Amber Fossil Enicocephalidae (Heteroptera) from the Lower Cretaceous of Lebanon and Oligo-Miocene of the Dominican Republic, with Biogeographic Analysis of *Enicocephalus*

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ABSTRACT

The oldest known enicocephalomorphans are reported and discussed, based on two adults in amber from Lebanon (Albian to Aptian, Lower Cretaceous, ca. 120 million years ago), apparently representing one species. This extends the fossil record for this family three times that of the previously known age. This amber species appears most closely related to the Murphyanellinae (Aenictopecheidae); several features are plesiomorphic for the Enicocephalomorpha, including the male genitalia.

Six additional species of fossil Enicocephalidae (sensu stricto), all adults, are described from Oligo-Miocene amber of the Dominican Republic: *Alienates brodzinskyi*, *A. electrodominicus*, *Enico-*cephalus omen, E. prius, E. seniculus*, and *E. subvitreous*. The closest living relatives of the two species of *Alienates* cannot be determined with certainty since adult material is lacking for most living species. They are, however, very similar to two living species, *A. millsi* and *A. insularis*. A specimen of a distinctive *Alienates* is reported. Most living species of *Enicocephalus* in the Greater Antilles and northern Lesser Antilles have extensive and vivid scarlet body coloration and form a monophyletic group. Two new living species are described, *Enicocephalus almanzari* and *E. bahorucensis*, both collected from isolated, wet montane forests in the Dominican Republic (island of Hispaniola). Cladistic analyses on the relation-

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ships of living *Enicocephalus* are affected very little by including fossil species. Biogeographic patterns, however, are affected by the fossils. One Dominican amber species, *E. seniculus*, belongs to a South American clade, indicating geographic extinction in the Caribbean. Another fossil species, *E. subvitreous* alters biogeographic hypotheses within the Caribbean. The two remaining fossil species of *Enicocephalus* have their closest living relatives also in the Dominican Republic, establishing an Oligo-Miocene endemism for those clades.

Cladistic morphological and molecular results by Schuh and others indicate that the Enicocephalomorpha is the sister group to the remaining Heteroptera (the Euheteroptera Stys). This information plus the paleontological results here indicate that the enicocephalomorphans are indeed ancient, perhaps Jurassic to Triassic in origin.

INTRODUCTION

The Order Heteroptera is an ancient group of insects, extending into geological time to the Permian (Bekker-Migdisova, 1960; 1991; Carpenter, 1992). Those earlies forms were transitional between Coleorrhyncha and Heteroptera, sensu stricto. According to Schuh's (1986) cladistic assessment of the Heteroptera, and recent molecular evidence (Wheeler et al., 1993), the Enicocephalomorpha are the sister group to the rest of the living Heteroptera, or Euheteroptera Stys, 1985. (Stys split the Enicocephalidae into two families, the Aenictopecheidae and the Enicocephalidae, sensu stricto. We will most often refer in the text to enicocephalids, which we are using synonymously with the Enicocephalomorpha, unless it is necessary to specify one of the two families.) At least 10 living families of Heteroptera cladistically more recently derived than enicocephalids are known from the Jurassic. In this light, the enicocephalids would probably have the oldest fossil record of living heteropteran families. But, par for the vicissitudes of fossilization, enicocephalid fossils are quite rare, which is no great surprise given the spotty abundance of these minute bugs in modern habitats. Until now the oldest enicocephalid was from the Eocene of England (Jarzembowski, 1986). This specimen is an incomplete head of a presumed nymph, but with intricate preserved detail and relief. We extend the known geological age of the Enicocephalidae by reporting here two remarkably well-preserved specimens in Lower Cretaceous amber (ca. 120 mya [million years ago]) from Lebanon.

Enicocephalids are curiously unknown from the huge deposits of Baltic amber (e.g., Larsson, 1978). In fact, the only amber fossils of Enicocephalidae besides the ones discussed here are from Burmese amber. The classification of those three fossil species was revised by Štys (1969), who placed them in two new genera (one of them as a new subfamily). Information on the geological age of the Burmese amber is anecdotal, but most references indicate lower Miocene (Langenheim, 1969). If cladistic rank reflects relative age (as it hypothetically should), the Burmese amber is surely older than Dominican amber, for the latter contains species so closely allied to modern, recently-derived species, as we show here.

Because of the antiquity of enicocephalids, study of essentially modern taxa in the younger Dominican amber (ca. 25–30 mya) provides really no information about higher relationships. However, when this study began, we felt that the Dominican amber fossils could offer valuable insight into the biogeography and history of the Caribbean insect fauna, for basically four reasons. One, small insects dwelling under bark and in leaf litter generally have poor dispersal ability, and subsequently have small areas of endemism (this aspect of their biology, some would also argue, might make geographic sampling less certain). Second, the known and postulated ages of the enicocephalids provide permissive evidence that the distributions of these bugs are likely to have been influenced by Mesozoic continental drift, thereby making an analysis of their distribution all the more amenable to vicariance methods.

