1983), both

Table B. Scoring of character states for the Areodina using the Heterosternina as the out-group.

	1a	2a	3a	4a	5a	6a	7a	8a	9a	10a	11a	12a	13a
Heterosternina	0	0	1	0	0	0	0	0	0	0	0	0	0
Cotalpa	1	0	0	1	0	0	1	1	0	0	0	0	0
Paracotalpa	1	0	0	1	0	0	1	0	0	0	1	0	0
Pseudocotalpa	1	0	0	1	0	0	1	1	0	1	0	1	0
Parabyrsopolis	1	0	0	1	0	0	1	0	1	0	0	0	0
Parachrysina	1	0	0	1	1	0	1	0	0	0	1	1	1
Viridimicus	1	0	0	1	0	0	1	0	1	0	0	0	2
Byrsopolis	1	0	0	1	0	0	0	1	0	0	0	0	0
Oplognathus	1	0	0	1	0	1	0	1	0	0	0	0	0
Areoda	1	0	0	1	0	1	0	0	0	0	0	0	0
Xenoproctis	1	1	1	0	0	0	1	1	0	0	0	0	0

sharing the plesiomorphy of a complete frontoclypeal suture. The character that separates the Areodina from the Heterosternina is the form of the mandible (1a). The Heterosternina are characterized by having a strongly developed preapical mandibular tooth, whereas all areodines possess an externally round-ed mandible and lack a strongly developed preapical tooth.

The presence of an externally rounded mandible is synplesiotypic for members of the Areodina, and, excluding *Xenoproctis*, all of the genera have an entirely rounded, lobe-like mandible (2a). In *Xenoproctis*, the mandibles are autapotypically sickle-shaped. Additionally, males of *Xenoproctis* possess enlarged hind femora (3a), a character common in the Heterosterina. In the Rutelini, enlarged hind femora are found in very few genera. I interpret this feature as derived based upon the general ruteline plan, and, as such, I score it as a derived trait.

Another unique feature of *Xenoproctis* is the presence of 10 or fewer spinules on the metatibial apex (4a). This character state is shared with the Heterosternina, yet not with the other Areodina. Therefore, I view this as a primitive character state.

Parachrysina is unique among the Areodina for having an 8- or 9-segmented rather than a 10-segmented antenna (5a). This is unique within the Rutelini and is interpreted as a derived trait.

A well-developed metasternal process (6a) extending from the metasternum anteriorly to the procoxae is present in *Areoda* and *Oplognathus*. This synapomorph joins these two genera as sister lineages and is a derived character state.

When the club of the antenna is longer than the stem (scape plus the remaining segments), it is scored as plesiotypic (7a). This character state is shared with Heterosternina, *Byrsopolis, Areoda,* and *Oplognathus.* The remaining areodine genera possess an antennal club subequal to or shorter than the stem.

In the out-group, the clypeal shape varies from subparabolic to semitrapezoidal. These shapes are considered primitive states. Subrectangular and subquadrate clypeal shapes describe the synapotypic states (8a) found in *Byrsopolis, Oplognathus, Xenoproctis, Pseudocotalpa,* and *Cotalpa.*

The apex of the mentum is apotypically notched (9a) (Fig. 12) in *Parabyrsopolis* and *Viridimicus.* In the remaining genera, the apex is bisinuate, deeply sinuate, or weakly emarginate (Figs. 9–11).

A distinguishing character for *Pseudocotalpa* is the terminal segment of the

Table C.   Polarization of character states for *Viridimicus* using *Parabyrsopolis* as the out-group.

No.	Character	Apotypic state	Plesiotypic state
1b	Apex of mentum	Notched (Fig. 12)	Sinuate, deeply sinuate, weakly emarginate (Figs. 9–11)
2b	Apex of parameres	Rounded (Fig. 15)	Subquadrate (Fig. 16)
3b	Color dimorphism	Present	Absent
4b	Dorsal color	Metallic green	Brown to black with only isolated weak metallic reflections
5b	Head profile	Not declivous with respect to frons (Fig. 25)	Declivous with respect to frons (Figs. 21–24)
6b	Mandibular surface plane	Not concave	Concave
7b	Head punctation	Large punctures of discal regions separated by one puncture diameter	Punctures of discal regions confluent to rugopunctate
8b	Punctation of pronotal margins	Punctures distinctly separated, not rugopunctate	Rugopunctate
9b	Punctation of pronotal disc	Sparsely punctate, punctures small	Moderately densely punctate to densely punctate, punctures small *and* moderate or large
10b	Punctation of pygidial disc	Finely, densely rugopunctate	Punctures discrete, not rugopunctate
11b	Punctation of sides of pygidium	Rugopunctate to rugulose	Confluent to discretely punctate
12b	Apex of third tarsomere	Not bilobed (FIg. 20)	Bilobed (Fib. 19)

maxillary palpus which is longer than the antennal club (10a). This character is autapotypic for *Pseudocotalpa.*

Paracotalpa* and *Parachrysina* both possess setose pronota (11a). In some species of *Paracotalpa,* this character manifests itself as sparsely setigerous punctures (such as *P. deserta,* which has only the lateral margins setigerous). Species of *Parachrysina* are setaceous over the entire pronotum or at least on the lateral edges. Other Areodina are setose ventrally, on the pygidium, or on the head, but not on the pronotum.

