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# THE BIOGEOGRAPHY AND PHYLOGENY OF *HOLOGYMNETIS* (COLEOPTERA: SCARABAEIDAE: CETONIINAE) WITH A REVISION OF THE GENUS

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## ABSTRACT

The Neotropical genus *Hologymnetis* (formerly *Cineretis*) is comprehensively reviewed. Descriptions and a key to the seven species are presented, including three new species (*H. kinichahau* from Guatemala and Mexico, *H. moroni* from Mexico, and *H. vulcanorum* from El Salvador). *Hologymnetis margaritis* is restored to species status. A cladistic analysis reconstructing the presumed phylogeny of the genus is provided, and a discussion of the characters and their states is given. *Hologymnetis cinerea* and *H. undulata* were found to be the most derived species, while *H. vulcanorum, H. margaritis* and *H. kinichahau* are the least derived; *H. moroni* and *H. argenteola* are sister species. The biogeographical study indicates that the genus is South American in origin with one species (*H. undulata*) now occurring there south of the Amazon Basin. Dispersal through Central America after the formation of the Panamanian land bridge is indicated. Descendent taxa then dispersed and speciated from El Salvador through southern and western Mexico and extreme southern Arizona. Subsequent formation of unfavorable habitat (primarily lowland rainforest) from Amazonia to Nicaragua eliminated species of ancestral *Hologymnetis* previously living there.

## RESUMEN

El género Neotropical *Hologymnetis* (anteriormente *Cineretis*) es revisado. Se describen tres nuevas especies: *H. kinichahau* de Guatemala y México, *H. moroni* de México, y *H. vulcanorum* de El Salvador. Para cada especie se comentan los datos conocidos de su biología y los registros precisos de localidad complementados con mapas y se incluye una clave para separar las siete especies hasta ahora conocidas.

Se propone un análisis cladístico que supone la filogénia de este género, discutiendo los caracteres y sus estados. *Hologymnetis cinerea* y *H. undulata* fueron encontradas las especies más derivadas, mientras que *H. vulcanorum, H. margaritis* y *H. kinichahau* son menos derivados; *H. moroni* y *H. argenteola* son especies hermanas.

Los estudios biogeográficos indican que el género es de origen sudamericano con una especie (*H. undulata*) ocurriendo en el sur de la Cuenca del Amazonas. La dispersión a través de Centroamérica despues de la formación del puente panameño es indicada. Los taxa descendientes se dispersaron y especieron en El Salvador a través del sur y oeste de México y extremo sur de Arizona. La subsecuente formación de habitats desfavorables (primariamente bosques lluviosos en las tierras bajas) de Amazonia a Nicaragua eliminó la especies ancestral de *Hologymnetis* anteriormente viva allí.

The purpose of this revision is to provide a key for identification, description of adults, locality and temporal data, and the little biological information available for the species belonging to the Neotropical genus *Hologymnetis.*

The genus *Hologymnetis* was previously composed of four species. We describe three new species here, two of which (the Guatemala and El Salvador species) were inadvertently discovered while studying possible variation in the male parameres of putative *H. margaritis.* Unlike related gymnetine genera such as *Cotinis, Argyripa,* and most *Gymnetis,* the form of the parameres is important in *Hologymnetis* because significant differences are present and consistently expressed.

In spite of a bewildering array of colors and patterns in the Gymnetini, there are relatively few robust characters available to separate taxa from an otherwise widespread, nearly homogenous matrix of body form and sculpturing. Our cladistic study of these characters for *Hologymnetis* and their phylogenetic information is discussed in the section dealing with phylogeny. Lastly, the genus is geographically divided between Mesoamerica and central South America, and we postulate in the section on biogeography as to how this might have occurred.

We believe the results of this study will now enable accurate and prompt identification of the species of *Hologymnetis* as well as add additional information to our efforts to understand the evolution and biogeography of scarabs.

METHODS

Traditional methods of alpha taxonomy were used to key and describe the species of *Hologymnetis* treated in this paper. Our database consisted of 1,692 specimens examined from the following institutions (acronyms are largely those used in Arnett and Samuelson 1986): (AMNH) American Museum of Natural History, New York (Lee Herman, Jr.); (BMNH) British Museum (Natural History), London (Michael Bacchus, Malcolm Kerley); (CASC) California Academy of Sciences, San Francisco (Norman Penny, David Kavanaugh); (CMNH) Carnegie Museum of Natural History, Pittsburgh (Robert Davidson, Ginter Ekis); (CNCI) Canadian National Collection, Ottawa (Ales Smetana, Jean McNamara); (DEIC) Deutsche Entomologisches Institut, Eberswald (H. Morge, H. Müller); (FMNH) Field Museum of Natural History, Chicago (Henry Dybas); (IEMM) Instituto de Ecologia, Mexico City (now Xalapa) (Miguel Morón); (INPA) Instituto Nacional de Pesquisas da Amazonia (Norman Penny, Victor Py-Daniel); (KSUC) Kansas State University, Manhattan (Derrick Blocker); (LACM) Los Angeles County Museum, Los Angeles (Roy Snelling); (MCZC) Museum of Comparative Zoology, Cambridge (Al Newton, Scott Shaw); (MHNG) Museum d'Histoire Naturelle, Geneva (Ivan Löbl); (MLUH) Martin Luther Universität, Halle (Manfred Dorn); (MNHN) Museum National d'Histoire Naturelle, Paris (Roger-Paul Dechambre); (MPEG) Museu Paraense Emilio Goeldi, Belem (William Overal); (MZSP) Museu de Zoologia, São Paulo (Cleide Costa); (QBUM) Museu Naçional, Rio de Janeiro (José Carvalho); (SEMC) Snow Entomological Museum, Lawrence (George Byers); (UAIC) University of Arizona Insect Collection, Tucson (Carl Olson); (UCCC) Universidad de Concepcion, Concepcion (Tomas Cekalovic); (UCEC) University of Colorado, Boulder (U. Lanham); (UCRC) University of California, Riverside (Saul Frommer); (UNSM) University of Nebraska State Museum, Lincoln (Brett Ratcliffe); (USNM) United States National Museum, D.C. (Robert Gordon);

and (ZMHU) Museum für Naturkunde der Humboldt Universität, Berlin (Manfred Uhlig, Fritz Hieke). Specimens were also examined from the following private collections: Dan Curoe, Palo Alto, CA; Cuauhtémoc Deloya, Xalapa, Mexico; John Glaser, Baltimore, MD; Alan Hardy, Sacramento, CA; Henry Howden, Ottawa, Canada; Paul Lago, University, MS; Antonio Martínez, Rosario, Argentina; Scott McCleve, Douglas, AZ; Miguel Morón, Xalapa, Mexico; Brett Ratcliffe, Lincoln, NE; Carlos Seabra, Rio de Janeiro, Brazil; Don Thomas, Tuxtla Gutierrez, Mexico; and William Warner, Chandler, AZ.

Field collecting was done by one or both of us in Brazil, Mexico, and the United States. We believe this to be an indispensible part of any revisionary study because it provides a greater understanding of the habitats, ecology, seasonality and actual abundance of the taxa under consideration.

Specimens in this genus can usually be sexed using external characters. Males normally have flat or slightly concave sternites whereas females have rounded or convex sternites. Males usually have the central region of the sternites velutinous while females have this region shining and bare. The apical spurs on the posterior tibia in males are usually both acute, and in females both are usually rounded. Finally, the anterior tibia in males has a length/width ratio of 4:1 whereas in females it is only 3:1, hence relatively broader.

It is important to note that the **length** measurements are from the anterior margin of the pronotum to the apex of the elytra. The head is not included in the measurement because it can be deflected at various angles upon preservation and, therefore, gives misleading indications as to overall length.

Coloration and color terms are frequently difficult concepts with which to deal, especially in groups such as this one where many subtle shades of earth colors are present. Some of the color terms are absolutes and need no interpretation. For those terms that are open to misinterpretation based on one's own experiences, we have used Smithe (1975) as a color standard in order to achieve objectivity. There are more complete color guides (*e.g.,* Ridgeway 1912), but they are not as widely available. The kind of light source is important when making color comparisons. Daylight, incandescent bulbs, and fluorescent tubes all give different color renditions, as does viewing with the unaided eye versus magnification. Except when stated otherwise, our use of color terms is made under magnification with incandescent scope lights striking the specimen at a 45° angle.

The gazeteers published by the Central Intelligence Agency (1956a, b, 1965) were used to corroborate place names.

The phylogeny analysis was conducted using cladistic methodology. The outgroup method of Watrous and Wheeler (1981) was used to polarize characters into ancestral and derived states. PAUP (release 3), a phylogeny reconstruction program developed by David Swofford, was utilized in tree construction. Short of employing mitochondrial DNA data, we believe that phylogeny analysis relying on phenotypic expression of characters is the best way to arrive at relationship hypotheses. We are also acutely aware, however, that parallel and mosaic evolution, ecophenotypy, and small sample size all contribute to obfuscation of any hypothesis we might care to make using this methodology.

Our biogeographical analysis is a straightforward use of vicariance and dispersal paradigms. It was also necessary to use a synthesis of data known for other organisms possessing a fossil record to aid in constructing dispersal patterns for our Scarabaeidae that do not have a fossil record. We have used a deductive approach to biogeographical reconstruction rather than narrative, inductive methods. "It is a normal practice in science to infer from what is

better and more completely known in order to discover the structure and meaning of that which is less well or only partly known. The similarity of facts known on both sides of a controversy suggests that the best documented will be taken as a good model for the reconstruction of the structures still unknown on the other side" (Lavocat 1980:93). Plate tectonics, as exemplified by sea floor spreading and continental drift, is implicitly assumed in this study.

## Taxonomic History

Schürhoff (1937) created the genus *Cineretis* for those species of Gymnetini lacking a strong, vertical, prosternal spine in combination with possessing three external teeth on the anterior tibia in both sexes. He included in this genus the species *argenteola* Bates, *cinerea* Gory and Percheron, and *undulata* Vigors. Unfortunately, he did not designate a type species for the genus (as required by Article 13b of the Code), and so the name is a *nomen nudum*. Martínez (1949) recognized this and created a new genus, *Hologymnetis,* as a replacement name and designated *Cetonia undulata* Vigors as the type species. Hardy (1975) correctly summarized these events.

The Code's (Ride *et al.* 1985) definition of a *nomen nudum* is "a name that . . . if published after 1930, fails to conform to Article 13. A *nomen nudum* is not an available name and therefore the same name may be made available later for the same or a different concept; in such a case IT WOULD TAKE AUTHORSHIP AND DATE [emphasis mine] . . . from that act of establishment. . . ." Krikken (1984), in his treatment of the cetoniine genera of the world, was apparently unaware of Article 13b when he designated a type species (*C. undulata*) for *Cineretis* (of Schürhoff) and declared *Hologymnetis* Martínez a junior synonym. According to Article 50g of the Code, Krikken became the author (though inadvertently) of *Cineretis* because "if a scientific name . . . is first published in the synonymy of an available name . . . its author is the person who published it as a synonym, even if some other originator is cited. . . ." Hardy (1987) again correctly summarized this situation.

Vigors (1825) described the first future *Hologymnetis, Cetonia undulata,* from Brazil. This species was then placed in the genus *Gymnetis* by Gory and Percheron (1833). These authors also described *Gymnetis consularis* from Brazil, on a relatively immaculate specimen of *G. undulata*. This was correctly recognized as a junior synonym of *G. undulata* by Schenkling (1921) (based possibly on the advice of Moser).

Gory and Percheron (1833) also described *Gymnetis cinerea* from Mexico. Blanchard (1850) and Casey (1915) then proceeded to describe an additional two and four species respectively that have since been placed in junior synonymy with *G. cinerea* (Blackwelder 1944). Examination of the types by one of us (Ratcliffe) confirms that they are all conspecific.

Bates (1889) described in the Biologia two additional species from Mexico, *Gymnetis argenteola* and *G. margaritis*. Casey (1915) added, in his characteristic view of things, a new subspecies (*laetula*) from Arizona. Lastly, Blackwelder (1944) reduced *G. margaritis* to a subspecies of *Cineretis argenteola.* We do not adhere to this interpretation because of substantial differences between the taxa, and we restore *margaritis* to species status. Among the six syntypes (or possibly nine; see treatment for *H. margaritis*), there was one specimen not conspecific with the others; it is one of the paratypes of *H. moroni* described herein (while, at the same time, retaining its nomenclatorial paratype status for *G. margaritis* Bates).

## *Hologymnetis* Martínez

*Cineretis* Schürhoff 1937:56, 69 (*nomen nudum*).
*Hologymnetis* Martínez 1949:15. Type species: *Cetonia undulata* Vigors (by
    original designation).
*Cineretis* Krikken 1984:60. Type species: *Cetonia undulata* Vigors.

DESCRIPTION. Cetoniinae, Gymnetini. FORM: Rhomboidal, robust, sides tapering api-
cally, dorsum weakly convex. Length from apex of pronotum to apex of elytra 11.5–
22.0 mm; width across humeri 6.4–12.7 mm. COLOR: Varying on dorsum from opaque,
velvety black to reddish brown to brown to cinnamon to olive gray or olive green to
yellowish green to smoke gray to buff, with or without cretaceous pattern of indistinct
fuscous cloudings. Ventrally, color varies from shining black to smoke gray with metallic
copper reflections to metallic pale yellowish green or blue with or without copper re-
flections; sternites with or without cretaceous or contrasting color markings. HEAD: Shape
subrectangular, longer than wide, weakly tumescent in center. Clypeus with apex slightly
to distinctly emarginate and reflexed. Antenna with 10 segments, club with 3 segments
not quite as long as stem. PRONOTUM: Widest at base, trapezoidal, attenuate apically,
center-base produced into posteriorly projecting lobe. Lateral margin usually slightly
sinuate before basolateral angle. ELYTRA: Widest at base, posthumeral emargination well
developed; weakly elevated sutural costa and two short, discal costae terminating at
apical umbone. PYGIDIUM: Surface transversely and concentrically strigate or coarsely
and transversely vermiculate. VENTER: Vertical prosternal spine absent. Mesometasternal
protrusion short to moderately long, ventral surface flat and in same plane as longitudinal
axis of body. Males with sternites concave, each sternite with only a small, dark, shining
patch or none. Females with sternites flat to slightly convex, sternites 2–5 in center with
large, dark, shining patch. LEGS: Foretibia tridentate in both sexes, slender in males,
wider in females. Metatibial spurs with apices acute in males, one or both rounded in
females.

DIAGNOSIS. The genus *Hologymnetis* may be distinguished from other New
World Gymnetini by the following: head unarmed, prosternum lacking a long,
vertical spine, foretibiae tridentate in both sexes, and dorsum velutinous and
largely unicolorous (except for the South American species that has distinctive
cretaceous markings).

RANGE. The combined ranges of the seven species extend from the south-
western United States to Honduras and from the southern half of Brazil to
eastern Bolivia and southern Paraguay.