Third, there are the morphological attributes of the enicocephalids themselves, which make them conducive to study as amber fossils. Enicocephalines and alienatines, in particular, are exceptional among most insects in having rather reduced male genitalia, with

most of the informative morphological variation instead being external; such as the spination of the forelegs, shape of the head and prothorax, and wing venation. Thus, there are very few morphological aspects that cannot be compared between living species and well-preserved amber specimens, which is a common limitation of fossils and even most other amber insect fossils. Fourth, this work would not have been possible without the recent comprehensive monograph on New World enicocephalids (Wygodzinsky and Schmidt, 1991). That monograph established an updated and detailed morphological and faunal context to which the Dominican fossils can now be added. In lieu of such revisionary treatments on living species, the isolated descriptions of amber fossils (unfortunately in vogue at present) are usually devoid of systematic and evolutionary meaning.

The two genera represented in Dominican amber, *Enicocephalus* and *Alienates*, provide convenient biogeographic comparisons. Both are quite unrelated (Wygodzinsky and Schmidt, 1991), but are similar in numbers of total species, species endemic to Caribbean islands, and because their overall ranges encompass the circum-Caribbean region (*Enicocephalus* actually extends further southward, to southern Brazil). We take this opportunity to describe two new species of *Enicocephalus* collected recently in isolated, wet montane forests in the Dominican Republic.
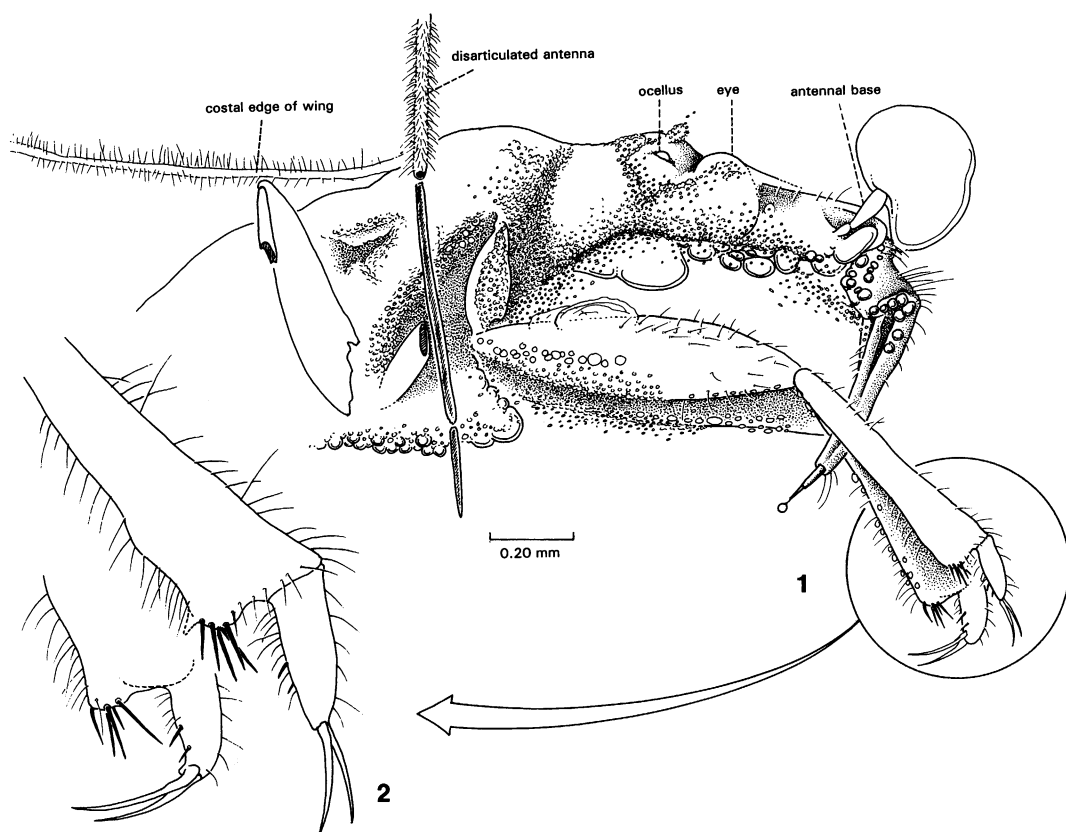
Lebanese amber that was studied here is from the private collection of the Acra family. Professor Aftim Acra, of American University in Beirut, originally collected the material with his son, Fadi, in the vicinity of Dar-al-Baidha. Schlee and Dietrich (1970) described the stratigraphy of amber deposits from Jezzine, Lebanon, which were Neocomian and Aptian (130-120 mya). These lower Cretacous deposits actually extend into Jordan and Israel. The other collection of Lebanese amber fossils is at the Stuttgart Museum, but Schlee and Dietrich (1970) did not mention enicocephalids as being present in that collection. A synopsis of Dominican amber paleontology has been given elsewhere (Krishna and Grimaldi, 1991; Grimaldi, 1991), and will not be repeated here. A minimum age of lower Miocene to upper Oligocene for the amber fossils at hand is a sufficient and reasonable estimate. Interestingly, enicocephalids are unknown from the large deposit of amber in southern Mexico (Hurd et al., 1962), which is of equivalent age and similar botanical origin as the Dominican amber (Langenheim, 1969).