The prothoracic peg is not developed (apotypic) (12a) in *Pseudocotalpa* and *Parachrysina.* The remaining genera, with the exception of *Areoda* and *Oplognathus,* possess this character state (plesiotypic). Because of the presence of a metasternal process in *Areoda* and *Oplognathus,* these two taxa are scored as plesiotypic with reference to the prothoracic peg.

While sexual dimorphism (pronotal horns, tubercles, size, color, enlarged appendages, etc.) is particularly noticeable in some subfamilies of Scarabaeidae (*e.g.,* Scarabaeinae, Dynastinae, Cetoniinae), it is an uncommon feature in nearly all Rutelinae and is scored as an apotypic character state. In the Areodina,

Table D. Scoring of character states for the species of *Viridimicus* using *Parabyrsopolis* as the out-group.

	1b	2b	3b	4b	5b	6b	7b	8b	9b	10b	11b	12b
Parabyrsopolis	0	0	0	0	0	0	0	0	0	0	0	0
V. unitus	0	1	1	1	0	0	0	0	0	1	0	0
V. cyanochlorus	0	1	1	1	0	0	1	1	1	1	1	0
V. ratcliffei	0	1	1	1	1	1	0	1	0	0	0	0
V. aurescens	0	1	1	1	0	0	0	1	0	1	0	0
V. nigroaeneus	0	1	1	1	0	0	1	1	1	1	0	0
V. impunctatus	0	1	1	1	0	0	1	1	0	1	0	1

males and females of *Xenoproctis*, some species of *Parachrysina* are separated due to the presence of enlarged hind femora in males (3a). Color dimorphism between males and females (13a) in the Areodina is observed in species of *Parachrysina* and *Viridimicus*. Of the two known specimens of females in the genus *Parachrysina* (Jameson, in press), both exhibit a dorsally dark greenish coloration while males are generally testaceous to lighter green (to the unaided eye). In *Viridimicus*, males are metallic green in coloration while females (at least the head and usually the entire dorsal surface) stand apart as either piceous or castaneous with only weak metallic green reflections.

Phylogenetic Relationships: Areodina

The phylogenetic relationships of the Areodina are based on the set of characters in Tables A, B and are presented in the cladogram (Fig. 34).

The unique traits of *Xenoproctis* (sickle-shaped mandibles and apex of the metatibia with 10 or fewer spinules) separate this genus from the other Areodina and place it closer (phylogenetically) to the Heterosternina. The fact that *Xenoproctis* is the most atypical areodine is congruent with its disjunct distribution in Africa. Although its character states are rather unlike other Areodina, the observed variation is within the range of variability seen in other subtribes of Rutelini.

Byrsopolis, *Areoda*, and *Oplognathus* (the South American Areodina), are all closely related genera as shown in the cladogram. *Areoda* and *Oplognathus*, by virtue of their shared apomorph (6a), are sister genera.

The Areodina north of the isthmus form the remaining clustered branch of the cladogram. Although these genera represent a trichotomy in the cladogram, the shared characters of antennal club length (7a) and clypeal shape (8a) serve to bind them together. *Paracotalpa* and *Parachrysina*, due to their shared character of dorsal setae (11a), are sister genera. *Parabyrsopolis* and *Viridimicus* are also sister genera due to the presence of a notched mentum (9a). *Cotalpa* and *Pseudocotalpa* also are contained in this clustered branch, but their relationships to the aforementioned genera could not be ascertained.

Character Analysis: Species of *Viridimicus* (Tables C, D)

The out-group chosen for this analysis was *Parabyrsopolis* as *Viridimicus* and *Parabyrsopolis* are sister genera (Fig. 34) and share the plesiomorph of a notched mentum (1b) (Fig. 12). This character state serves to root the cladogram and join the two lineages. Characters used in this analysis are summarized in Tables C, D.

Two characters separate *Viridimicus* from *Parabyrsopolis*: the apex of the parameters (2b) (Figs. 15, 16) and the presence of color dimorphism (3b) between males and females of *Viridimicus*.

Metallic green coloration (whether brassy green as in *V. unitus* and rare specimens of *V. aurescens* or dark green) on the entire dorsal surface of males of *Viridimicus* (4b) is regarded as apotypic in comparison to *Parabyrsopolis*.

With the exception of *V. ratcliffei*, the other species of *Viridimicus* and the outgroup possess a declivous clypeus with respect to the frons (5b) (Figs. 21–24). In *V. ratcliffei*, the clypeus and frons are autoapotypically nearly flat (Fig. 25).