### KEY TO SPECIES OF *HOLOGYMNETIS*

1. Venter largely shiny black in both sexes, sternites *laterally* often with
    cretaceous markings .................................................................................................... 2
1'. Venter brown to grayish brown or pale brassy green or blue, weakly
    shining or weakly to strongly metallic; females with central third of
    sternites bare, piceous ................................................................................................ 3
2. Dorsum unicolorous (smoke gray, grayish olive, cinnamon brown,
    or black) (Fig. 1), rarely strongly punctate (Fig. 2). Mexico to Gua-
    temala (possibly Honduras) ...................................................... *cinerea* (G. & P.)
2'. Dorsum black or piceous and distinctly patterned with cretaceous
    lines; lines present longitudinally on pronotum and radiating from
    midline on elytra (Fig. 5); occasionally reduced or nearly absent (Fig.
    6). Southern Brazil, Paraguay, eastern Bolivia ..................... *undulata* (Vigors)
3. Venter brassy green (usually with coppery reflection) or dull grayish
    olive or bluish gray (rarely blue), with or without coppery reflections
    .................................................................................................................................... 4

3'. Venter grayish brown or yellowish brown, weakly shining .............. 5
4. Venter a bright, shining brassy green, usually with distinct coppery reflection. Protibia with teeth subequally spaced from one another. Parameres as in Figure 7. Arizona, northern Mexico ..... *argenteola* (Bates)
4'. Venter dull grayish olive or bluish gray (rarely blue), with or without coppery reflections. Protibia with median tooth distinctly closer to apical tooth than to basal tooth. Parameres as in Figure 11. West-central Mexico ......................................... *moroni* Ratcliffe & Deloya, n. sp.
5. Mesometasternal process with shining apex usually sharply and transversely delineated from shaft (Fig. 16). Parameres with apical, median ridges tapering to a point (Fig. 13). El Salvador ..................................
......................................................... *vulcanorum* Ratcliffe & Deloya, n. sp.
5'. Mesometasternal process with shining apex and shaft usually broadly joined by a broad, piceous region (Figs. 14–15). Parameres apically not acuminate ............................................................................. 6
6. Parameres in caudal view subquadrate (Fig. 9). Pronotum lacking pale, longitudinal median line. Southwestern Guatemala and Chiapas, Mexico ............................... *kinichahau* Ratcliffe & Deloya, n. sp.
6'. Parameres in caudal view rounded at base, expanded at apex (Fig. 10). Pronotum with pale, longitudinal, median line. Southern Mexico
............................................................................................. *margaritis* (Bates)

<div align="center">

*Hologymnetis argenteola* (Bates)
(Figs. 7, 17)

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*Gymnetis argenteola* Bates 1889:354. Holotype male, labeled "Pinos Altos, Chihuahua, Mexico," "Sp. figured," "Buchan-Hepburn," "Type;" at BMNH (London), examined.
*Gymnetis argenteola laetula* Casey 1915:280. Type locality: "Nogales, Arizona." Holotype at USNM, examined.

DESCRIPTION. Length 13.5–20.5 mm; width across humeri 7.6–11.1 mm. Color dorsally varying from entirely velvety dusky brown to clay to olive gray to olive green to yellowish green; vermiculate impressions and punctures shining black, piceous, or metallic pale green; ventrally metallic pale yellowish green with strong copper reflection, at least rim of punctures or strigae shining black. Occasional specimens with distinct cobalt blue suffusing pale green of venter. Other specimens lacking strong metallic lustre, instead weakly shining pale yellowish green or copper (depending on angle of light). HEAD: Surface moderately to moderately densely punctate; punctures small to moderately large, round to nearly crescent-shaped, with minute, pale setae in fresh specimens; declivous sides of clypeus rugulose. Clypeus feebly tumescent at center; apex strongly reflexed, usually strongly arcuate (best seen in anterior view). Interocular width 5.0–6.0 transverse eye diameters as seen from above. Antenna with basal segment at apex with dorsal fringe of 10 or fewer pale, slender setae. PRONOTUM: Surface usually moderately densely punctate; punctures small to large (largest in lateral one-third of pronotum), small punctures round, larger punctures crescent-shaped, setigerous in fresh specimens; setae short, pale; some specimens with entire field of punctures smaller throughout. Anterior margin lacking tubercle. Lateral border with complete marginal line, weakly emarginate before basolateral angle. Mesepimera moderately to densely punctate or rugopunctate; punctures moderate to large, round to vermiculate, setigerous; setae pale, often dense. ELYTRA: Surface moderately to densely punctate (denser in center of disc); punctures small to large, round to transverse to U-shaped, some setigerous; setae short, pale. Weakly elevated sutural costa and two discal costae terminating at apical umbone usually present in posterior half of elytra. PYGIDIUM: Surface coarsely, transversely vermiculate; impressions moderate to dense (occasionally confluent), C-shaped to elongate, setigerous; setae
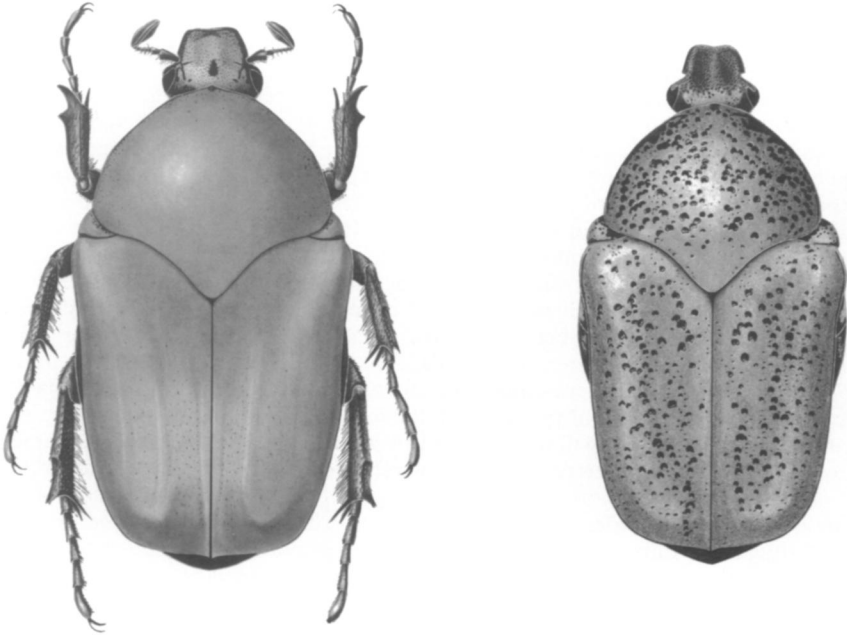
Figs. 1–2.   Habitus of *H. cinerea*. Fig. 1 (left) is typical. Fig. 2 (right) shows extreme in dorsal sculpturing.

short, pale. Discal area flattened in both sexes. VENTER: Setae tawny. Meso-metasternal protrusion short, extending anteriorly to just beyond mesocoxae; anterior and ventral faces acute relative to one another, but angle rounded; ventral face flat, in same plane as longitudinal axis of body; anterior face with long, slender setae that curl around apex of protrusion. In ventral view, sides of mesometasternal protrusion diverging to broadly rounded apex. Last sternite at apex usually with fringe of slender, short, testaceous setae. Sternites completely yellowish green or with central area variably lacking green, instead shining black; punctures moderate to large, C-shaped to crescent-shaped, moderately dense laterally, becoming sparser medially. LEGS: Colored similarly to venter. Anterior tibia with 3 subequally spaced teeth. PARAMERES: Figure 7.

DISTRIBUTION. *Hologymnetis argenteola* is found on the western slopes of the Sierra Madre Occidental in northwestern Mexico as well as in its northern extension, the Huachuca and Santa Rita mountains of extreme south-central Arizona in the United States.

LOCALITY RECORDS (Fig. 17). 82 specimens examined. Specimens were seen from the following collections: AMNH, BMNH, CASC, CNCI, DEIC, LACM, MCZC, MFNH, MNHN, SEMC, USNM, ZMHU, Alan Hardy, Scott McCleve, Henry Howden, Miguel Morón, Brett Ratcliffe, and William Warner. MEXICO (26): CHIHUAHUA (2): Moris, Pinos Altos; DURANGO (2): Canelas, Durango; SINALOA (2): No data; SONORA (5): Agua Zarca, La Chiripa, 9 mi. NE Imuris, Nogales, Rio Mayo; NO DATA (15). UNITED STATES (54): ARIZONA (48): COCHISE CO. (41): Carr Canyon, Chiricahua Mts., Coronado National Memorial, Hereford, Huachuca Mts. 2 mi. E. Nicksville, Palmerlee; PIMA CO. (1):

Madera Canyon; SANTA CRUZ CO. (6): Nogales, Peña Blanca Canyon (Oro Blanco Mts.), Santa Rita Mts. NO DATA (9). TEMPORAL DISTRIBUTION. May (2), July (32), August (17).

REMARKS. *Hologymnetis argenteola* is distinctive because of its unicolorous dorsum (similar to but usually greener and paler than *H. cinerea*) and venter metallic pale yellow green with strong copper reflections. The parameres are substantially different from those of *H. cinerea* because the apex is more strongly toothed and the shaft of each paramere strongly curved (Fig. 7). Some slight variation was observed in the slenderness in the middle of each paramere.

The dorsal coloring and degree of punctation of this scarab varies considerably with no apparent correlation to geography or altitude. So, too, does the ventral coloration. Metallic pale yellowish green with strong coppery reflections is most common. Some specimens have metallic bluish green reflections beneath. Bates' holotype is similar to this, as is the holotype of Casey's *laetula*. The presence of a distinct carina ventrally and laterally near the base of each paramere (Fig. 7), in combination with the form of the apices of the parameres and geographic origin, will distinguish this species. The ventral color of these two species is also different but is not as reliable a character for separation.

Biological information is sparse for *H. argenteola,* but presumably the adults are flower and sap feeders and the larvae develop in organic debris or compost-like situations. Label data indicate that some specimens were collected from gumming sites on *Baccharis sararthroides* Gray, from banana traps and from "desert willow" at elevations ranging from 1,212–2,273 m. Adults have occasionally been found competing with species of *Euphoria* and *Cotinis* at gumming sites on *Baccharis* sp. (William Warner, pers. comm. 1989).

This species is apparently not abundant.

*Hologymnetis cinerea* (Gory and Percheron)
(Figs. 1–2, 8, 17)

*Gymnetis cinerea* Gory and Percheron 1833:73, 371. Lectotype male, labeled "Mexico" here designated; at MHNG (Geneva) with Ratcliffe's lectotype label. Also two male paralectotypes labeled "Mexico" at Geneva and one female paralectotype labeled "Mexico, Gory," "Coll. Helfer," "Typus," "Exemplaire typique du cabinet de M.H. Gory," and "Field Mus. Coll., F. Psota Coll. (ex. Aug. Ondrej Coll.)" at FMNH (Chicago).

*Gymnetis punctata* Blanchard 1850:36. Type locality: "Mexique." Holotype at MNHN (Paris), examined.

*Gymnetis uniformis* Blanchard 1850:36. Type locality: "Mexique." Holotype at MNHN (Paris), examined.

*Gymnetis cuneata* Casey 1915:282. Type locality: "Durango City, Mexico." Holotype and allotype at USNM (Washington, D.C.), examined.

*Gymnetis lobiculata* Casey 1915:282. Type locality: "Mexico, probably near Jalapa." Holotype at USNM (Washington, D.C.), examined.

*Gymnetis simulans* Casey 1915:283. Type locality: "Mexico (Guerrero)." Holotype and allotype at USNM (Washington, D.C.), examined.

*Gymnetis aequalis* Casey 1915:284. Type locality: "Cuernavaca, Morelos, Mexico." Holotype at USNM (Washington, D.C.), examined.

DESCRIPTION. Length 14.7–21.7 mm; width across humeri 8.5–12.7 mm. Color dorsally varying widely from entirely velvety or opaque black to dark gray to dark plum to light or dark cinnamon to grayish or brownish olive to light or dark smoke gray to buff; black where punctate or velvety surface absent (head occasionally entirely black); ven-

trally shining, black. HEAD: Surface usually sparsely to moderately punctate either side of raised midline; punctures small to moderate in size, setigerous in fresh specimens; where velutinous covering absent, surface densely rubopunctate; declivous sides of clypeus rugulose, clypeal apex rugulose to finely punctate; setae tawny, short. Clypeus with apex reflexed, distinctly arcuate (curve bowed posteriorly) to subtruncate. Interocular width equalling 5.0–6.0 transverse eye diameters. Antenna with basal segment at apex with dorsal fringe of 10 or fewer pale or dark colored, slender setae. PRONOTUM: Surface usually completely velutinous, sculpturing obscured; otherwise, varying from sparsely punctate in anterior half with punctures small and round to moderately densely punctate all over with punctures small, round mixed with moderate to very large round, crescent-shaped or U-shaped punctures. Anterior margin with small tubercle. Lateral margin completely beaded, not or only weakly emarginate before basolateral angle. Mesepimera largely velutinous, usually with a few small to moderate punctures in anterior half. ELYTRA: Surface entirely velutinous, punctation varying from absent to sparsely to moderately punctate; punctures varying from small and round (in which case punctures usually in partial lines representing striae and random in intervals between striae) to moderate and large mixed; larger punctures crescent shaped (in which case, punctation seemingly random). Weakly elevated sutural costa and 2 discal costae terminating at apical umbone usually present in posterior half of elytron. PYGIDIUM: Surface usually transversely, concentrically strigulose around a point at center apex; otherwise (in specimens with coarse pronotal and elytral sculpturing) surface transversely strigate in basal half, apical half with sparse, transverse, moderate to large punctures; strigae and/or punctures setigerous; setae short, pale, dense at base, becoming sparser apically (some specimens seen with dense setae over entire surface). In some specimens surface velutinous, obscuring sculpturing. VENTER: Setae testaceous to mostly black. Mesometasternal protrusion moderately long, extending well past mesocoxae, but not quite reaching forecoxae; anterior and ventral faces form sharply acute angle. Ventral surface flat, in same plane as longitudinal axis of body; anterior face with short, stout setae. In ventral view sides subparallel to slightly divergent to broadly rounded apex. Sternites 1–5 occasionally with small area of velvety color (as on dorsum) on lateral margin and apical edge of each segment (usually seen only in specimens with pygidium similarly colored). LEGS: Markings absent, color piceous to black, shining. Anterior tibia with 3 subequally spaced teeth, basal tooth often reduced. PARAMERES: Figure 8.

DISTRIBUTION. Except for the Baja peninsula and extreme north-central Mexico, *H. cinerea* is found throughout Mexico west of the isthmus of Tehuantepec. There are several records east of the isthmus in Chiapas but not in the Yucatan peninsula. There are few records for Guatemala and questionable records for El Salvador, Honduras, Arizona, and Texas.

LOCALITY RECORDS (Fig. 17). 1,238 specimens examined. Specimens were seen from the following collections: AMNH, BMNH, CASC, CMNH, CNCI, DEIC, FMNH, IEMM, KSUC, LACM, MCZC, MHNG, MLUH, MNHN, MCSP, SEMC, VCEC, VCRC, UNSM, USNM, ZMHU, John Glaser, Alan Hardy, Henry Howden, Antonio Martínez, Miguel Morón, Cuauhtémoc Deloya and Brett Ratcliffe. EL SALVADOR (1): Cafetalera. (1). GUATEMALA: (21) BAJA VERAPAZ (16): San Geronimo, No data; CHIQUIMULA (2): Candiza, Chiquimula; SANTA ROSA (3): Barcena. HONDURAS (3) NO DATA (3). MEXICO (1,212): AGUASCALIENTES (5): Aguascalientes; CHIAPAS (3): Santa Rosa (Lagunas de Montebello), Sumidero Cnyn. Nat. Pk., No data; CHIHUAHUA (3): San Isidro, Temosachic; COLIMA (71): Colima, Tonila, Volcan de Colima, No data; DF (22): Mexico City, Temascaltepec, No data; DURANGO (35): Durango, 5 mi. W Durango, 18 mi. W Durango, Nombre de Dios, Ventanas, Villa Lerdo, No data; GUANAJUATO (9): Acambaro, 11 mi. SW Acambaro, No data; GUERRERO (41): Acahuizotla, Acapulco, Amuco de la Reforma, Chilpancingo, 3 mi. N Chilpancingo, 10 km E Chilpancingo, Cuacoyula, Taxco, 3 mi. N