MATERIALS, METHODS, ACKNOWLEDGMENTS

Methods for preparation of the amber and observation of inclusions are given elsewhere (e.g., Grimaldi, 1993). Measurements of the *Alienates* were done using a Leitz Wetzlar stereoscope with an ocular micrometer at $144 \times$ magnification. The *Enicocephalus* specimens, being much larger, were measured with a digital stage micrometer mounted to the stage of a Zeiss SV-8 stereoscope, using $64 \times$ magnification. With such tiny specimens positioned at odd angles in amber, the error of measurement derives principally from orientation of specimens. Each specimen was repositioned several times and respective measurements averaged. FW refers to fore wing in length measurements, and BL to body length. Length of the head (HL) is that distance between the apex of the collum (pedicel, for other insects) and the posterior margin of the segment bearing the ocelli; this length is divided by the length of pronotum (PL). FF is the fore femur (length) and FT is the fore tibia (length). Citations of most major and historically important taxonomic references for enicocephalids are omitted here since they are provided by Wygodzinsky and Schmidt (1991).

Figs. 1, 2.   Lebanese amber specimen JG 83/1 (Acra collection). **1.** Right lateral view of anterior half; most of specimen is covered by a frothy coating. All scales are in mm. **2.** Detail of foretibiae.

SYSTEMATICS

LEBANESE AMBER SPECIMENS
Figures 1–8

Specimen JG 83/1 (figs. 1, 2): A partially preserved adult approximately 2.9 mm long in a piece of very fractured amber, ca. 14 × 6 × 10 mm. Specimen lies near an edge. Synthetic resin was applied to crumbling surfaces of the piece and over the enicocephalid specimen. A chip of glass coverslip was placed on top of the mountant over the bug, which greatly improved the visibility and should better protect the specimen from surface oxidation.

Both forelegs very well preserved; head (with rostrum) present. Eyes and most of thorax obscured by dense froth of fine bubbles. Antennae detached, one is displaced and lies vertically over right side of thorax. Remnants of right wing present; no venation discernible. Left mid and hind legs present, but greatly obscured by depth of amber and internal fractures. Right mid and hind legs partially preserved (only coxa and femur, respectively). Abdominal sclerites not observed; masses of brown granular material present where abdomen is, perhaps the original tissue. Dorsal surface is obscured by a crusted surface close to the specimen.

Placement of the specimen in the Enico-
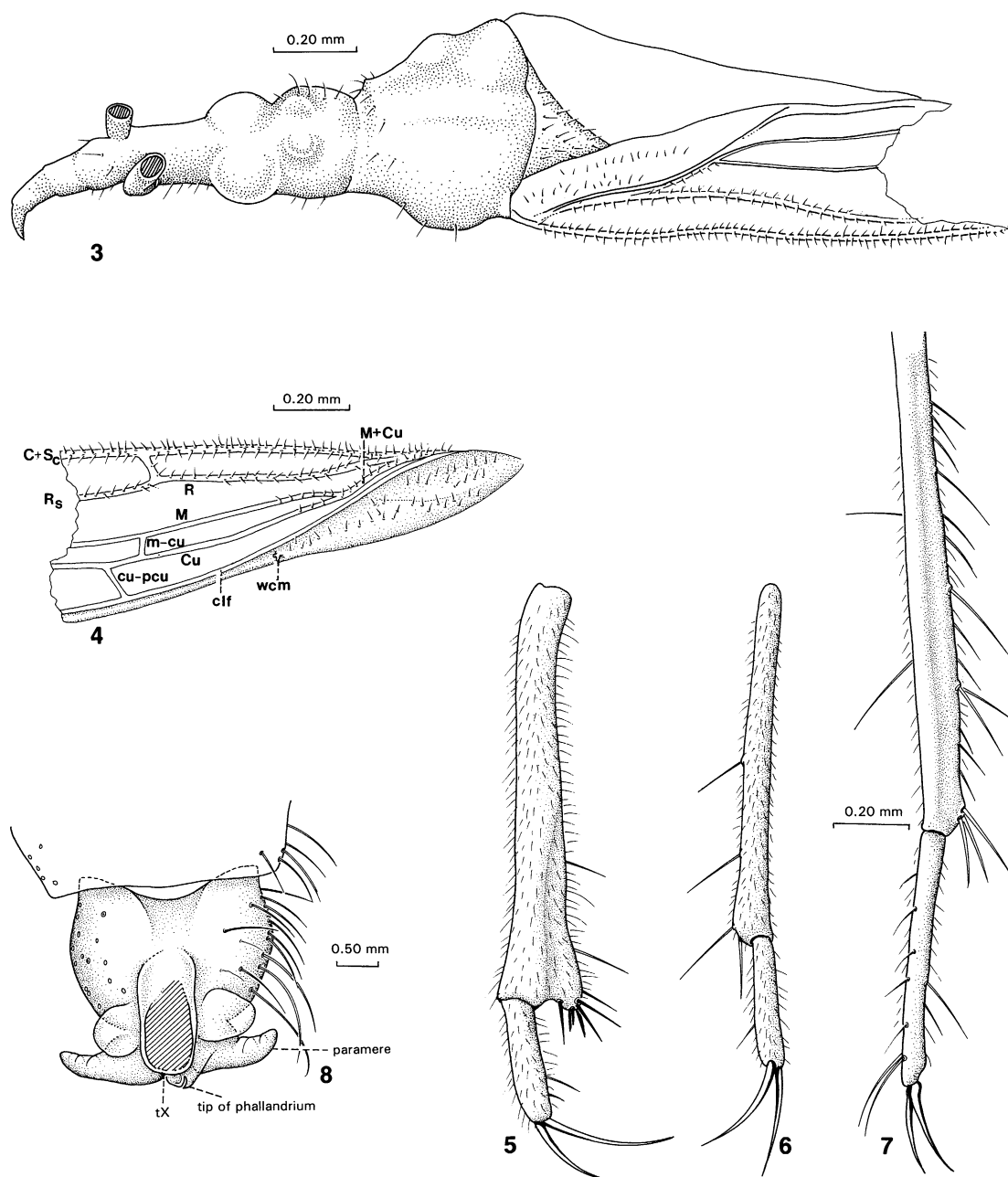
Figs. 3–8. Lebanese amber specimen (JS673). **3.** Dorsal view of anterior half. A milky coating covers most of the specimen; distal halves of wings are lost. **4.** Right forewing. 5-7: tibiae and tarsi. **5.** Left foreleg. **6.** Left midleg. **7.** Left hindleg (mesal view). **8.** Male genitalia, dorsal view.