Mandibles (6b) in *Viridimicus* and all Areodina are broadly rounded externally. In *Viridimicus* the plesiotypic state of the manidbular plane is concave and the mandibles are hidden (6b). Only in *V. ratcliffei* are the mandibles not concave (rather, they are flat) and broadly exposed.

In the derived state, the large punctures of the discal regions of the frons and the clypeus are separated by at least their own diameters (7b). This state is seen in *V. cyanochlorus, V. impunctatus,* and *V. nigroaeneus.* The plesiotypic state is punctures confluent or rugopunctate and is present in the other species of *Viridimicus*.

Both *Parabyrsopolis* and *V. unitus* have the anterolateral margins of the pronotum confluently punctate or rugose (8b). I view this as a plesiotypic state. In all other *Viridimicus,* the punctures in this region are separated by one puncture distance or more. In places where muscles attach interiorly, the punctures may coalesce, but these areas are small and isolated near the mediolateral margin of the pronotum.

The pronotal disc of *V. impunctatus* is sparsely punctate with the punctures being very small (9b), thus the pronotum almost appears smooth and impunctate. All other species of *Viridimicus* possess moderately densely punctate pronota with the punctures being characterized as small (sparse) *and* moderate or large (dense).

The pygidial disc of *V. cyanochlorus* and *V. nigroeaneus* is finely, densely rugopunctate (the rugae being very small) (10b). This character varies in other species from sparsely punctate (*Parabyrsopolis* and *V. ratcliffei*) to moderately densely punctate (*V. unitus* and *V. aurescens*).

Laterally, the pygidium of *V. unitus, V. cyanochlorus, V. aurescens, V. impunctatus,* and *V. nigroaeneus* is densely, finely rugopunctate (11b). The plesiotypic state is moderately densely punctate, never rugopunctate, and is manifested in *Parabyrsopolis* and *V. ratcliffei*.

The diagnostic and unshared apomorph of *V. cyanochlorus* is the entire rather than bilobed (Fig. 20) apex of the third anterior tarsomere (12b).

Phylogenetic Relationships: *Viridimicus*

The relationships of the species of *Viridimicus* using *Parabyrsopolis* as the out-group are based on the characters in Tables C, D and are presented in the cladogram in Figure 35.

The species of *Viridimicus* form a nested set with *V. nigroaeneus* and *V. cyanochlorus* being the most derived species and *V. unitus* being most closely related to *Parabyrsopolis*.

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BOOK REVIEWS

BOUSQUET, YVES. 1990. **Beetles associated with stored products in Canada: An identification guide.** Agriculture Canada Publication 1837, 240 pp. Price: $29.95 (Canada), US$35.95 (outside Canada).

This is a very well presented book. It is convenient to handle being 6″ × 9″ with a good spiral binding and it has a rather spectacular cover featuring a line drawing of *Anthrenus scrophulariae*. One hundred and twenty species (adult stage only), representing 20 families, are keyed and described in the text which is copiously illustrated with original drawings of the highest quality. The species chosen are those commonly found in storage situations in Canada. Apart from *Trogoderma granarium,* species found only on imports are merely mentioned in family or species descriptions. The book is arranged in two parts; the first covering identification and the second giving a general account of the species.

The first part contains a general key in which families, certain genera and species are keyed out, and separate keys to species within particular families. All of the keys are straight forward, have well thought out couplets and are complemented by 17 pages of excellent line drawings (168 figures) illustrating the diagnostic characters used in them. In addition, there are 7 pages of habitus figures 'Identification Plates' showing 63 species and presented as a further identification aid.

The second part of the book contains short notes on the families and for each of the 120 species a diagnosis, a description of sexual dimorphism and notes on distribution and economic importance. A list of selected biological and taxonomic references is given for each family. Apart from the concise and informative text this part contains magnificent full page reproductions of the 63 habitus drawings presented in the 'Identification Plates' plus two others. Following the species descriptions there are line drawings and scanning electron micrographs depicting secondary sexual characters, particularly useful for those wishing to sex storage beetles. A glossary, two figures illustrating the major morphological features of a beetle, a listing of literature cited and an index complete the second part.

The author only uses external characters for identification even with such difficult genera as *Cryptophagus* where genitalia can be very useful. However, the accurate figures of external characters and the habitus drawings in combination with the keys and diagnoses leave little room for doubt when dealing with most of the Canadian storage fauna. Although it seems rather churlish to find fault with such beautifully executed and accurate figures, I believe that the artist must have had atypical specimens before him when producing the habitus figures of *Dermestes maculatus* (Fig. 197) and *Tribolium confusum* (Fig. 239). The figure of *D. maculatus* does not show the white (or pale) setae which are usually present at the sides of the pronotum although the diagnostic character of the elytral apex is well illustrated. That of *T. confusum,* particularly due to the form of the pronotum but also the lack of any indication of the narrowing of the eye at the side of the head, gives the wrong overall impression for this species. A more typical pronotum for this tenebrionid is illustrated in Fig. 161.

With regard to nomenclature, the author uses the name *Ptinus ocellus* Brown for the