Taxco, Teloloapan, Tierra Colorada, La Venta, 7 km E Xochipala, No data; HIDALGO (4): Barranca Venados, Melchor Ocampo, No data; JALISCO (229): Ajijic, Chapala, Chamela Biol. Sta., 12 mi. S Encarnación de Díaz, Guadalajara, 8 and 10 and 23 mi. S Guadalajara, 28 and 53 mi. E Guadalajara, 7 and 16 and 19 and 25 mi. W Guadalajara, Huejotitán, Jacotopec, 6 mi. NE Jolostitlán, Lagos de Moreno, 15 mi. NE Lagos de Moreno, 13 mi. SE Lagos de Moreno, 22 mi. NW La Piedad, 20 mi. N La Quemada, Ocotlán, 8 mi. W San Juan de los Lagos, 8 mi. SW San Juan de los Lagos, 9 mi. W Tepatitlán (El Refugio), El Tuito, 10 mi. E Union de Tula, Zapopan; MEXICO (5): Canalejas, Ixtapan de la Sal, Tejupilco; MICHOACAN (13): Acahuato, Cotija, Huetamo, Jungapco, 10 mi. N Morelia, 4 mi. W Morelia, Palo Alto, Tacámbaro; MORELOS (127): Cañada de Lobo, Cuautla, 10 mi. W Cuautla, Cuernavaca, Jojutla, Morelos, Puente de Ixtla, Tepoztlan, Tequesquitengo, Tlaltizapán, Tlaquiltenango, Yautepec, Xochicalco, Km 6 on Hwy 160 from Jonacatepec to Atotonilco; NAYARIT (19): Compostela, 18 mi. W Compostela, Jesús María, 40 km SE Peñitas, 5 mi. S Rio Santiago ferry, Tepic, 24 mi. SE Tepic, Tuxpan; NUEVO LEON (8): 15 mi. SW China, Monterrey, 5 mi. S and 20 mi. S and 50 mi. S of Monterrey, Villa Santiago; OAXACA (61): La Asunción (12 mi. NW Oaxaca), Etla, Juquila Mixes, Mitla, Oaxaca, 10 mi. S Oaxaca, Tamaulapan, 56 mi. NW Tehuantepec, Teotitlan Tlacolula, No data; PUEBLA (64): Acatlán, Atlixco, Guadalupe, Izúcar de Matamoros, Tehuacán, 6 mi. NE Tehuacán; QUERÉTARO (2): No data; SAN LUIS POTOSI (4): El Naranjo, Ciudad Valles, San Luis Potosi; SINALOA (31): 5 mi. NW Choix, E La Concordia, 17 km E La Concordia, Mazatlán, 5 mi. N Mazatlán, Presidio, Venodio, Villa Union; SONORA (48): Alamos, 7 mi. and 10 mi. S Alamos, Arispe, Estrella Alamo, Guirocoba, 15 mi. E Navajoa, San Bernadino (Rio Mayo), Ventanas, No data; VERACRUZ (64): Acatlán, Cordoba, Cotaxtla, Jalapa, Misantla, Orizaba, Plan del Rio, Sierra Mixteca, Tierra Blanca, Tuxpan, Veracruz, No data; ZACATECAS (2): Monte Escobido, Tlaltenango de Sánchez Román; NO DATA (373). UNITED STATES (2): ARIZONA (1): No data; TEXAS (1): No data. TEMPORAL DISTRIBUTION. January (1), March (1), April (1), May (1), June (22), July (85), August (103), September (123), October (68), November (18), December (4).

REMARKS. *Hologymnetis cinerea,* in spite of its wide variety of color forms, is easily distinguished from its congeners by the presence of both a unicolorous dorsum and a shiny black venter. The parameres of the male genitalia were seen to vary in the degree to which the subapical flanges or "teeth" were produced. In most specimens, they are produced (Fig. 8) while in others they are not raised appreciably from the surface plane of the paramere. This difference did not correlate with any altitudinal or geographic parameters. Similarly, some specimens are coarsely punctate on the pronotum and elytra (Fig. 2). As Bates (1889) noted, punctation is present in certain specimens of all the color forms and is seemingly of little taxonomic importance. We concur with this, having noted no correlation between the degree of punctation and locality or altitude.

This species is often locally abundant feeding on flowers. It has been taken feeding on *Acacia angustissima* (Mill.) and *Baccharis glutinosa* Pers. in Nayarit and Jalisco states. Adults have also been found in the detritus piles of leafcutter ants (*Atta* sp.) (Deloya 1988) in Hidalgo, Morelos, and Nayarit states and have been taken in fruit-baited traps in Guerrero. *Hologymnetis cinerea* has a broad tolerance of different habitats inasmuch as it has been found from the lowland forests (150 m elev.) of Veracruz to the open pine highlands (2,000 m elev.) of Michoacan.

*Hologymnetis kinichahau* Ratcliffe and Deloya, **n. sp.**
(Figs. 3, 9, 15, 17)

TYPE MATERIAL. Holotype labeled, "GUAT., Finca San Rafael Olimpo, Cuyotenango, Such., X-10-1965, J.M. Campbell, 1700." Allotype labeled, "MEXICO: Chiapas, San Cristobal de las Casas, VII-1988, A. Morón col." Five paratypes with the following data: "MEXICO: Chiapas, Municipio Motozintla, Ridge between Cerro Boqueron & Niquivil, 2438–2743 M, 15-XII-1976, D.E. & J.A. Breedlove, Cal. Acad. Sci. Coll." (1); "Rincon Chamula, Chis., MEX. 7-VII-1969, L.A. Kelton" (1); "Chiapas, MEXICO, San Cristobal, 22-23 Jun. 1989, P.K. Lago" (1); "MEXICO, Chiapas, San Quintin, 27-VII-1978, P. Hubbell" (1); "MEXICO, Chiapas, Rancho Santa Rosa, 17-XI-1975, P. Hubbell" (1). Holotype at CNCI. Allotype in the collection of Miguel Morón. Paratypes at CASC, UAIC, and in the Paul Lago and Brett Ratcliffe collections.

HOLOTYPE. *Male:* Length 17.2 mm; width across humeri 10.6 mm. Color dorsally an opaque brown to olive brown, punctures and sculpturing piceous to black; venter weakly shining, light brown to darker smoke gray with faint coppery reflection; sculpturing black. HEAD: Surface moderately densely punctate; punctures small on frons, becoming large on clypeus, round to oblong; setae not present; declivous sides of clypeus rugulose. Clypeus slightly convex on disc; apex broadly reflexed, distinctly emarginate at center, apices either side of emargination broadly rounded. Interocular width equaling 5.0 transverse eye diameters as seen from above. Antenna with basal segment at apex with fringe of 12 testaceous, slender setae on dorsal edge. PRONOTUM: Surface with sparse, minute punctures on center of disc, becoming moderately dense on lateral thirds of pronotum where punctures large, round, deep. Anterior margin at center not tumid. Lateral margin with bead broken up by sculpturing; side margin just anterior of basolateral angle distinctly emarginate in dorsal view. Mesepimera moderately punctate; punctures large, round, deep, setigerous; setae short, testaceous, most apparently abraded away. ELYTRA: Surface sparsely punctate on disc, becoming denser behind apical umbones; punctures large, mostly round on disc to mostly kidney-shaped apically. Sutural costae weakly elevated. PYGIDIUM: Surface coarsely, densely punctate/vermiculate; impressions kidney-shaped to transverse to elongate, deep, setigerous; setae short, testaceous. VENTER: Setae testaceous. Mesometasternal protrusion short, extending anteriorly just beyond mesocoxae; anterior and ventral surfaces weakly acute relative to one another, angle rounded; ventral surface flat, in same plane as longitudinal axis of body; anterior surface with long, slender setae that curl around apex of protrusion. In ventral view, sides of mesometasternal protrusion diverging to broadly rounded apex. Sternites with large punctures in lateral thirds; punctures moderately dense, round to mostly kidney-shaped, setigerous; setae short, testaceous. LEGS: Colored similarly to venter. Anterior tibia with 3 subequally spaced teeth. PARAMERES: Figure 9.

ALLOTYPE. *Female:* Length 17.7 mm; width 10.4 mm across humeri. As holotype except in following respects: Color light brown; elytra with broad, transverse, diffuse lighter yellowish brown band just behind middle (Fig. 3); venter light brown with weak metallic reflection. ELYTRA: Punctures very large, about twice size of those in holotype, U-shaped to C-shaped with opening facing posteriorly.

VARIATION. *Males* (2 paratypes): Length 19.8–21.9 mm; width across humeri 12.0–12.9 mm. Color and pattern as allotype. Other than the "freshness" of the specimens (reflected in distinct color and pattern), there is little variation from the holotype. The three teeth on the anterior tibiae in both specimens are nearly obsolete.

*Females* (3 paratypes): Length 6.1–9.0 mm; width across humeri 9.9–11.2 mm. Color as allotype (1 specimen) to darker brown (2 specimens). HEAD: Punctation a little denser in one specimen. ELYTRA: Punctures large and round in one specimen as opposed to C-shaped.

DISTRIBUTION. *Hologymnetis kinichahau* is known only from the Pacific slope of the Sierra Madre in Guatemala and Chiapas state in Mexico (Fig. 17).
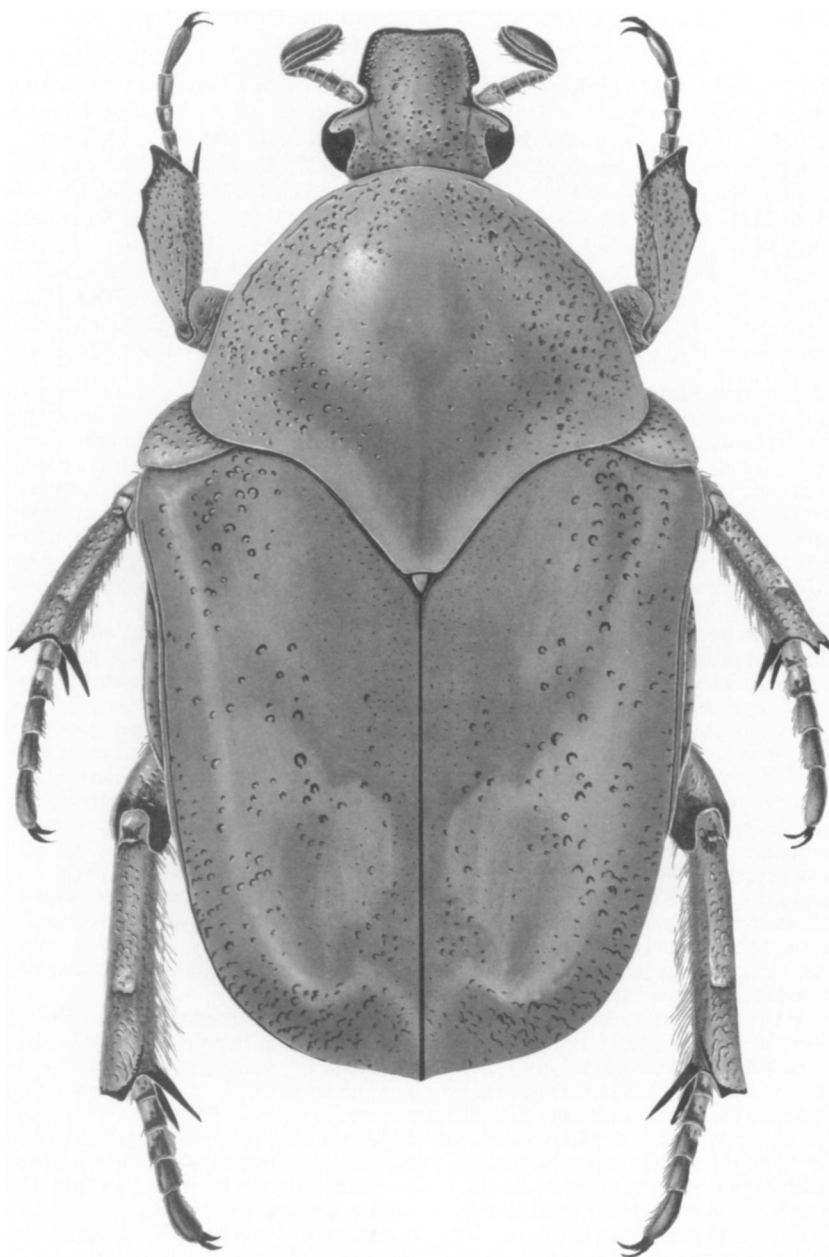
Fig. 3.    Habitus of *H. kinichahau.*

REMARKS. *Hologymnetis kinichahau* is similar in external appearances to *H. margaritis*. Whereas there is a lighter, longitudinal line on the pronotum of *H. margaritis*, there is no such line in *H. kinichahau*. If anything, this part of the pronotum is a little darker with an irregular, fuscous clouding. The parameres of the male genitalia are distinctive because they are so short and stout.

ETYMOLOGY. Being a diurnal species that is most active in bright sunlight, we name this species after the sun god, Kinich Ahau, of the ancient Maya indians of Guatemala.

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*Hologymnetis margaritis* (Bates)
(Figs. 4, 10, 14, 18)

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*Gymnetis margaritis* Bates 1889:354. Lectotype male, labeled "Tehuantepec," "B.C.A., Col. II (2), *Gymnetis*," "Type, sp. figured," "Mexico, Salle coll.," and "B.C.A. figured," here designated; at BMNH (London) with Ratcliffe's lectotype label. Female lectoallotype, labeled "Acapulco, Guerrero," "B.C.A., Col. II (2), *Gymnetis*," and "Hoge" here designated; at BMNH with Ratcliffe's lectoallotype label. Also, one male paralectotype labeled as lectoallotype, one male paralectotype labeled "Guatemala," "*margaritis* var.," "Salle coll.," and one unsexed paralectotype labeled "Oaxaca, Mexico, Hoge," "B.C.A., Col. II (2), *Gymnetis*" here designated; all at BMNH with Ratcliffe's paralectotype labels. One additional male paralectotype, labeled "Oaxaca, Mexico, Hoge," "B.C.A., Col. II (2), *Gymnetis margaritis* Bates," and "Cotype CNCNo. 8676, *G. margaritis* Bates" at CNCI (Ottawa) with Ratcliffe's paralectotype label. One specimen labeled "Acapulco" and two labeled "Etla" are at MNHN and may be part of the original type series because their label data match those in the original description. Bates indicated there was only one specimen from Etla, however, and did not mention numbers for Acapulco. Due to these uncertainties, lectotype designations were not made for the specimens at Paris.