cephalomorpha is based on the elongate head; ocelli (only right one visible) on a hind lobe of the head; a long, projecting rostrum; and the unique, chelate forelegs. Foretibia and tarsus well preserved, with apical spines fully

visible (special preparation was necessary with the resin, plus 144× magnification [Leitz Wetzlar] with high-intensity fiber optic illumination). Foretibia with five stout apical spines: row of three equal-size ones on lateral

edge; two slightly longer ones on medial edge. Foretarsus with two small spines on distal half of adaxial surface [it is possible that four exist, but they are not visible]. Each tarsus with two claws of equal size. The stout, crescentic spine close to the base of outer claw (seen in Aenictopecheidae and Enicocephalidae sensu stricto) definitely not present. Inner apex of foretibia obscured, bristle comb (if present) not observed.

Specimen JS/673 (figs. 3–8): A virtually complete, adult male in a thin slice of clear, dark yellow amber, with a few cracks. Piece is 17 × 8 × 4 mm. Most of the body is covered with a thin, milky coating ("Schimmel"), similar to what is seen in many Baltic amber inclusions. Antennae are missing, as well as distal third of wings.

HEAD: Entirely covered with Schimmel, thus obscuring exact boundaries and shapes of sclerites and other structures. Hind lobe of head about same width as anterior lobe; eyes apparently large. Anteocular distance large, slightly greater than diameter of eye.

THORAX: Wings with apical third sheared off. Venation as shown in figure 4. R (+ Rs?) virtually parallel to C + Sc. M and Cu separate off very close to base of wing. X-veins m-cu, cu-pcu present. Clavus slightly sclerotized, with scattered setae. Hind wings diaphanous; costal edge barely visible, rest of wing not visible.

Lobes of pronotum difficult to discern due to Schimmel. Scutellum triangular, with ca. 40 fine, unevenly distributed setae. Forelegs with excellent preservation, without milky coating. Femur without thicker, stiff setae; no fine granular areas apparent on ventral surface. Greatest width of tibia (apically) slightly less than width of femur. Posterior edge of tibia with two thicker, stiff setae, lengths ca. 0.6× width of femur. Distance from tibial apex ca. equal to length of seta; other stiff seta ca. 2× its length from more apical seta. Posterior corner of tibial apex with rounded mound bearing five stout, stiff setae; one distinctly smaller than others (ca. 0.5× the length). Stiff setae on adaxial edge of tarsus difficult to see. Claws of equal length; long, ca. 1.0× length of tarsus (measured for left foreleg). No comb apparent on mesal-apical edge of tibia. Ratio length femur:tibia:tarsus (exclusive of claws): 2.7:3.4:1.

Midlegs with right femur having milky covering. Numerous fine cracks ring the femur and are filled with Schimmel, resembling thick setae. Ventral edge of tibia with row of three longer, stiff setae; apex with pair of ventral, stiff setae. All tarsi one-segmented. Claws of equal size. Ratio length mid-femur:tibia:tarsus 2.5:2.7:1. Preservation of hind femora similar to that of right mid femur, with fine cracks and Schimmel. Hind tibia long and thin; with ventral row of 5 longer, stiff setae (lengths slightly greater than width of tibia); preapical setae paired; ventral half of apex with 3 stiff setae; no apical bristle comb. Claws of equal size; long, ca. 0.45× length of tarsus. Tarsus preapically with long, fine pair of setae on dorsal surface. Ratio length hind-femur:tibia:tarus 2.3:2.6:1.

Abdomen mostly covered with Schimmel. Male genitalia: genital capsule large, subspherical, with numerous long setae, especially laterally. Tergite X a long, thin oval, but apex lost at surface of amber. Parameres long, fleshy lobes with narrow, rounded tips; base of paramere with broad, rounded plate. Guide (or tip of phallandrium? [sensu Stys, 1985] extended slightly beyond posterior margin of tX, but most of it is obscured.

DISCUSSION: Both specimens probably represent one species, based on the distinctively large anteocular distance and general spination of the foretibia. There are slight differences, however, in the foretibial spination. Features of this fossil species which are plesiomorphic at the level of the Enicocephalomorpha include: long, equal-size claws (present in several taxa throughout the group, such as *Systelloderes*); apex of foretibia with group of 5–6 thin spines, not stout ones as seen in the Aenictopecheidae; a rather well developed clavus; male genitalia well developed, with a pair of large, unfused parameres and an indistinct, composite phallus. The genitalic features and the one-segmented tarsi most closely match the Murphyanellinae (Aenictopecheidae) (cf. Wygodzinsky and Stys, 1982). This subfamily is represented by two living genera known from Singapore. Presence of a preapical bristle comb on mesal surface of foretibia is expected but could not be confirmed since it is obscured. Also, since female terminalia were unavailable, it could not be determined whether or not a rudi-

mentary ovipositor is present, as seen (plesiomorphically) in the Aenictopecheidae. Autapomorphies of the fossil species include a very distinctive r-c crossvein, and male genitalia with large, disc-shaped bases of parameres.

We have chosen not to provide a name for the fossils and designate types because of the incomplete nature of the specimens, and because they are as yet still in a private collection.

## DOMINICAN AMBER AND LIVING TAXA

Genus *Alienates* Barber

DIAGNOSIS: Males with fully developed wings, eyes, and ocelli (females lacking these); fourth antennal segment longest; all tarsi one-segmented; tarsal spines absent; apex of foretibia with two to three straight spines; forewing venation reduced, with at least a marginal and submedian vein (hind wings lacking venation).

Restricted to Central America and the Caribbean, with one species known from Arizona. Seven of the 12 described species are endemic to Caribbean islands: *brevilobus*, *iviei*, and *muchmorei* are from the U.S. Virgin Islands (St. John and St. Thomas); *millsi* is from Cuba; *maldonadoi* is from Jamaica; *insularis* from Key Largo, Florida and South Bimini, Bahamas; and *dudichi* from St. Lucia, Lesser Antilles. Two species from Central America are undescribed, being based on an incomplete male and on females and nymphs (Wygodzinsky and Schmidt, 1991).

Alienates brodzinskyi, new species
Figures 9–11

DIAGNOSIS: Similar to the living species *millsi*, except for (most notably) the upturned flange on the hind margin of the metanotum in the fossil; forewing setulae longer than in *millsi*; and a fine furrow between the ocelli not present in the fossil. Easily distinguished from the other species of amber *Alienates* since *brodzinskyi* is smaller (body length 1.05–1.25 mm); wing venation in *brodzinskyi* comprises a single, incomplete longitudinal vein (apex forked in *A. electrodominicus*); and forefemur is same length or slightly shorter than foretibia in *brodzinskyi*.
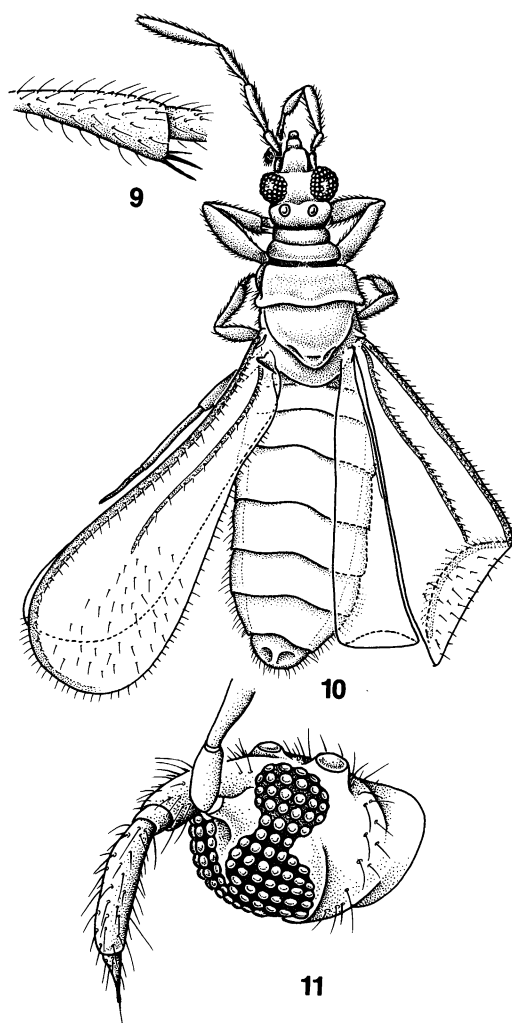
Figs. 9–11. *Alienates brodzinskyi*. **9.** Detail of apex of foretibia. **10.** Dorsal habitus. **11.** Oblique frontal view of head and proboscis.

DESCRIPTION: General body color brown, without distinctive markings. Head rather wide and short. Distance between outer margins of eyes much wider than hind lobe of head. Length of head (excluding rostrum) only slightly more than length of hind lobe. Eyes with about 60 facets, of standard size. Hind margin of eye deeply excavated (to depth of three facet rows); anterior margin slightly excavated (about two facets only); eyes almost contiguous ventrally. Ocelli very close to hind margins of eyes; separated by 1.5× diameter of ocellus. Cuticular granules on gula and ventral part of thorax not observable. Setae

without tuberculous bases. Antennal segment IV 1.7–1.9× the length of segments II and III. Hind lobe of head narrow, ribbonlike; constricted between middle lobe of head (bearing ocelli) and prontoum; slightly narrower and shorter than anterior lobe of pronotum. Pronotum with posterior margin flanged. Scutellum small, without distinct suture between it and mesonotum. Posterior margin of metanotum rounded, simple; without surface sculpturing. Forewing venation highly reduced: C+Sc present, extended to slightly past apex of wing; with single row of setae. M+Cu incomplete: extended from base of wing to ca. 0.6× its length. Membrane at apex of wing with ca. 40 fine setae. Hind wing without venation. Foretibia with two stouter, one fine apical setae. Cuticular granules not observable.