DESCRIPTION. Length 11.6–17.2 mm; width across humeri 6.4–10.2 mm. Color dorsally varying from opaque light to dark brown; pronotum usually with light brown, narrow, longitudinal line in center; elytra usually with broad, transverse, *diffuse* light brown 'band' just behind middle (Fig. 4) and usually with weakly raised costae (terminating in apical umbone) darker than background color (not noticeable in dark brown specimens); venter weakly shining, darker smoke gray, occasionally with faint metallic copper reflection; punctures and other sculpturing piceous to black. HEAD: Surface moderately densely to occasionally densely punctate; punctures small to large (frequently larger on frons than on clypeus), round to kidney-shaped, setigerous; setae minute, straw colored; declivous sides of clypeus rugulose. Clypeus feebly tumescent at center; apex strongly reflexed, distinctly emarginate at center, apices usually distinctly angulate either side of center. Interocular width 4.0–5.0 transverse eye diameters as seen from above. Antenna with basal segment at apex with 10 or fewer pale, slender setae on dorsal edge. PRONOTUM: Surface moderately (most common) to densely punctate; punctures small to larger (larger and denser laterally), round to kidney-shaped, setigerous in fresh specimens; setae minute, pale. Anterior margin at center not tuberculate or noticeably timid. Bead of lateral margin varying from complete to broken or missing in basal half; margin just anterior of basolateral angle varying from entire to distinctly emarginate. Mesepimera moderately to densely punctate; punctures small to mostly large, round to crescent-shaped to vermiculate, setigerous; setae pale, often dense, long. ELYTRA: Surface moderately to densely punctate (much less so basomedially); punctures varying from small to mostly large, round to transverse to kidney-shaped to U-shaped to vermiculate near apex. Weakly elevated sutural costa and 2 discal costae terminating at apical umbone present in pos-
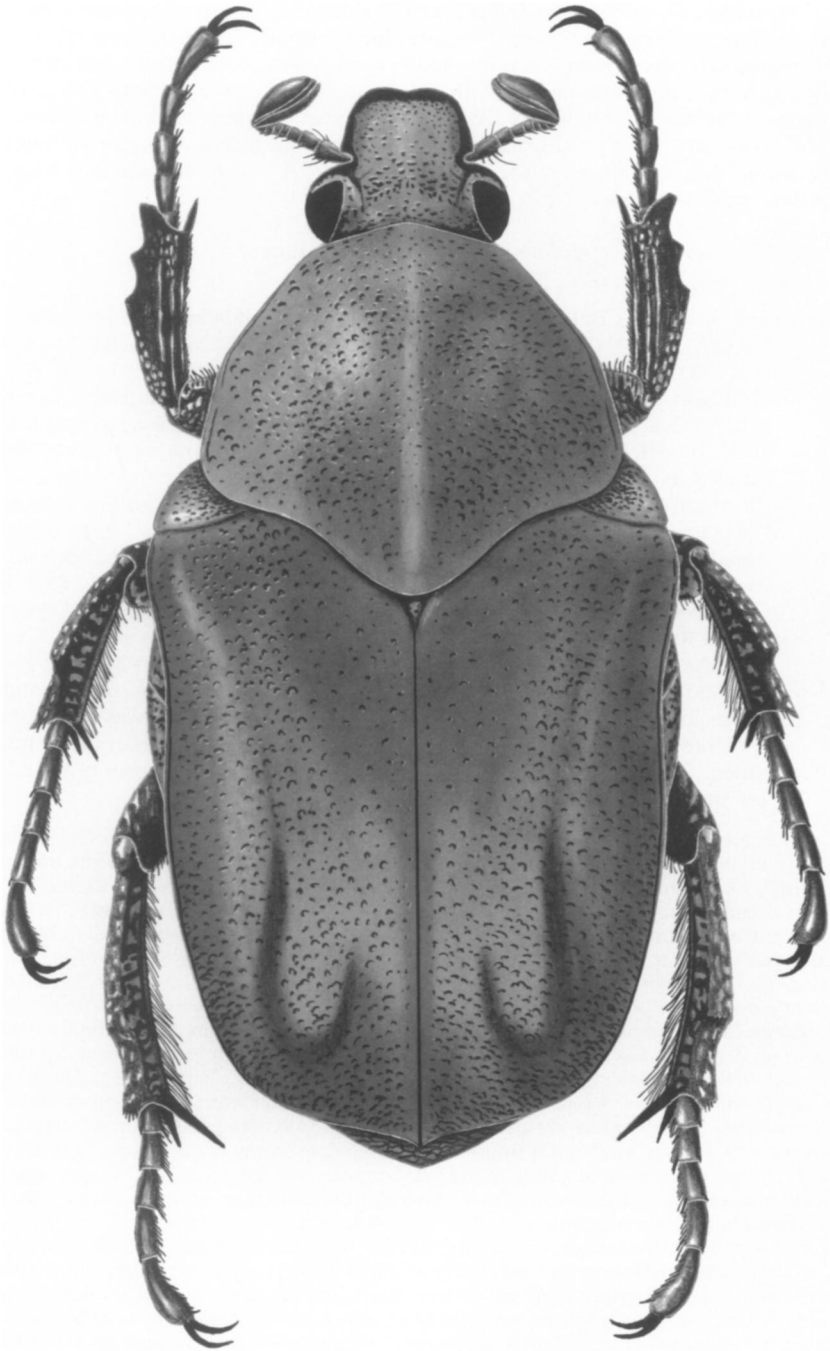
Fig. 4.    Habitus of *H. margaritis.*

terior half of elytra. PYGIDIUM: Surface coarsely, transversely vermiculate (rarely with large, transverse punctures only); impressions moderate to dense (occasionally confluent), C-shaped to elongate, setigerous; setae short, pale. VENTER: Setae testaceous. Mesometasternal protrusion short, extending anteriorly beyond mesocoxae but not reaching procoxae; anterior and ventral surfaces weakly acute relative to one another, but angle rounded; ventral surface flat, in same plane as longitudinal axis of body; anterior surface with long, slender setae that curl around apex of protrusion. In ventral view, sides of mesometasternal protrusion slightly diverging to rounded apex. Apex of protrusion piceous, shining, broadly connected by similar colorations to shaft of protrusion (Fig. 14). Last sternite at apex with fringe of slender, short, testaceous setae. Sternites completely smoke gray or with small piceous spot basomedially (males) or with central area variably shining black (females); punctures moderate to large (larger laterally), kidney-shaped to C-shaped. LEGS: Colored similarly to venter. Anterior tibia with 3 subequally spaced teeth. PARAMERES: Figure 10.

DISTRIBUTION. *Hologymnetis margaritis* is found in the Sierra Madre del Sur in southwestern Mexico and in the Sierra Madre of southern Chiapas. There is a country record only for El Salvador.

LOCALITY RECORDS (Fig. 18). 53 specimens examined. Specimens were seen from the following collections: AMNH, BMNH, CNCI, MNHN, SEMC, USNM, ZMHU, Henry Howden, Cuauhtémoc Deloya, Miguel Morón, Don Thomas, and Brett Ratcliffe. GUATEMALA (1): NO DATA (1). MEXICO (51): CHIAPAS (4): Ciudad Cuauhtémoc, El Aguacerro, Tapachula; GUERRERO (9): Acahuizotla, Acapulco, Amula, No data; JALISCO (2): Chamela Biol. Sta., 10 km NW El Tuito; MICHOACÁN (1): Uruapan; NAYARIT (4): 14 mi. E San Blas, Tepic; OAXACA (21): Ayoquesco, Etla, Hiway 190 at Chiapas border 19 mi. S Matias Romero, Monte Alban, Oaxaca, Pochutla, San Mateo Macuilzochitl Tehuantepec, 56 mi. NW Tehuantepec; NO DATA (9). TEMPORAL DISTRIBUTION. May (1), June (15), July (8), October (3), November (1).

REMARKS. *Hologymnetis margaritis*, although variable in its dorsal markings and color, is nearly always characterized by having an irregular, lighter band across the elytra just past the middle (best seen by the unaided eye). Only three of the 45 specimens studied lacked this band. Frequently, this band is delimited posteriorly by the darker, raised costae terminating at the apical umbone. Normally, the pronotum has a lighter, longitudinal, narrow band at its center that is absent in the other species of the genus (best seen with magnification). The ventral coloring of smoke gray or grayish brown is also distinctive. Little variation was observed in the form of the parameres, which are also unique. They resemble most closely those of *H. argenteola* but lack the apicolateral tooth.

Life history information for this species is lacking. Label data indicate that specimens have been taken at elevations ranging from 150 m at Tapachula, Chiapas to 1,936 m at Monte Alban, Oaxaca.

*Hologymnetis moroni* Ratcliffe and Deloya, **n. sp.**
(Figs. 11, 18)

TYPE MATERIAL. Holotype labeled "V. Carranza, Nay. [prob. Jalisco], 28-VIII-1980, H. Mendoza." Allotype labeled "La Yerba, Nay. [prob. La Yerbabuena, Michoacan], 19-XI-1980, J. Morales." Twenty-one paratypes with the following data: "Mexico: Jalisco, Amatitlán [Amatitan], 8-VII-87, en suelo maíz, Reyes-Rueda, J. Col." (1); "Guatemala," "Sallé Coll.," "1300," "*margaritis* var. male," "B.C.A., Col., II (2), *Gymnetis margaritis* Bates," "*Cineretis* new species, det. at B.M., H.F. Howden '62," "*Gymnetis margaritis* Bates,

B.C. Ratcliffe 1981" (1); "Monte Escobido (11 mi. E.), Zacat., Mexico, 19 July 1954, 7000 ft. alt.," "R.H. Brewer leg., field no. 1836" (1); "Mexico: Jal., 8 mi. NW Tequila, 4400', VIII-5-65," "H.E. Evans collector" (1); "Compostela 1937, Nayarit, Mexico, E.J. Rosenbauer," "O.L. Cartwright Collection 1962" (4); "Ocotlan, Jalisco, Mex., IX-1910," "Coll. by L.H. Weld," "H. & A. Howden collection" (1); "MEXICO: Nayarit, Tepic, Ejido Platanitos, en frutas de guayaba, VIII-1990, J. Cuevos Leg." (8); "Mesillas (near Compostela), Nayarit, 26/X/86, Curoe coll." (3); "Mex: Jal, El Tuito, Curoe coll., 25/X/86" (1). Holotype and allotype in the collection of Miguel Morón. Paratypes at CNCI, UNSM, USNM, FMNH, UNAM, and in the collection of Dan Curoe, Cuauhtemoc Deloya, Henry Howden, Miguel Morón, and Brett Ratcliffe.

HOLOTYPE. *Male:* Length 15.0 mm; width across humeri 8.4 mm. Color dorsally velutinous grayish olive with faint metallic coppery reflections on head and mesepimera; sculpturing reddish brown, piceous, or black; venter weakly shining, a lighter grayish olive than dorsum and with metallic copper reflections; sculpturing reddish brown, piceous, or black. HEAD: Surface moderately punctate; punctures small to mostly moderately large, round to weakly kidney-shaped. Clypeus feebly convex on disc, apex broadly reflexed, emarginate medially, apices either side of emargination rounded. Interocular width 5.0 transverse eye diameters as seen from above. Antenna with basal segment at apex with only 4 testaceous, slender setae on dorsal edge. PRONOTUM: Surface moderately densely punctate; punctures mostly small in median third with a few larger punctures basally and apically, small and large mixed in lateral thirds, smaller punctures round, larger punctures weakly crescent-shaped and setigerous; setae short, sparse, testaceous. Anterior margin at center not swollen. Marginal line complete laterally; margin just anterior of basolateral angle feebly emarginate in dorsal view. Mesepimera moderately densely punctate; punctures moderately large, transverse, setigerous; setae short, testaceous. ELYTRA: Surface moderately densely punctate; punctures small to mostly moderately large, round to transverse to weakly kidney-shaped, setigerous; setae short, sparse, testaceous. Sutural costa and 2 short costae terminating at apical umbone present. PYGIDIUM: Surface coarsely, concentrically vermiculate; impressions long, many confluent, setigerous; setae short, numerous, testaceous. VENTER: Setae testaceous. Mesometasternal protrusion short, extending anteriorly just beyond mesocoxae; anterior and ventral surfaces acute relative to one another; ventral surface flat, in same plane as longitudinal axis of body; anterior surface with long, slender setae curling around apex of protrusion. In ventral view, sides of mesometasternal protrusion subparallel, then expanding slightly before rounded apex; apex of protrusion piceous, shining, connected to shaft by broad, piceous band. Sternites with large kidney-shaped punctures laterally grading to small, round punctures medially. Sternites 2–5 each with a complete or nearly complete, narrow, longitudinal, piceous line in center. LEGS: Femora colored similarly to venter, tibiae predominantly piceous with grayish olive or light green punctures. Foretibia with 3 teeth, middle tooth much closer to anterior tooth than basal. PARAMERES: Figure 11.

ALLOTYPE. *Female:* Length 15.4 mm; width across humeri 8.9 mm. As holotype except in the following respects: HEAD: Frons and disc of clypeus with punctures nearly all large. Apex of basal segment of antenna with 5 testaceous setae on dorsal edge. PRONOTUM: Surface with punctures denser and larger throughout. ELYTRA: Punctures larger and denser. VENTER: Sternites with punctures larger. Sternites 2–5 each with large, piceous area in middle.

VARIATION. *Males* (7 paratypes): Length 15.3–19.3 mm; width across humeri 9.0–11.3 mm. Color dorsally as holotype to slightly darker (3 specimens) to dark purplish red with blue/green reflections on head, sides of pronotum and epimera (3 specimens) to entirely dark reddish brown (nearly black to the unaided eye) (1 specimen); color ventrally varying from grayish olive (with strong copper reflections) (holotype and 3 paratypes) to pale bluish gray with a faint metallic blue reflection (3 paratypes) to a strongly metallic, cerulean blue (1 paratype). Otherwise the male paratypes do not differ appreciably from the holotype.

*Females* (2 paratypes): Length 15.7–16.1 mm; width across humeri 9.1 mm. Color dorsally and ventrally as allotype (1 paratype) to piceous (one paratype; possibly discolored from fluid immersion). The female paratypes do not differ appreciably from the allotype.

DISTRIBUTION. *Hologymnetis moroni* is known from the Pacific slope to the Sierra Madre Occidental in west-central Mexico and from "Guatemala." There is a possibility that the Guatemala specimen could be mislabeled inasmuch as it lacks specific data and was given or sent to Sallé in France prior to 1890. We believe that under such circumstances its provenance is questionable. Coincidentally, that would also help to explain the apparent disjunct distribution.

REMARKS. *Hologymnetis moroni* may be distinguished from other members of the genus by the distinctive form of the parameres in the male and by the fore tibiae where the median tooth is distinctly closer to the anterior tooth than the basal tooth. In the other Central American species with a non-black venter, the median tooth is roughly equidistant from both the basal and apical teeth.

The ventral color in this species is distinctly duller than the strongly shining venter of *H. argenteola* to the north. Dorsal coloration varies extensively and is not a reliable character.

ETYMOLOGY. We take great pleasure in naming this species after our friend and colleague, Miguel A. Morón, who is making substantial contributions to our knowledge of Scarabaeidae, particularly in Mexico.

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*Hologymnetis undulata* (Vigors)
(Figs. 5–6, 12, 19)

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*Cetonia undulata* Vigors 1825:415. Type locality "Brazilia." Holotype at BMNH
    (London), examined.
*Gymnetis consularis* Gory and Percheron 1833:71, 347. Type locality: "Bresil."
    Holotype at MNHN (Paris), examined.

DESCRIPTION. Length 12.9–19.7 mm; width across humeri 7.0–11.9 mm. Background color reddish brown (rarely) to piceous or black; opaque or velvety dorsally, shining ventrally; markings on dorsum and venter cretaceous, opaque or velvety, ranging from creamy white to pale yellow to ochre (rarely). HEAD: Markings consist of longitudinal band either side of middle, extending from frons to clypeus, band usually broken into variably sized spots. Surface of frons and clypeus densely punctate, becoming rugulose on declivous sides and apex of clypeus; punctures large, deep, setigerous in fresh specimens; setae short, erect, reddish brown. Clypeus nearly flat or weakly depressed either side of weakly tumescent, longitudinal ridge; apex broadly rounded either side of broadly V-shaped, median emargination. Interocular width equaling 5.0 transverse eye diameters. Antenna with basal segment at apex with dorsal fringe of 15–20 stout, dark bristles. PRONOTUM: Cretaceous marking present on lateral margins from just behind eye to not quite reaching apex of basomedian lobe, as a sinuous line extending from behind eye posteriorly to apical third of pronotum (occasionally connected to lateral margin), and as a straight line extending anteriorly from apex of basomedial lobe (where expanded) to near center of disc; markings vary in width from slender (not common) to "normal" (most common) to very wide (least common). Surface usually sparsely punctate with punctures becoming a little denser along lateral and anterior margins and in basomedian lobe; punctures usually large (often made to appear smaller or completely covered by cretaceous markings), setigerous along lateral margins in fresh specimens; setae short, stout, reddish brown. Anteromedian half of pronotum with weak, longitudinal keel. Lateral margin with bead broken up by large punctures, side weakly to distinctly emarginate before basolateral angle. Mesepimera dorsally entirely cretaceous or cretaceous with anterior margin dark (most common) or with small cretaceous spot only (least
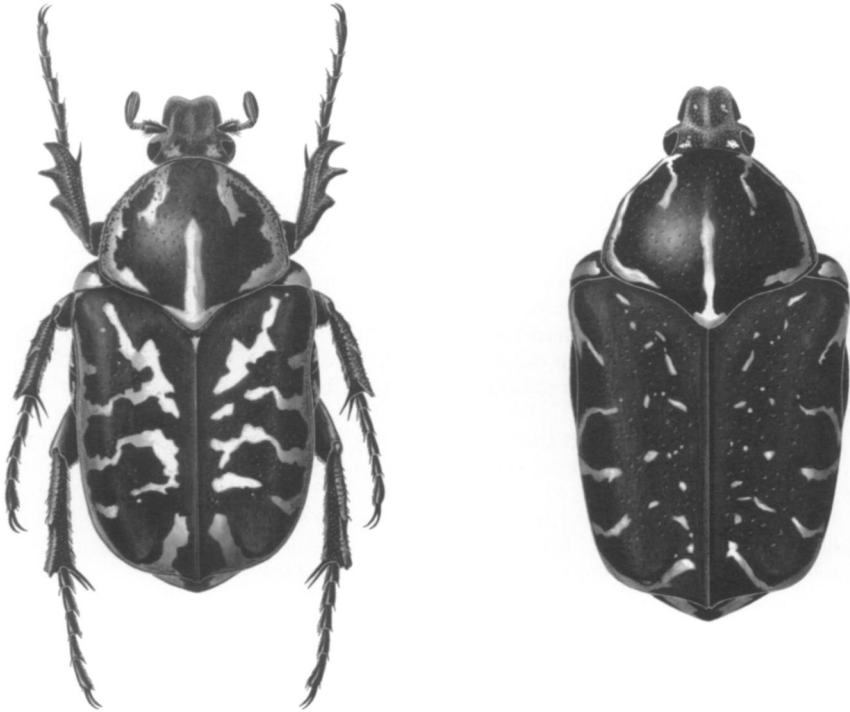
Figs. 5–6.    Habitus of *H. undulata*. Fig. 5 (left) is typical. Fig. 6 (right) shows extreme reduction of dorsal pattern.