HOLOTYPE: Specimen no. AMNH DR-10-35A, which occurs in a dark yellow, small round piece of amber (ca. 6 mm diameter). This piece also contains another adult male of the same species (specimen DR-10-35B), a male keroplatine mycetophilid, and fine particulate debris. The holotype is closer to the surface and better displayed. Measurements: ratio of antennal segments 2:3:4 = 1.1:1:1.7; FW length = 1.04 mm; BL = 1.25 mm; HL/PL = 2.27; FF and FT not measured (at odd angles).

PARATYPES: Five additional adult males in three pieces of amber, all designated as paratypes. AMNH 3077: in dark oval piece (25 × 16 mm), which also contains a phorid, cecidomyiid, mymarid wasp, small bits of frass and loose debris, and bubbles. The specimen is very close to the surface and part of the body is lost. Measurements: ratio of antennal segments 2:3:4 = 1.2:1:1.9; FW length = 0.87 mm; BL = 1.13 mm; HL/PL = not measured (odd angle); FF/FT = 1.00. AMNH DR-10-35B: occurs in the same piece as the holotype, described above. Measurements: ratio of antennal segments 2:3:4 not measured (odd angle); FW length = 1.05 mm; BL = 1.11 mm; HL/PL not measured (odd angle); FF/FT = 0.91. AMNH DR-10-53: a dark yellow, oval piece (17 × 28 mm), containing three males of *Alienates brodzinskyi* (numbered DR-10-53A,B, and C), and a male of *Alienates electrodominicus*. This piece also contains three sciarid midges, one cecido-

myiid, two chalcidoid wasps, a salticid spider, and three tiny pselaphid beetles. Measurements of DR-10-53A: ratio of antennal segments 2:3:4 = 1.2:1:1.8; FW length = 0.94 mm; BL = 1.06 mm; HL/PL not measured (odd angle); FF/FT = 0.88.

ETYMOLOGY: Patronym, in honor of Mr. Jacob Brodzinsky, whose help and indefatigable enthusiasm with Dominican amber made this research and much else possible.

DISCUSSION: The similarity of this species with *A. millsi* is based on the presence of a single submedian longitudinal vein (M + Cu), which apically does not extend to the wing margin. The fossil also has a deeply excavated hind margin of the eye (fig. 11), as seen in male *millsi* (females are unknown). It shares with *millsi* and *insularis* the presence of scattered, sparse setulae on the posteroapical portion of the wing membrane. These similarities say nothing of the relationships, since for only 3 of the 12 described living species are the males known.

Alienates electrodominicus, new species
Figure 12

DIAGNOSIS: Similar to the living species *A. insularis* on the basis of wing venation, but *A. electrodominicus* distinct as follows: antennal segments II and III very similar in length, segment III much shorter than II in *insularis*; face is more projected; margin behind the eyes is more constricted; hind lobe of head slightly narrower than "HW across eyes," but lobe extends slightly more laterally than eye margins in *insularis*; forelobe of pronotum much more constricted between it and hind lobe; mesonotum more rounded, with a distinct but small scutellum; metanotum distinctly triangular; setulae at apex of wing sparser; male genitalia without pointed guide as in *insularis*.

Differs from *Alienates brodzinskyi* based on larger body size and wing length (1.49–1.70 mm; 1.09–1.15 mm, respectively); the wing venation; the forefemur being longer than the foretibia (FF/FT, values below); and ratio of head length/pronotal length longer than in *A. brodzinskyi*.

DESCRIPTION: General body color brown, no markings visible. Head with rostrum slightly longer than length of eye. Eyes of
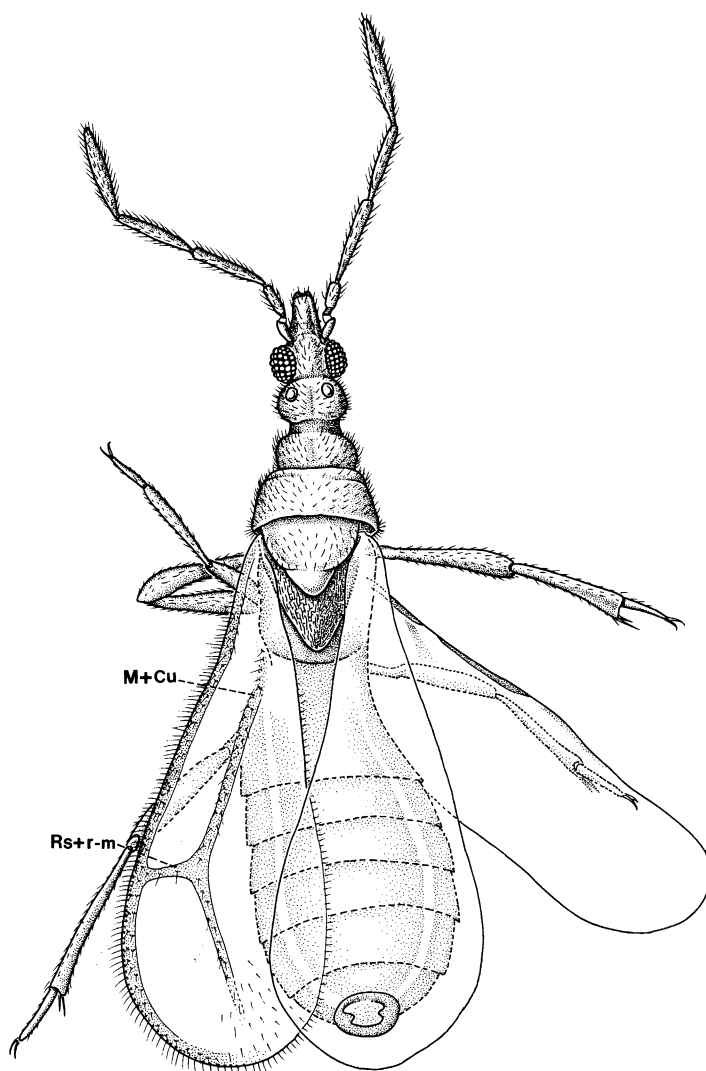
Fig. 12.　Dorsal habitus of *Alienates electrodominicus*.

standard size; distance between outer margins nearly equal to width of hind lobe of head. Hind margins of eyes virtually complete, only slightly excavated. Distance between eyes equal to dorsal width of eye. Distance between ocelli about 2× diameter of ocellus; ocelli slightly anterior to midline of hindlobe. Slight longitudinal furrow present between ocelli. Cuticular granules on gula and underside of thorax not observable in specimen. Setae on head simple, apparently without raised or tuberculous bases. Length of hind lobe of head slightly greater than pro-

notum. Antennal segment IV 1.6–1.8× the length of segments II + III.

Forelobe of pronotum slightly wider than hind lobe of head. Lengths of meso- and metanotum about equal. Scutellum small; width and length at least one-half that of mesonotum; triangular. Metanotum triangular, finely crenulate; length approximately equal to that of mesonotum + metanotum + scutellum. Forewing with typical reduced venation. C + Sc well developed and extended to slightly past apex of wing. Fringe of evenly spaced fine setae on costal edge;
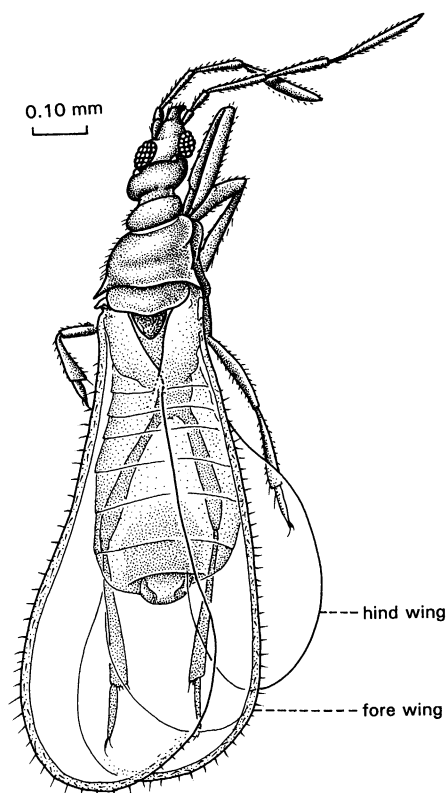
0.10 mm

--- hind wing

------- fore wing

Fig. 13. Undescribed *Alienates* species (see text).

lengths of setae about equal to width of vein C + Sc. Other setae irregularly arranged on this and other veins. Crossvein r-m present, connecting vein M + Cu. All veins approximately of equal width. Base of M + Cu obscure; apex incomplete, extended to only slightly more than halfway between r-m and wing apex. Membrane at apex of wing with about 20 scattered fine setae. Hind wing with only vestige of C + Sc present on proximal half. Forefemur length/width 6.0. Cuticular granules present on lateral surface of apical half of tibia. Foretibia length/width ca. 5.0; with two apical spines, one ca. 1.3× longer than other. Bristle comb not observable. Claws simple, equal in length.

HOLOTYPE: Specimen no. AMNH DR-8-32, which occurs in a yellow, oval piece of amber (21 × 9 mm). The specimen is perfectly preserved, entirely intact, and close to the surface, with the wings and legs spread and entirely visible. This piece also contains

a small female trichopteran, bubbles, and fine debris. Measurements: ratio of antennal segments 2:3:4 = 1.1:1:1.6; FW length = 1.15 mm; BL = 1.71 mm; HL/PL = 2.75; FF/FT = 1.14.

PARATYPE: Specimen no. AMNH DR-10-53D; the piece of amber is described above under *Alienates brodzinskyi* paratypes. Measurements: ratio of antennal segments 2:3:4 = 1.2:1:1.8; FW length = 1.09 mm; BL = 1.49 mm; HL/PL not measured (odd angle); FF/FT = 1.20.

ETYMOLOGY: from Greek, *elektron*, referring to the static charge given by amber; and *dominicus*, referring to the country of origin.

DISCUSSION: Features that the fossil shares with *A. insularis* males are the following: forewing venation almost identical (x-vein r-m between C + Sc and M + Cu; M + Cu incomplete at distal end of wing); and, in both the recent and fossil species, the metanotum is finely crenulate (with "reticulated sculpturing" in Wygodzinsky and Schmidt [1991]). Again, because only 3 of 12 described living *Alienates* species are known as males, the similarities of this fossil with *insularis* are not necessarily indicative of a close relationship.