common); surface usually with a few large punctures. ELYTRA: Cretaceous markings consisting of line along lateral margin from behind mesepimeron extending posteriorly to wrap around apical umbone; additionally, 4 cretaceous lines extending mesad and nearly perpendicular from lateral margin at subequal intervals, and 1 cretaceous line extending from behind mesepimeron obliquely mesad onto elytron; markings varying in width (similar to those of pronotum) and lines may be variably broken into spots or reduced almost entirely (Figs. 5–6). Surface sparsely punctate; punctures large, deep, round to more commonly horseshoe-shaped; border of cretaceous marks with punctures or long, deeply impressed furrows; furrows of variable length, seeming random, but always outlining marking; immaculate (or nearly so) specimens with punctures in loose rows corresponding to striae. PYGIDIUM: Markings consisting of triangular maculation either side of middle, maculations connected at their bases or at middle and occupying most of surface except for base, margins, and midline; markings variably reduced or (rarely) absent. Surface (where not maculate) transversely vermiculate; vermiculae deep, large, weakly shining. Disc occasionally with only sparse, transverse punctures. Apical third occasionally with sparse, short, testaceous setae. VENTER: Setae dark. Mesometasternal protrusion short, barely extending past mesocoxae; anterior and ventral faces nearly right angled to weakly acute; ventral surface flat, in same plane as longitudinal axis of body; anterior face with short, stout setae; in ventral view sides subparallel to slightly divergent toward apex, apex broadly rounded. Last sternite at apex with fringe of stout, dark bristles. Sternites 1–5 with cretaceous band in apical half of each segment but immaculate in broad band down middle; sternite 1 with band rarely connected; markings variably reduced to small spot on lateral edge of each sternite, sternite 5 occasionally lacking markings altogether. LEGS: Markings (ventral view) varying from

metafemur in anterior half cretaceous with additional spot in posterior half of apical third and mesofemur with cretaceous spot near apex in anterior half, to all legs without markings. Anterior tibia with 3 strong teeth, basal tooth a little farther from middle tooth than apical tooth is from middle tooth. PARAMERES: Figure 12.

DISTRIBUTION. *Hologymnetis undulata* is found in south-central Brazil, Paraguay, and eastern Bolivia.

LOCALITY RECORDS (Fig. 18). 276 specimens examined. Specimens were seen from the following collections: BMNH, CASC, CMNH, DEIC, FMNH, INPA, MLUH, MNHN, MPEG, MZSP, QBUM, UCCC, USNM, ZMHU, Antonio Martínez, Carlos Seabra, and Brett Ratcliffe. BOLIVIA (1): SANTA CRUZ (1): San José de Chiquitos. BRAZIL (268): DF (1): Brasilia; GOIAS (56): Bananeiras, Campinas, Goiatuba, Jatai, Leopoldo de Bulhões, Mineiros, Rio Verde, Trinidade, Vila Tenorio; MATO GROSSO (12): Buriti, Chapada dos Guimares, Cuiba, Jacaré, Rancho Grande; MINAS GERAIS (16): Belo Horizonte, Diamintina, Pouso Alegre, Sabara, Serra do Paraça, St. Catarina; PARANA (1): Curitiba; RONDONIA (1): Vilhena; SÃO PAULO (1): No data; RIO DE JANEIRO (13): No data; RIO GRANDE DO SUL (3): No data; NO DATA (55). PARAGUAY (5): LA CORDILLERA (5): Asunción. TEMPORAL DISTRIBUTION. January (3), February (9), March (2), April (1), May (1), August (4), September (5), October (21), November (27), December (7).

REMARKS. *Hologymnetis undulata,* the only species of this genus in South America, is immediately recognizable because of its bold and distinctive markings. These markings may be variably reduced but are always of the same general configuration. Enough of these markings remain in nearly immaculate specimens so as to still enable easy identification. The center of the elytral disc lacks the elevated stria present in *H. cinerea;* consequently, each elytron appears very flat between the elevated sutural and lateral striae.

Immature stages have not been reported or described in the literature, and we are unaware of any specimens in collections. Habits of the adults are also unknown, and label data indicate that they have been collected by "beating." They are presumably diurnal flower feeders in the relatively dry, shrubby caatingas and cerrados of south-central Brazil.

<p style="text-align:center"><em>Hologymnetis vulcanorum</em> Ratcliffe and Deloya, <strong>n. sp.</strong><br>(Figs. 13, 16, 18)</p>

TYPE MATERIAL. Holotype labeled "El Salvador, Alvarenga." Allotype labeled "Sta. Tecla, SALVADOR," and "27-VIII-51, P.A. Berry Collector." One paratype with same data as holotype, one paratype with same data as allotype, one paratype labeled "Candelaria, EL SALVADOR, VIII-31-55," and "*Cineretis* n. sp., det. at B.M., H.F. Howden '62," and last paratype labeled "No. 444-202A, date. 30-XI-53, loc. Rosario, Cuzcatlan [Cuscatlan, El Salvador], Col. M.S." Holotype and allotype at USNM. Paratypes at CNCI, UNSM, and in the collections of Brett Ratcliffe and Miguel Morón.

HOLOTYPE. *Male:* Length 16.8 mm; width across humeri 9.6 mm. Color dorsally an opaque darker smoke gray suffused with darker brown on elytral costae and lateral and basomedian portions of elytra, center of pronotum with faint, lighter, longitudinal line; sculpturing piceous; venter weakly shining, light smoke gray with faint trace of coppery reflection; sculpturing piceous to black. HEAD: Surface with frons moderately densely punctate; punctures moderately large, round to mostly kidney-shaped, setigerous; setae sparse, short, testaceous. Surface of clypeus moderately punctate; punctures small and round (primarily at apex) mixed with large, confluent, crescent-shaped punctures (either

side of midline), setigerous; setae sparse, small, testaceous. Clypeus weakly tumid on disc, apex broadly reflexed, emarginate medially, apices either side of emargination angulate. Interocular width equals 3.5 transverse eye diameters as seen from above. Antenna with basal segment at apex with fringe of 12 testaceous, slender setae on dorsal edge. PRONOTUM: Surface moderately densely punctate; punctures small to moderate medially, becoming large laterally and apically, smaller punctures round, larger punctures kidney-shaped to C-shaped, deep, setigerous; setae short, testaceous. Anterior margin at center not tuberculate. Marginal bead laterally broken up by sculpturing; margin just anterior of basolateral angle weakly emarginate in dorsal view. Mesepimera moderately densely punctate; punctures moderate to large, crescent-shaped, setigerous; setae short, testaceous. ELYTRA: Surface moderately punctate, becoming denser laterally and especially apically where punctures become confluent; punctures small to moderately large, round to kidney-shaped to elongate, setigerous; setae short, testaceous. Sutural costa and 2 short costae terminating at apical umbone distinctly elevated. PYGIDIUM: Surface coarsely, transversely vermiculate; impressions elongate, confluent, setigerous; setae dense, short, testaceous. VENTER: Setae testaceous. Mesometasternal protrusion short, extending anteriorly just beyond mesocoxae; anterior and ventral surfaces weakly acute relative to one another, angle rounded; ventral surface flat, in same plane as longitudinal axis of body; anterior surface with long, slender setae curling around apex of protrusion. In ventral view, sides of mesometasternal protrusion diverging to broadly rounded apex. Apex of protrusion abruptly separated from shaft by piceous, shining color, connected to shaft by only a thin line of same color (Fig. 16). Sternites with large punctures in lateral third; punctures moderately dense, round to mostly kidney-shaped, setigerous; setae short, testaceous. Center third of sternites 2–6 with shining, piceous spot anteriorly in center. LEGS: Colored similarly to venter. Anterior tibia with 3 subequally spaced teeth, basal and median tooth nearly obsolete. PARAMERES: Figure 13.

ALLOTYPE. *Female:* Length 17.0 mm; width across humeri 10.8 mm. As holotype except in the following respects: Color dorsally olive brown; ventrally, center of sternites 2–5 with large, shining, piceous spot from anterior to posterior margins of each sternite. HEAD: Frons with punctures a little denser. Clypeus with similar but denser (many confluent) crescent-shaped punctures either side of midline. Interocular width equaling 4.0 transverse eye diameters as seen from above. PRONOTUM: Mesepimera a little more densely punctate, some punctures confluent.

VARIATION. *Males* (3 paratypes): Length 16.6–18.1 mm; width across humeri 9.5–10.4 mm. Specimens do not differ appreciably from holotype.

*Female* (1 paratype): Length 17.8 mm; width across humeri 10.4 mm. Aside from being darker overall (specimen is greasy or was fluid-preserved), the paratype does not differ from the allotype.

DISTRIBUTION. *Hologymnetis vulcanorum* is known only from El Salvador (Fig. 18).

REMARKS. This species is nearly identical in external features to both *H. margaritis* and *H. kinichahau.* We could not, at first, find any way to separate *H. vulcanorum* from *H. margaritis* and *H. kinichahau* except by the form of the male genitalia (an internal character) and by locality (largely unreliable even though only one species is known from El Salvador). We have found, however, that the color pattern (normally unreliable) of the mesometasternal protrusion is unique in *H. vulcanorum* (Fig. 16) and is consistently expressed in every specimen of the type series. The shining apex is sharply and transversely delineated form the smoke gray shaft of the protrusion, and the two regions are

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Figs. 7–9.   Parameres of (7) *H. argenteola,* (8) *H. cinerea,* (9) *H. kinichahau* (9a is slightly oblique). Lateral view (a), caudal view (b), opposite side of caudal view (c).
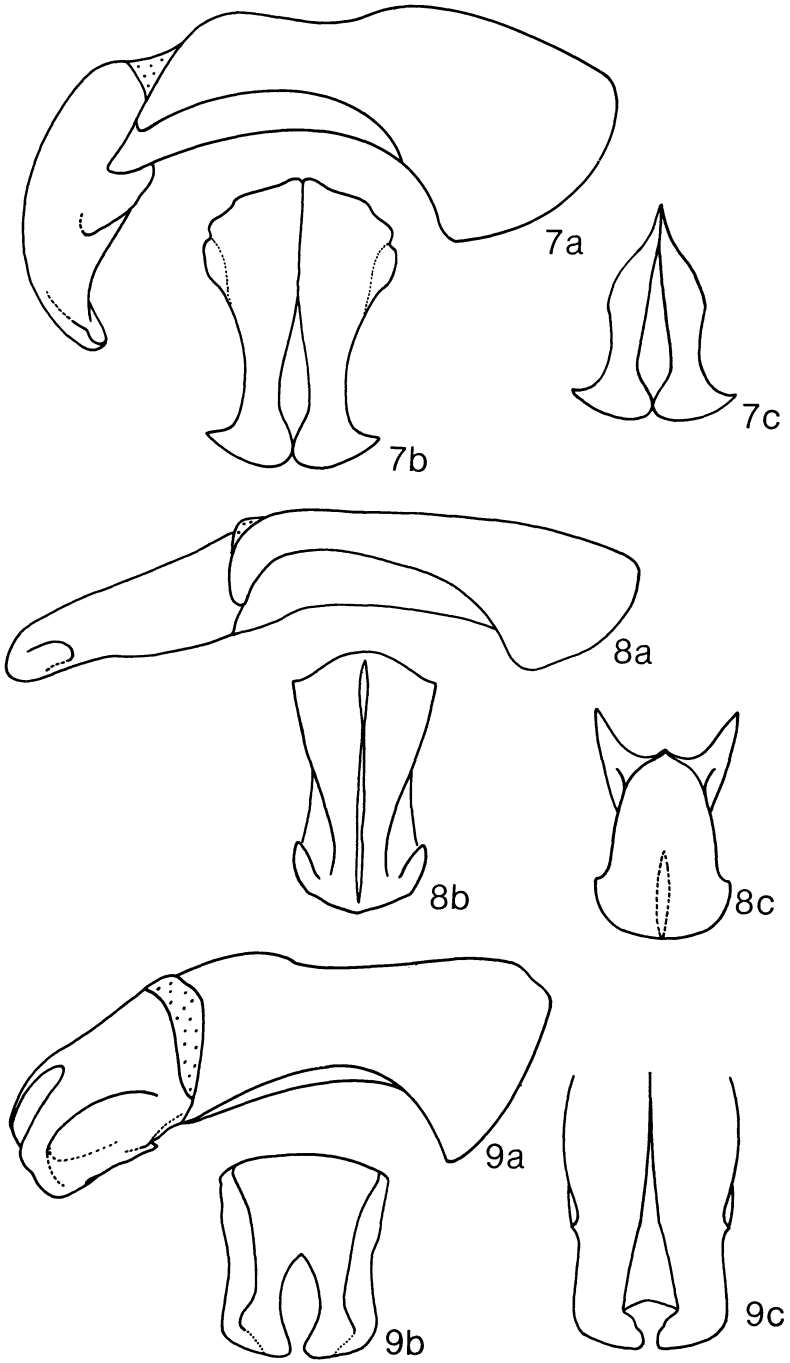
joined by a very slender, longitudinal, piceous line. In every example of both *H. margaritis* and *H. kinichahau,* the apex of the protrusion is not sharply and transversely delineated and the two regions are joined by a broad piceous region. The shape of the protrusion as seen in the illustrations should not be construed as a means of separation of species because it is somewhat variable intraspecifically, it changes slightly depending on the angle of viewing, and is not different enough interspecifically to be of value.

In all but the darkened (greasy) specimen of the type series, there is a faint (but distinct), transverse, angulate, darker band just behind the middle of the elytra. This is formed by denser, darker punctures and is best seen by the unaided eye. Magnification shows the punctures clearly but not the pattern. The interocular width does not exceed 4.0 transverse eye diameters, a character shared only with *H. margaritas*; all other species have a relatively broader frons compared to the eye (5.0 or larger).

The parameres (Fig. 13) are distinctive because, in caudal view, no other species has apical, median ridges that taper to a point. The name "Alvarenga" on the label of the holotype probably refers to the collector's name inasmuch as there is no town by that name according to maps, gazeteers (Central Intelligence Agency 1956), the Embassy of El Salvador in Washington, D.C., and other Salvadorians contacted by Ratcliffe.

ETYMOLOGY. From the Latin "*Vulcanus,*" god of fire; the "*Hologymnetis* of the volcanoes," so named because El Salvador is a country of volcanoes with over 20 in only 21,000 km$^2$.

## PHYLOGENY

Cladistic methods were used to obtain our hypothesis of relationship among the species of *Hologymnetis.* The methodology establishes relationship based on taxa sharing derived states of the same homologous characters (synapomorphies). The operational philosophy for this methodology is that of Hennig (1966) and the many subsequent developers of cladistic methods. While cladistic methods are not without their pitfalls, we believe the method's accountability, repeatability, and objectivity warrant its use above all other methods for phylogeny reconstruction presently available. The characters we used were polarized into ancestral and derived states using the outgroup method of Watrous and Wheeler (1981). The outgroup chosen for our comparative analysis were the species in the genus *Hoplopyga.* Although an analysis of generic relationships within the Gymnetini has not yet been completed, it is suspected that *Hoplopyga* may be the sister lineage of *Hologymnetis* (Ratcliffe, in prep.).

Phylogenetic relationships among these cetoniines have not been previously addressed. We believe that the genus *Hologymnetis* is viewed most parsimoniously as a monophyletic lineage. The characters that bind the taxa together in a phylogenetically unified lineage are (1) foretibia tridentate in *both* sexes, (2) prosternal spine *short,* and (3) head unarmed. Initially, we had reservations about the inclusion of *H. undulata* in the genus because of its radically different color and pattern and because of its extremely disjunct distribution. Short of
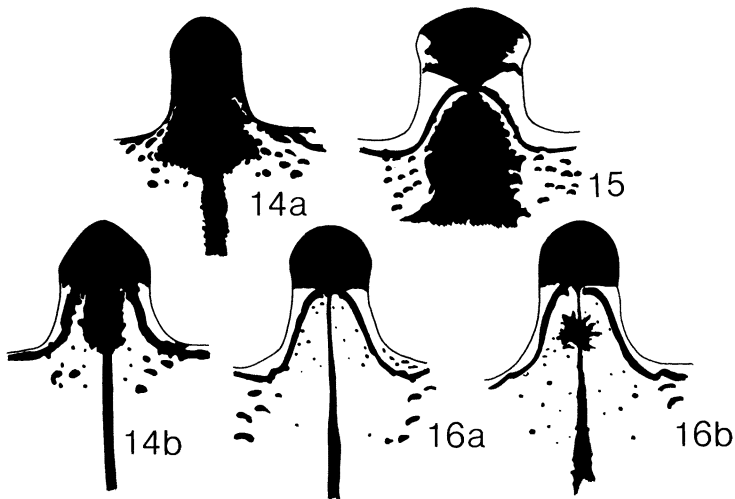
$\longrightarrow$

Figs. 10–13.   Parameres of (10) *H. margaritis,* (11) *H. moroni,* (12) *H. undulata,* (13) *H. vulcanorum.* Lateral view (a), caudal view (b), opposite side of caudal view (c).

10a  10b  10c

11a  11b  11c

12a  12b  12c

13a  13b  13c
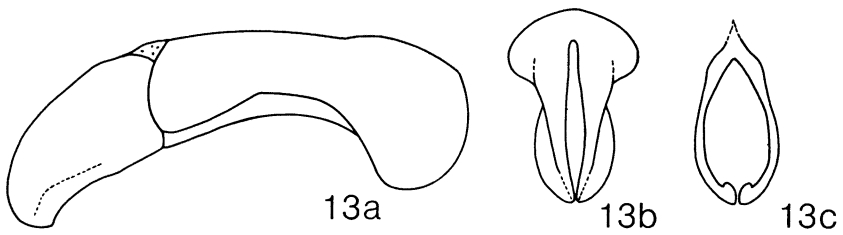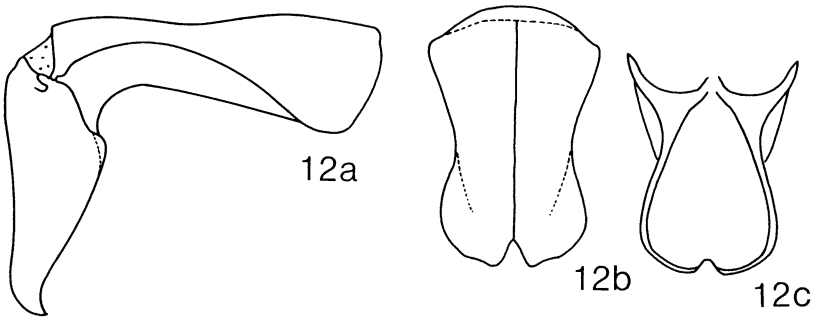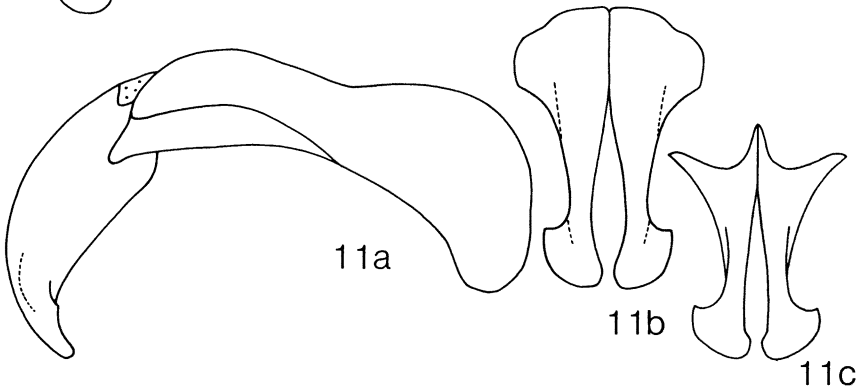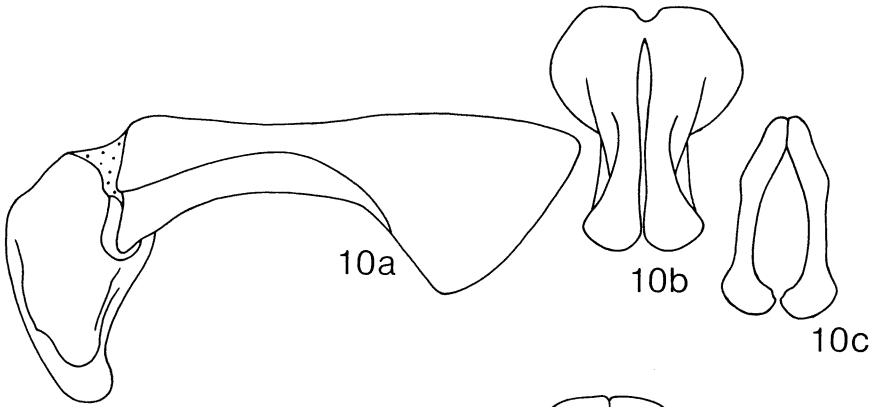
Figs. 14–16.    Mesometasternal projections of (14) *H. margaritis* (showing variation), (15) *H. kinichahau* (holotype), (16) *H. vulcanorum*; holotype (a), allotype (b).

creating a new, monobasic genus that could be separated from *Hologymnetis* only with difficulty, we chose to retain its current generic placement.

We would like to have identified numerous characters in order to achieve a robustness in our resulting hypothesis. We found, however, only eleven characters that are consistently expressed in states usable in the analysis. In spite of a bewildering array of colors and patterns in the Gymnetini, there are relatively few solid characters available to separate taxa from an otherwise widespread, nearly homogenous matrix of body form and sculpturing. This may be indicative of relatively recent speciation resulting in little morphological distance between taxa. For example, the posterolateral angle of the hind coxa was noticeably different, being either rounded or acute, but it also varied within a single species, thus rendering this character useless. Surprisingly, the form of the male genitalia is diagnostic within *Hologymnetis,* whereas it is not in many other gymnetine genera. Color and pattern are usually very different between many species but, because they are so variable *within* a species, they must be used in both keys and cladograms with extreme caution.

<div align="center">CHARACTERS</div>

Table 1 shows, in a conventional data matrix, the scoring of the characters used in our analysis. The number 1 represents the ancestral state, and 2 or above indicate a derived condition. The %D figures suggest, in a general way, the relative degree of "derivedness" of each species. This reflects the observation by Edmonds (1972) and others that the frequency of synapomorphy is a valid measure of inferred cladistic relationship. The %D is arrived at by dividing the number of derived character states by the total number of characters being used.

What follows is a list of the characters we found useful and our rationale for scoring character states.

Table 1.  Characters and distribution of phylogenetically classified character states among the species of *Hologymnetis*. The %D figure represents relative degree of derivedness.

| No. | Character | Species and character states | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | *undulata* 64% D | *cinerea* 64% D | *margaritis* 9% D | *kinichahua* 18% D | *vulca-norum* 9% D | *moroni* 55% D | *argenteola* 55% D |
| 1 | Metallic venter | 1 | 1 | 1 | 1 | 1 | 2 | 2 |
| 2 | Ventral coloration | 2 | 2 | 1 | 1 | 1 | 2 | 2 |
| 3 | Pygidial sculpturing | 1 | 2 | 1 | 1 | 1 | 2 | 2 |
| 4 | Elytral punctation | 2 | 2 | 1 | 1 | 1 | 2 | 2 |
| 5 | Anterior pronotal margin shape | 2 | 2 | 1 | 1 | 1 | 1 | 1 |
| 6 | Elytral costae | 2 | 1 | 2 | 2 | 1 | 2 | 2 |
| 7 | Parameres | 2 | 2 | 1 | 1 | 1 | 1 | 1 |
| 8 | Dorsal pattern | 3 | 2 | 1 | 1 | 1 | 2 | 2 |
| 9 | Mesometasternal peg | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 10 | Mesotibial carina | 1 | 1 | 1 | 1 | 2 | 1 | 1 |
| 11 | Pygidial pattern | 2 | 1 | 1 | 1 | 1 | 1 | 1 |

1. METALLIC VENTER. Metallic reflectivity is, in our view, a character different from actual coloration. Dorsal metallic reflection, common in some groups of Scarabaeidae, is relatively rare in the Gymnetini. It is found in some species of *Argyripa, Corvicoana, Cotinis,* and *Allorrhina.* The presence of a metallic luster on the ventral surface occurs a little more commonly than on the dorsum but is still uncommon. A metallic venter does not occur in the outgroup genus, *Hoplopyga,* nor in any but two of the species of *Hologymnetis.* Only *H. argenteola* and *H. moroni* possess a metallic venter, a state we consider derived.

2. VENTER COLORATION. The 'hoplopygaform' ventral coloration is a gray-brown and is the ancestral state. A shiny, entirely black surface is found in *H. undulata* and *H. cinerea* and is considered derived. Similarly, *H. argenteola* and *H. moroni* have a blue-green venter, and this is also considered derived.

3. PYGIDIAL SCULPTURING. The form of pygidial sculpturing found in *Hoplopyga* consists of large, concentric, vermiform impressions. *Hologymnetis cinerea* has a pygidium that is closely, concentrically strigulose, hence derived. The pygidium in *H. moroni* and, to a lesser extent in *H. argenteola,* we consider derived because the form and degree of sculpturing is different from that of the outgroup.

4. ELYTRAL PUNCTATION. The relatively large, often U-shaped punctures found on the elytra of *H. margaritis, H. kinichahau,* and *H. vulcanorum* are like those found in species of *Hoplopyga* and are scored ancestral. Punctation in the remaining species of *Hologymnetis* is usually greatly reduced and is considered derived.

5. SHAPE OF ANTERIOR PRONOTAL MARGIN. The shape of the margin is evenly rounded in *Hoplopyga* and in all but two species of *Hologymnetis.* In *H. undulata* and *H. cinerea* this margin is angularly produced or tumescent, a derived state for this character.

6. ELYTRAL COSTAE. In *H. margaritis* and *H. vulcanorum,* the sutural costa and those coalescing to form the apical umbone are most like the state seen in the outgroup and are plesiotypic. The other species of *Hologymnetis* have these costae a little more produced, which we consider derived.

7. PARAMERES. The shape of the parameres in all but two species of *Hologymnetis* is basically 'hoplopygaform,' *i.e.,* with a relatively narrow shaft with apical or subapical lateral expansion of shaft. The parameres of *H. kinichahau* and *H. undulata* are short and blunt, an apotypic state.

8. DORSAL PATTERN. Species of *Hoplopyga* and *H. margaritis, H. vulcanorum,* and *H. kinichahau* possess an elytral pattern characterized by darkening of the costae forming the apical umbone and a lighter, obliquely transverse 'band' just behind the middle of the elytra. This is the ancestral state. *Hologymnetis argenteola, H. moroni,* and *H. cinerea* all have unicolorous elytra, and we have scored this state as derived. The bold, black and cream elytral pattern seen in *H. undulata* is even more derived relative to the outgroup.

9. MESOMETASTERNAL PROTRUSION. This protrusion is short in the outgroup and in all but one species of *Hologymnetis.* Only in *H. cinerea* does this protrusion extend well past the mesocoxae, a state that is derived relative to the outgroup.

10. MESOTIBIAL CARINA. The mesotibial carina is located past the middle of the tibia in *H. vulcanorum* and is considered apotypic. All other species of *Hologymnetis* and species of *Hoplopyga* have the carina at the middle of the tibia, which is the plesiotypic state.

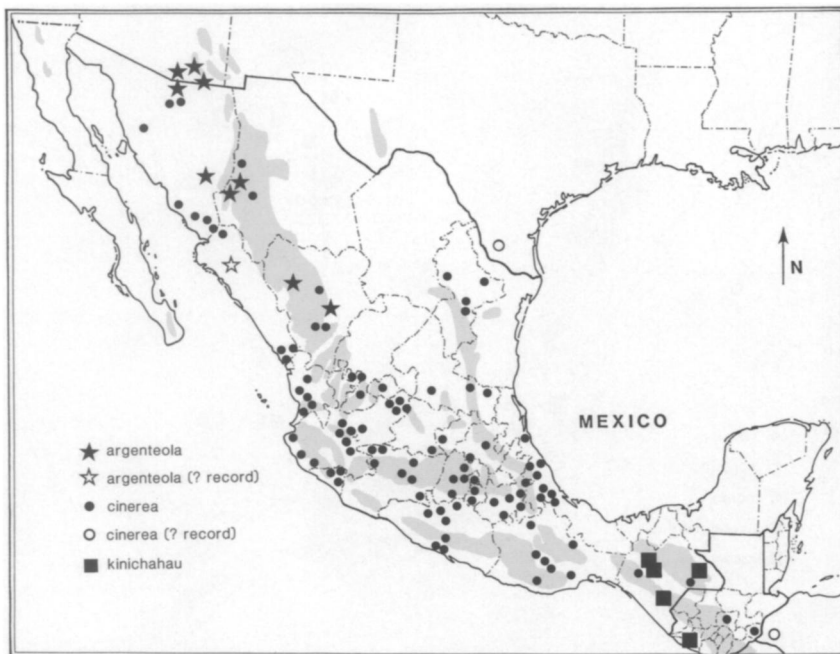11. PYGIDIAL PATTERN. All species of *Hologymnetis,* except *H. undulata,*

Fig. 17. Distribution map for *H. argenteola, H. cinerea,* and *H. kinichahau.* Grey area represents highlands. Dark symbol equals point data, open symbol indicates questionable record.

share the 'hoplopygaform' color pattern (such as it is) on the pygidium, a state characterized as ancestral. Only *H. undulata* has a large, cretaceous spot either side of the middle, and we consider this derived.

### RESULTS

Only one phylogenetic tree resulted from the PAUP analysis of our data set. The cladogram was constructed with the assumption that the most parsimonious arrangement of shared, derived character states with the fewest homoplasies (parallelisms, reversals) best infers genealogical relationship. The cladogram is shown in Figure 23. The overall consistency index of the tree was high at 0.857 (suggesting compatability of character interactions, *i.e.,* few homoplasies). The consistency index, after exclusion of uninformative characters (unique apomorphies), remained high at 0.818.

*Hologymnetis vulcanorum,* followed successively by *H. margaritis* and *H. kinichahau,* retains the most ancestral character states. These three species also "cluster" on an area cladogram in that they are all basically restricted to regions encompassing the Sierra Madre del Sur, Sierra Madre de Chiapas, and the Central American Nucleus.

*Hologymnetis argenteola* and *H. moroni* are sister species and, although allopatric, both inhabit the Sierra Madre Occidental and the western portion of the Transverse Volcanic Belt. They share the same degree of "derivedness"
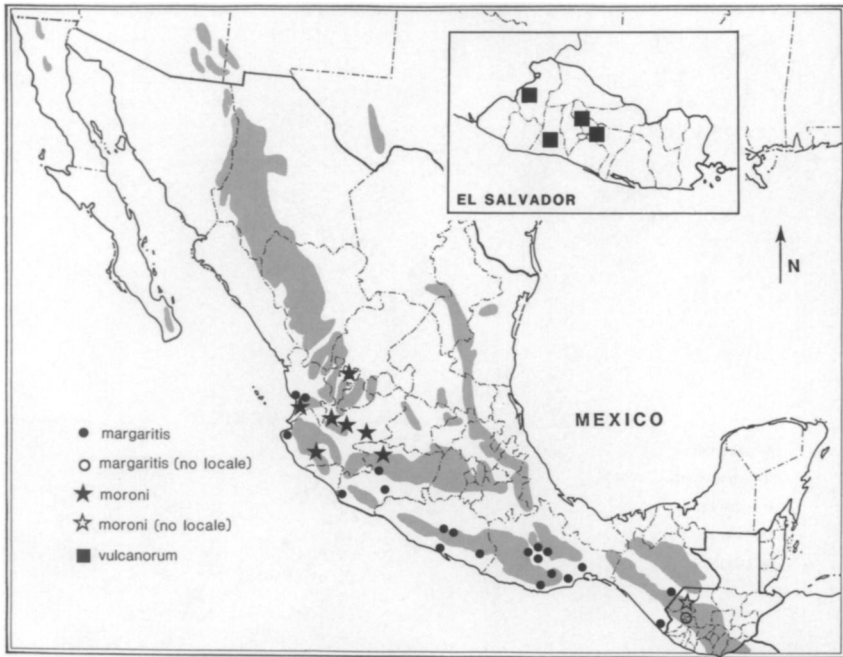
Fig. 18.    Distribution map for *H. margaritis, H. moroni,* and *H. vulcanorum.* Grey area represents highlands. Dark symbol equals point data, open symbol indicates country record only.

but are different from one another because of the form of the protibia and parameres and the ventral coloration.

The most derived species in the genus are *H. cinerea* and *H. undulata,* each at opposite ends of the generic range. Both are widespread in the areas they inhabit. Due to its apparent longer isolation, we might have thought that *H. undulata* would have retained more ancestral character states because of reduced genetic interchange. This is clearly not the case and suggests either continued evolution in isolation or long retention of shared traits that evolved prior to genetic separation.

## BIOGEOGRAPHY

*The top of Mt. Everest is marine sandstone.*

—John McPhee

## ORIGINS

The genus *Hologymnetis* is found only in the New World. One species occurs in the southern half of Brazil, eastern Bolivia, and Paraguay. The other six species are found from El Salvador north to southern Arizona. Inasmuch as we believe the genus to be monophyletic (see Phylogeny), we propose a biogeographic model that uses a deductive approach to explain the current dis-
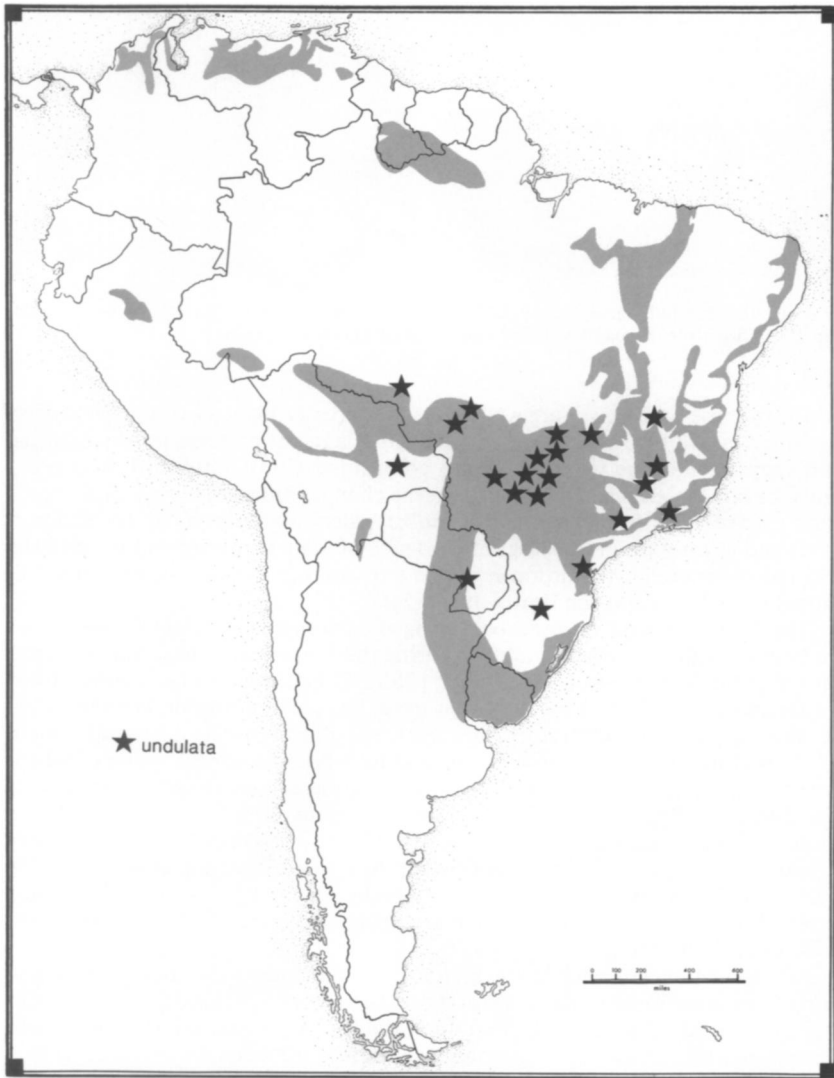
Fig. 19.    Distribution map for *H. undulata*. Grey area represents zone between the 1,000 and 1,500 mm annual precipitation isohyets (isohyets after Brown 1982).

tribution of these beetles. It is a maximum parsimony hypothesis congruent with the cladogram and is a blend of vicariance and dispersal paradigms of biogeography.

Lacking fossil evidence for the Gymnetini, we are forced to rely upon data from plate tectonics, present and paleodistribution of other plants and animals, and ecological factors to formulate a model to best explain the current distri-
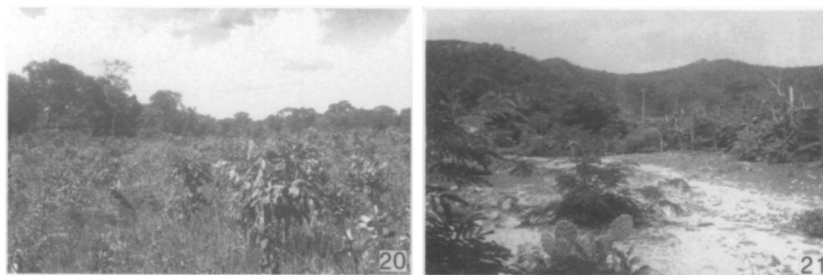
Fig. 20.   Cerrado near Goiania, Goias, Brazil, in February during the wet season.
Fig. 21. Thorn scrub near Hwy 190 southeast of Oaxaca, Mexico.

bution of these beetles. We are well aware of Mares' (1985) caveat that biologists
straying beyond the broadest interpretation of ancient patterns must recognize
that they are moving from science to conjecture. Continents shift their posi-
tions, ocean currents and weather patterns change, mountains rise, and organ-
isms evolve. The hard-science portion of paleobiogeography is based upon
plant and animal fossils, geological evidence of plate tectonics and orogenesis,
and paleoclimatology. Caution must be exercised in making deductions that
propel us well beyond the limits of the data.

   The fragmentation of Pangaea during the Mesozoic with subsequent con-
tinental drift and mountain building during the Tertiary are the main historical
causes of biotic differentiation (Haffer 1982). This biotic change resulted from
the formation of effective barriers between a previously continuous biota which
became increasingly subdivided through time. The Gymnetini (*sensu* Krikken
1984) is composed of 25 New World and four African genera, none of which
are shared between continents. Their distribution is clearly Gondwanan. Our
Gondwana model suggests that the Gymnetini is an old lineage with origin and
some radiation at least prior to 110 MYBP, which coincides with the early
Albian break between Africa and South America (Dietz and Holden 1970,
Tarling 1971, Veevers *et al.* 1971). Ancestral New World Gymnetini then
evolved in isolation in South America during that continent's long westward
drift away from Africa.

   "By the Miocene, after 'drifting' for 70 million years, South America had
moved into a position quite close to its present-day one" (Tarling 1980). Moun-
tain building along the western margin of the continent was just beginning, and
we can infer that much of the continent supported tropical forests (*e.g.*, Axelrod
1970, Vuilleumier 1971, Simpson 1975, Raven and Axelrod 1975). Of course,
as Axelrod has pointed out repeatedly (Axelrod 1950, 1958, 1970, 1972; see
also Raven 1963), there have very likely always been climatic fluctuations that
would cause wet forest habitat to give way to drier vegetation in some portions
of tropical America. Moreover, since the broad vegetation bands are established
by the position of a continent on the rotating sphere of the earth (Beaty 1978),
we can also infer that tropical forest habitats graded into more xeric vegetation
areas in southern South America (Webb 1978). By late Miocene times, after
the Andes had achieved some elevation, the wind patterns were greatly altered
and this resulted in the formation of major habitats differing significantly in
precipitation patterns (*e.g.*, Vuilleumier 1971, Solbrig 1976, Webb 1978). Hab-
itat alteration due to orogeny also occurred in North America. Although the
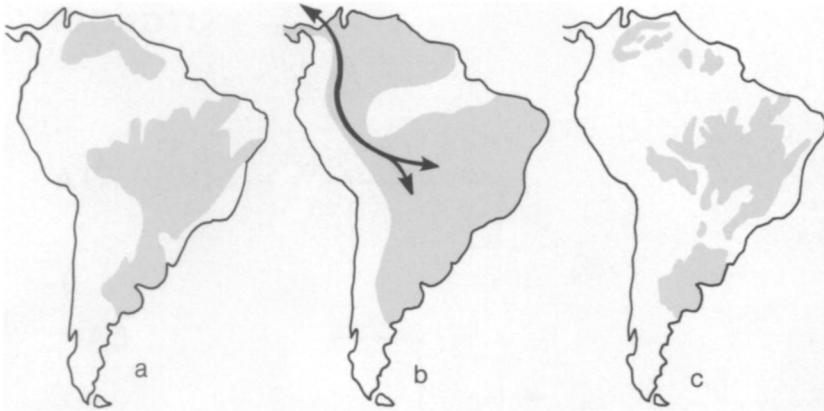
Fig. 22. Maps showing approximate distribution of savannas (grey areas) in South America at (a) about 4.0 MYBP, (b) during glacial maxima and (c) today. Arrow in (b) shows dispersal route of taxa living in savanna habitats (after Marshall 1985).

changes in South American landscapes that occurred during the Cenozoic roughly paralleled those of North America in both timing and pattern (Axelrod 1970, Bailey *et al.* 1977), semiarid habitats developed somewhat earlier in South America (Webb 1978, Mares 1985).

### SOUTHERN HEMISPHERE DISTRIBUTION

Ancestral *Hologymnetis* were present in South America although we cannot really know whether this was north or south of the present Amazon basin. Given their current distribution and ecological requirements, it is assumed that their evolution has been in drier habitats. Based upon the occurrence of fossil mammals showing grazing adaptations, drier habitats like savannas have been present in South America since middle Tertiary time (Webb 1978).

The Quaternary (*i.e.,* the last two million years) is characterized by great environmental instability (Bigarella and Andrade-Lima 1982, Whitmore and Prance 1987). These climatic changes caused, in relatively short geologic time, successive expansions and contractions of either forest or open, drier vegetation. Forest and nonforest biomes broke up into isolated blocks or expanded and coalesced depending on varying humid or arid climatic conditions (Haffer 1982). The evidence for increases and reductions in forest and nonforest vegetation, popularly known as the refuge theory, is discussed extensively in Haffer (1969), Vuilleumier (1971), Müller (1973), Prance (1973, 1982), Brown *et al.* (1974), Brown (1977), Tricart (1974), and Simpson and Haffer (1978). Most of the evidence for South America consists of pollen profiles and inferences from extant biotas because studies of core samples and other paleontological data are lacking. These changes led to the disruption of formerly continuous ranges when habitats became so climatically altered that they could no longer support the survival of certain taxa. Concurrently, the range of other taxa was able to expand in concert with a broadening favorable habitat.

With the reduction of forest vegetation during drier periods, there was a corresponding increase in nonforest formations which penetrated into the Am-
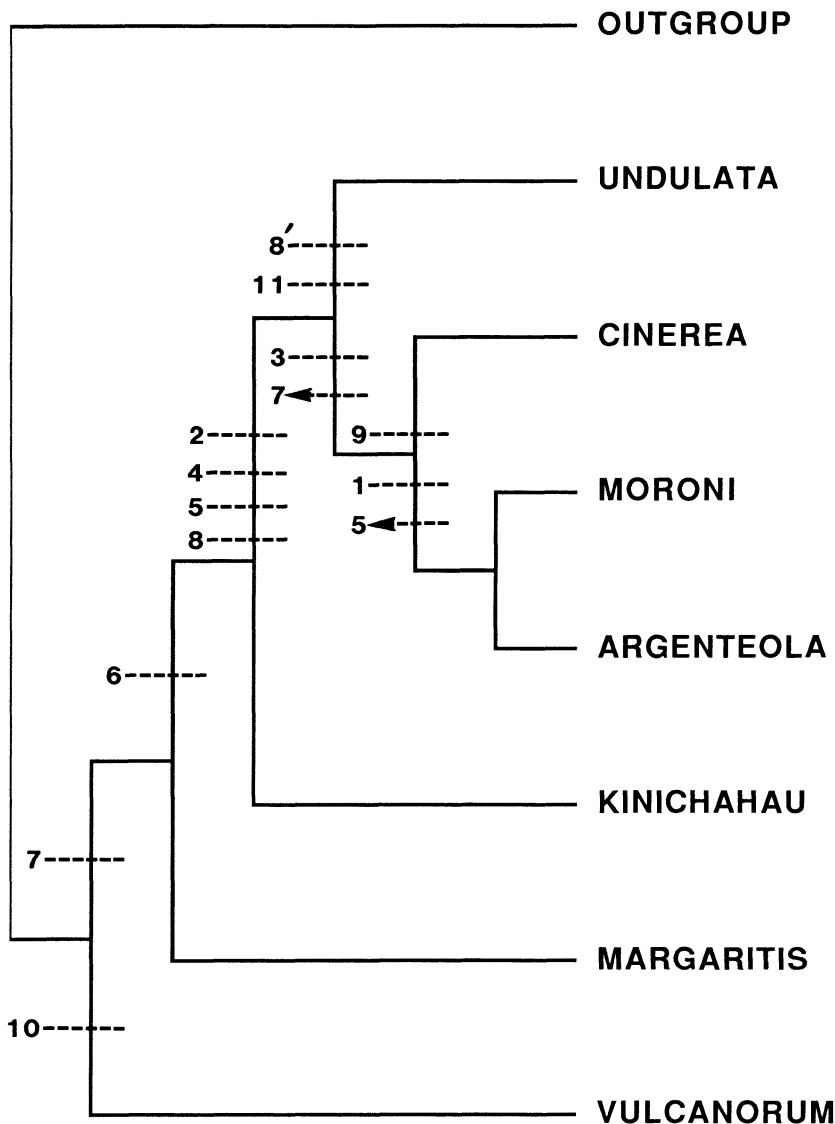
Fig. 23.    Cladogram for the species of *Hologymnetis*. Numbers refer to characters; line next to number indicates character transformation to more derived state; reverse arrow refers to character transformation to more ancestral state.

azon region from both north and south. Such formations consisted of large blocks or corridors connecting the open vegetation associations of the Central Brazilian Plateau with those of Venezuela and the Guianas (Fig. 22) (Eden 1974, Sarmiento 1975, Bigarella and Andrade-Lima 1982, Marshall 1985).

These savannas (or campos) were covered by an open scleromorphic or xe-romorphic primary vegetation comprising an ecologically dominant ground layer which consisted mainly of densely associated grasses, sedges and/or herbs with or without trees and/or shrubs (Huber 1982).

*Hologymnetis undulata* inhabits the mesic to semiarid, relatively open veg-etation of the cerrados and caatingas of central and southern Brazil (Fig. 19). Cerrados (Fig. 20) include a number of different vegetation types ranging from closed forests to open savannas with savanna woodland being most common (Walter 1971). They cover an area of about 1,500,000 km², dominate the Planalto region of central Brazil, and border the southern limit of present-day Amazonia. Cerrado is characterized by markedly seasonal rainfall of 1,000–1,500 mm (Brown 1987). Characteristic tree species of the cerrado are *Byr-sonima verbascifolia, Bowdichia virgilioides, Caryocar brasiliensis, Curatella americana, Dimorphandra mollis, Hancornia speciosa, Qualea grandiflora*, and *Stryphnodendron barbatima*. The high degree of local endemism suggests that the cerrado is an old formation (Brown 1987). Caatingas consist of arboreal or shrubby formations that are deciduous with many members being spinous (Andrade-Lima 1982). This tropical thorn scrub occurs today mainly east of Amazonia in northeast Brazil. Rainfall is low, rarely exceeding 1,000 mm per annum, and plants produce flowers and leaves during the brief rainy season. Typical genera of the Brazilian caatinga include *Bromelia, Caesalpinia, Cap-paris, Euphorbia, Jatropha, Manihot, Mimosa*, and *Opuntia* (Brown 1987). Brown noted that Brazilian caatinga has considerable physiognomic similarity with the vegetation of the arid regions of northern Venezuela/Colombia and Central America. Typical genera of the Venezuela/Colombia arid region include *Acacia, Bulnesia, Bursera, Caesalpinia, Capparis, Cercidium, Cereus, Croton, Jacquinia, Lemaireocereus, Opuntia*, and *Prosopis*.

The distribution of *Hologymnetis undulata* matches very closely the 1,000–1,500 mm annual precipitation isohyet south of the Amazon Basin (Fig. 19). Cerrados and caatingas are also found primarily in this area. This species, like others in the genus, is not a denizen of rainforests but, rather, of mesic to semiarid habitats. Consequently, the broad, continuous band of present-day Amazonian rainforest is a barrier preventing further northward dispersal. We propose that this was not always the case, however.

Ancestral *Hologymnetis*, if not already present in either northern or southern South America, would have been afforded suitable avenues for traversing pre-viously inhospitable lowland forested regions in Amazonia by the extensions of savanna-like habitat. With the establishment or re-establishment of rain forest in the Amazon basin, populations of ancestral *Hologymnetis* became divided and isolated both to the north and south of the Amazon region. The northern lineage ultimately dispersed to nuclear Central America, and the southern lineage became isolated in the woodland savannas south of the Am-azon basin. As habitats changed through time, ancestral *Hologymnetis* disap-peared entirely from Nicaragua south to Amazonia.

## The Interamerican Biotic Interchange

Pre-Miocene dispersal of the biota between North and South America prob-ably occurred uncommonly. A small amount of biotic interchange agrees with the geologic evidence suggesting a relatively wide separation of the Americas in Cretaceous through Oligocene times (Raven and Axelrod 1974, Smith and

Bredin 1977, Gose *et al.* 1980). Initial contact was probably through a filter route consisting of a peninsula and islands. Even after the formation of a continuous land connection, a filter bridge, rather than a corridor, was in operation due to probable unfavorable conditions along the route or at either end. As Stehli and Webb (1985*b*) point out, consideration of climate is important both before and after establishment of a connection. For example, the existence of clear evidence of mountain glaciation along the continental divide in Guatemala suggests that simply extending present-day conditions back in time will not suffice to allow a real understanding of the physical nature of the link between the two Americas or of its effect on biotic interchange.

After Mesoamerica coalesced during the Pliocene 3.0 MYBP (Marshall 1988) to 5.7 MYBP (Lloyd 1963, Kaneps 1979), an extensive faunal exchange began (Webb 1978, Stehli and Webb 1985*a*). Formation of the isthmian dispersal route permitted separate invasions of plants and animals at widely separated periods when climates and topographic features were different. We hypothesize that after the formation of the isthmus of Panama, the Gymnetini began their northward dispersal into Central America and Mexico.

Webb (1978, 1985) has provided an excellent analysis of the interamerican biotic exchange, appropriate parts of which are mentioned here. The interval from 2.5–1.5 MYBP shows an extensive movement of savanna-adapted mammal faunas from south temperate to north temperate latitudes and vice versa. All of the animals that are known to have dispersed between the Americas in the late Tertiary were tolerant of, or specifically adapted to, savanna woodland habitats. The savanna elements were not incidental parts of the interchange but represent the vast majority of the taxa involved. Notable among them were horses, llamas, armadillos, and ground sloths. The extent of savanna adaptations among the land mammals of the interchange indicates the presence of a uniformly nonforested corridor or a moving mosaic of such habitats between South America and North America. The more arid conditions that must be postulated for the isthmian region during its early history probably supported seasonal forests grading into thorn scrub savannas. Similar habitats exist today in northern Venezuela and eastern Colombia and on the Pacific slopes of Central America from western Panama northward.

Less mesic conditions in the isthmian corridor were a result of a combination of factors having to do with climatic fluctuations associated with northern hemisphere glaciations, lowering of sea levels (with a concomitant increase in land area), regional uplift with large-scale volcanic extrusion, and creation of rainshadow regions. The data of Shackelton and Opdyke (1977) and Cronin (1981) indicate that glacial maxima at and following the emergence of the Panamanian land bridge, combined with the presence of a north-south corridor over the bridge, occurred only twice in the late Tertiary. These times (2.5 and 1.8 MYBP) represent "optimal ecological windows" that permitted dispersal of taxa living in savanna habitats between the Americas (Marshall 1985). The earliest known South American mammals to disperse to North America across the Panamanian land bridge occur in rocks dated at 2.8–2.6 MYBP. This reciprocal event favoring savanna-adapted forms could not have occurred earlier due to absence of a suitable corridor, habitat, and climate. Subsequent opportunities did not exist until the next glacial maxima at about 2.0–1.9 MYBP (Marshall 1985).

"Thus, two synchronous and reciprocal dispersal events of late Tertiary age are recognized. The first event (2.8–2.6 Ma) included dispersal of *Erethizon, Neochoerus, Glyptotherium, Glossotherium, Nothrotheriops, Kraglievichia,* and

*Dasypus* (and the ground bird *Titanis*) to North America, and *Conepatus, Hippidion,* and *Platygonus* to South America. The second event (2.0–1.9 Ma) included dispersal of *Hydrochoerus, Eremotherium,* and *Holmesina* to North America, and *Arctodus, Galictis, Felis, Smilodon, Tapirus, Hemiauchenia, Onohippidium,* and *Cuvieronius* (and possibly *Stipanicicia, Dusicyon,* and *Protocyon*) to South America. Only one dispersal event of early Pleistocene age is evident, and this occurred at about 1.4 Ma. It corresponds to the earliest of the Pleistocene glacial maxima recognized by Cronin (1981) and follows the one at 2.0–1.9 Ma. During this event *Canis, Lutra, Chrysocyon, Cerdocyon, Leo,* and *Stegomastodon* dispersed to South America, and *Didelphis* and *Palaeolama* dispersed to North America" (Marshall 1985).

The last glacial maximum permitting dispersal of savanna biotas over the land bridge occurred 12,000–1,000 years B.P. (Bradbury 1982, Markgraf and Bradbury 1982). A savanna corridor formed along the eastern side of the Andes connecting the now disjunct habitats in South America (Fig. 22). The major obstacles to such dispersal were distance and potential competitive exclusion.

Given that cetoniines are capable of such powerful flight, distance may not have been such a deterrent to long distance dispersal. The Japanese beetle (*Popillia japonica* Newman), for example, has spread from the east coast of North America (where it was introduced) to the central states (1,900 km away) in only 70 years; that averages 27 km/year. *Aphodius fimetarius* (L.), introduced into North America from Europe probably in colonial times, is now found over much of the continent. The tussock moth, monarch butterfly, European corn borer, and honeybee all represent contemporary examples of long distance dispersal by insects in short periods of time. The Africanized honeybee, *Apis mellifera scutellata* Lepeletier, has dispersed 300–500 km per year from southern Brazil to northern Mexico in only 30 years (Camazine and Morse 1988). The rapid and historically near-instantaneous colonization of the Australian continent by the European hare, *Lepus europaeus* Pallas, highlights the staggering dispersal ability of a small mammal (Marshall 1985). The opossum, *Didelphis marsupialis* L., had an average dispersal rate of 50 km/year during the 26 years following its introduction into California (Tyndale-Biscoe 1973). At such a rate this species could extend its range 25,000 km in only 500 years (Savage and Russell 1983). Martin (1973) noted that a conservative dispersal rate of 16 km/year would have permitted prehistoric man to spread from Canada to Tierra del Fuego in less than 1,000 years.

The dispersal of insects between the mid-continental regions of North and South America may have occurred in only a few thousand years with the availability of suitable habitat. The vertebrate fossil evidence clearly indicates that dispersal of savanna-adapted animals occurred twice in the late Tertiary. South American ancestral *Hologymnetis,* adapted to seasonally dry habitats, was part of that dispersal. While it may be difficult for some biologists to accept so short a time scale for such evolutionary change, the paleontological record of the interamerican interchange demonstrates that two or three million years is sufficient time to produce fundamental evolutionary reorganization of a major biota (Webb 1978).

The late Pleistocene shift to more humid conditions in lower Central America produced a major set of savanna disjunctions spanning the isthmian gap (Webb 1978). The disjunct distribution across the American tropics shared by many present-day organisms provides additional evidence of a previous woodland savanna corridor. Within the temperate to subtropical Areodina (Scarabaeidae: Rutelinae: Rutelini), six genera are found ranging from the United

States to Guatemala, and three genera are found in South America (Jameson 1990). None of these genera occur in the remainder of Central America, which, for the most part, has been historically covered by tropical rainforest. This Central American gap might seem like a paradox until, noticing its occurrence in other groups, we recognize a pattern.

Many birds adapted to savanna or thorn scrub show a wide interamerican disjunction. These include the Green Jay, Military Macaw, Melodious Blackbird, Horned Lark, Vermillion Flycatcher, small woodpeckers, and the Grasshopper Sparrow (Griscom 1950, Mengel 1970). Cricetid rodents such as *Reithrodontomys* skip from semiarid habitats in Nicaragua to similar habitats in the Andes, and *Crotalus* vipers (preferring scrub habitats) now have a large gap across the rainforest of the isthmus (Webb 1985).

The distributional gap across the isthmian region is well known for many plants as well as many bees that specialize on these plants (Raven 1963, Solbrig 1972, Rzedowski 1973, Simpson and Neff 1985). Webb (1985) observed that one of the most convincing indications of former continuity is a string of relict populations such as the outposts of *Larrea* in Peru and Bolivia partly connecting its main south temperate and north temperate ranges. This idea is strengthened by the fact that one of the principal foods of the extinct ground sloth (*Nothrotheriops*), as indicated by its dung, was *Larrea,* and that both genera clearly came to North America from temperate South America (Martin *et al.* 1961, Hunziker *et al.* 1973).

By the late Pleistocene, as now, woodland savanna taxa were excluded from the isthmian region due to the dissolution of savanna habitats and replacement by tropical rainforest. Late Pleistocene pollen samples from Lake Gatun in Panama reveal a forest flora much like that of present lowland Panama (Webb 1978). About 1,700 km of tropical wet forest extending from Costa Rica and Panama through northern Colombia now separates the nearest areas of savanna and thorn forest (Sarmiento 1976). Consequently, ancestral *Hologymnetis* were also excluded from this region because they could not survive in tropical wet forests. Northern Central America retained a woodland savanna fauna as evidenced by the present biota and Pleistocene samples from Guatemala, Honduras and El Salvador (Stirton and Gealey 1949, Carr 1950, Duellman 1966, Savage 1966, Woodburne 1969, Howell 1969). Species of *Hologymnetis* are today found on the drier Pacific slopes of Guatemala and El Salvador and have dispersed northward into Mexico and extreme southern Arizona.

NORTHERN HEMISPHERE DISTRIBUTION

All but the single South American species of *Hologymnetis* are found in Halffter's (1987) Mexican Transition Zone. This area includes the southwestern United States, all of Mexico, and that part of northern Central America extending south to the Nicaraguan Depression. The Nicaraguan Depression is a tropical lowland located between the mountains of El Salvador, southern Honduras and northern Nicaragua and the Talamanca Range in Costa Rica and Panama. It now constitutes a dispersal barrier to many organisms because of its tropical lowland nature.

*Hologymnetis vulcanorum* and *H. kinichahau,* found in El Salvador and southern Guatemala respectively, are possibly isolated remnants in the Andes Centroamericanas and Altiplano of Guatemala. We postulate that if these two species are indeed represented by small and isolated populations, then their existence is threatened due to the severe habitat alteration caused by humans

during the last 50 years there. Neither area has apparently been very well collected judging from material found in collections.

Based on his analysis of the entomofauna, Halffter (1976) formulated several different dispersal patterns to explain the present distribution of taxa in the Mexican Transition Zone. Our ideas regarding the distribution of species in the genus *Hologymnetis* coincide well with Halffter's Typical Neotropical Dispersal Pattern. In this pattern, South American elements penetrated into the Mexican Transition Zone and the southern United States after the formation of the Panamanian land bridge and after most of the elevation of the Mexican Plateau. The north-south direction of dispersal corridors in the physiographically complex Mexican Transition Zone has been a major factor in the displacement of biotas during times of climatic change, and this seems to be particularly true for the species of *Hologymnetis*.

As ancestral *Hologymnetis* spread northward, they used as their principal expansion route from Central America the mountains of Oaxaca and Guerrero. The transverse Volcanic Belt and the Sierra Madre del Sur funneled the dispersal of *Hologymnetis* to the west toward the Sierra Madre Occidental. All of the species of *Hologymnetis* west and north of the Isthmus of Tehuantepec (*margaritis, moroni, argenteola, cinerea*) are now found along the Sierra Madre Occidental. This range is the longest (1,400 km) and most continuous in the Mexican Transition Zone. It runs parallel to the Pacific coast from its juncture with the Transverse Volcanic Belt in Nayarit and Jalisco states to the U.S.–Mexican border. Limited penetration of *Hologymnetis* into isolated areas of southern Arizona has been enabled by such a dispersal corridor. As also noted by Jameson (1990) for *Parabyrsopolis* (Scarabaeidae: Rutelinae), the continuity of this mountain system and local climate has prevented further 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.

According to the research of Axelrod (1958) and Findley (1969), no extensive desert area appeared in the Sonoran or Chihuahuan regions until the Pleistocene. The fossil evidence indicates that an extensive pine-oak savanna existed prior to desert formation in what is now the Texas panhandle (Rogers 1976) and adjoining areas of northern Mexico and southern Arizona. Expansion of *Hologymnetis* northward through the Sierra Madre Occidental as far as the Huachuca and Santa Rita mountains in Arizona was facilitated by suitable habitat and climate. Isolation of *H. argenteola* and *H. moroni* into more equable mountain islands surrounded by a sea of desert then occurred with the establishment of the current post-glacial vegetation. Only *H. cinerea,* with its apparently broader ecological valency (150 m elevation in Veracruz to open pine highlands at 2,000 m in Michoacan) has spread to the plains of the Gulf Coast and along the Sierra Madre Oriental.

Species of *Hologymnetis* in Mexico occur from near sea level sites to the open pine highlands at 2,000 m, as just noted for *H. cinerea.* Most records are from tropical subdeciduous forests where the average annual rainfall is 1,000–1,500 mm (see Toledo 1982, and Rzedowski 1986 for climatic requirements of Mexican vegetation types). There is a remarkable similarity between distribution as it relates to precipitation for both the Mesoamerican and South American species, *i.e.,* they both occur largely between the 1,000 and 1,500 mm average annual rainfall isohyets. Their occurrence elsewhere, especially in pine-oak forests, where precipitation generally tends to be lower, is indicative of their adaptability and competitiveness.

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## 1992 E.C.N. MEETING

The 1992 Entomological Collection Network meeting will be held Saturday morning, 5 December, through Sunday morning, 6 December 1992, hosted by USDA–ARS Systematic Entomology Laboratory in Beltsville, Maryland and Maryland Center for Systematic Entomology. Planned sessions include materials conservation in entomological collections, biodiversity sampling methods, data security and ownership, and demonstrations of collections- and systematics-related software.

If you haven't received a notice and wish to be get further notices, contact Margaret K. Thayer, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496; tel. (312) 922-9410, ext. 404; FAX (312) 922-2572 or 427-7269; Internet: thayer@fmnh785.fmnh.org. For additional program info: Richard L. Brown, Dept. of Entomology, Drawer EM, Mississippi State Univ., Mississippi State, MS 39762; tel. (601) 325-2085; FAX (601) 325-8837.

—F. Werner