Alienates sp.

There is a minute alienatine in Dominican amber, with total body length ca. 1.0 mm. It is being described by J. Maldonado C., J. Santiago-Blay, and G.O. Poinar, Jr. as a new genus, but is apparently just a highly modified *Alienates*. Placement in this genus is based on the shape of head and pronotal lobes; relative length of antennal segment IV (longer than other segments); and reduction of wing veins. Of the living and amber fossil species of *Alienates*, this one has the most extreme reduction in wing venation: no veins are present on the hind wings; forewings have only vein C + Sc, which is sparsely setose and extended slightly past the wing tip. The species is also distinct for the spinelike tip on the posterolateral corner of the hind lobe of the pronotum; the very short mesonotum; and the small, crenulate scutellum.

The specimen we examined is AMNH DR-8-387 (fig. 13); its specific provenance within the Dominican Republic is unknown. The bug occurs in a dark, clear yellow piece 4 ×

9 × 10 mm, with debris and a fulgoroid nymph in it; it is close to the surface, allowing one to reliably confirm the virtual absence of wing venation. The foretibiae are folded under the body, so spines on their apices could not be observed. The head and thorax are slightly distorted, so relative sizes of lobes could not be measured. The other known specimen of this species is also a male, in the personal collection of George O. Poinar, Jr. (Dept. of Entomology, University of California, Berkeley).

Genus *Enicocephalus* Westwood

DIAGNOSIS: An undoubtedly monophyletic group restricted to the Caribbean region, Central America, and South America, defined by the following synapomorphies (Wygodzinsky and Schmidt, 1991): outer claw on foreleg very small relative to inner one (0.3× its length or less); tarsal spine III strongly crescentic; apex of tibia with five spines, innermost one (VI) long, slender, curved toward remaining spines, and with a distinctive subbasal hump (figs. 14, 33, 43) in all but one species (*E. sturmi* Wygodzinsky and Schmidt).

LIVING SPECIES

Enicocephalus almanzari, new species
Figures 14–18

DIAGNOSIS: Easily distinguished from other, scarlet Caribbean species (particularly *E. cubanus*) based on distinctive pattern of brown areas as follows: entire rostrum and antenna; lateral areas of scutellum and postnotum; posterolateral corners of posterior lobe of pronotum. Wing dusky brown with white tip (as in *E. cubanus*), but with costal segment proximal to R scarlet. Also, apical flagellomere slightly shorter in *almanzari* than in *cubanus*; pronotum slightly longer relative to head in *cubanus* (see description, below). *Enicocephalus almanzari* smaller than *E. cubanus*; ranges of body sizes do not overlap (see below). Females unknown.

DESCRIPTION: Based entirely on males. Body length 3.5–3.8 mm (4.3–5.4 in *E. cubanus*). Body mostly scarlet in color. Head entirely scarlet, except for brown rostrum and

brown space between base of antenna and eye. Antennae dark brown, with apical half of distal flagellomere lighter. Forelobe of pronotum mostly scarlet, with light brown around margin of coxal articulation. Hind lobe of pronotum scarlet with brown posterior corners. Dorsal surface of forecoxa scarlet; ventral surface and trochanter light brown. Base of wing scarlet; membrane of fore and hind wings dusky brown. Veins of forewing much darker than membrane; segment of C + Sc proximal to R scarlet. Vein C + Sc white at tip of wing from apex of Rs to slightly past M. Forefemur scarlet; foretibia reddish brown. Mid and hind coxae scarlet dorsally, ventral surface and trochanters white. Mid and hind femora scarlet; mid and hind tibiae and tarsi reddish-brown. Scutellum and metanotum mostly scarlet, laterally with brown areas. Abdomen entirely scarlet.

Head, pronotum, and scutellum with dense, even covering of fine setae. Metanotum bare. Ratio of HL to HW across eyes 1:0.6. Ratio width across eyes to synthlipsis 1:0.50. Ratio L:W of hind lobe of head 1:1.6. Eyes (male) of medium size in lateral view, attaining level of ventral surface and barely reaching dorsal margin. Antennal segments I–IV 1:1.8:3.1:2.25. Rostrum as in figure 18.

Pronotum as in figure 18; with deep incision on posterior margin. Pronotum 1.23 times longer than head (1.4× in *E. cubanus*). Fore and hind wings fully developed and apparently not caducous. Venation of wings as in figures 16 and 17. Setae on forewing veins in two rows, one row on each edge. Small patch of setae (as in *E. cubanus*) present on radial vein of hind wing where it departs from costal edge. Hind wing without apical setae. Setae on forefemur of uniform length, not interspersed with smaller spines. No granular surface structures apparent on forefemur. Tibial spine VI with distinct subbasal hump (figs. 14, 15). Apex of tibia with standard arrangement of five spines. Tarsal spine VI crecentic. Outer claw 0.25 length of inner one. About 23 teeth in tibial comb.

HOLOTYPE: Male. DOMINICAN REPUBLIC: Duarte Province, 8 mi. N. San Francisco de Macoris, Loma Quita Espuela, 800 m, Victor Almanzar, IV/91. In the AMNH.

OTHER MATERIAL: Paratype series of nine specimens with same label data as holotype,
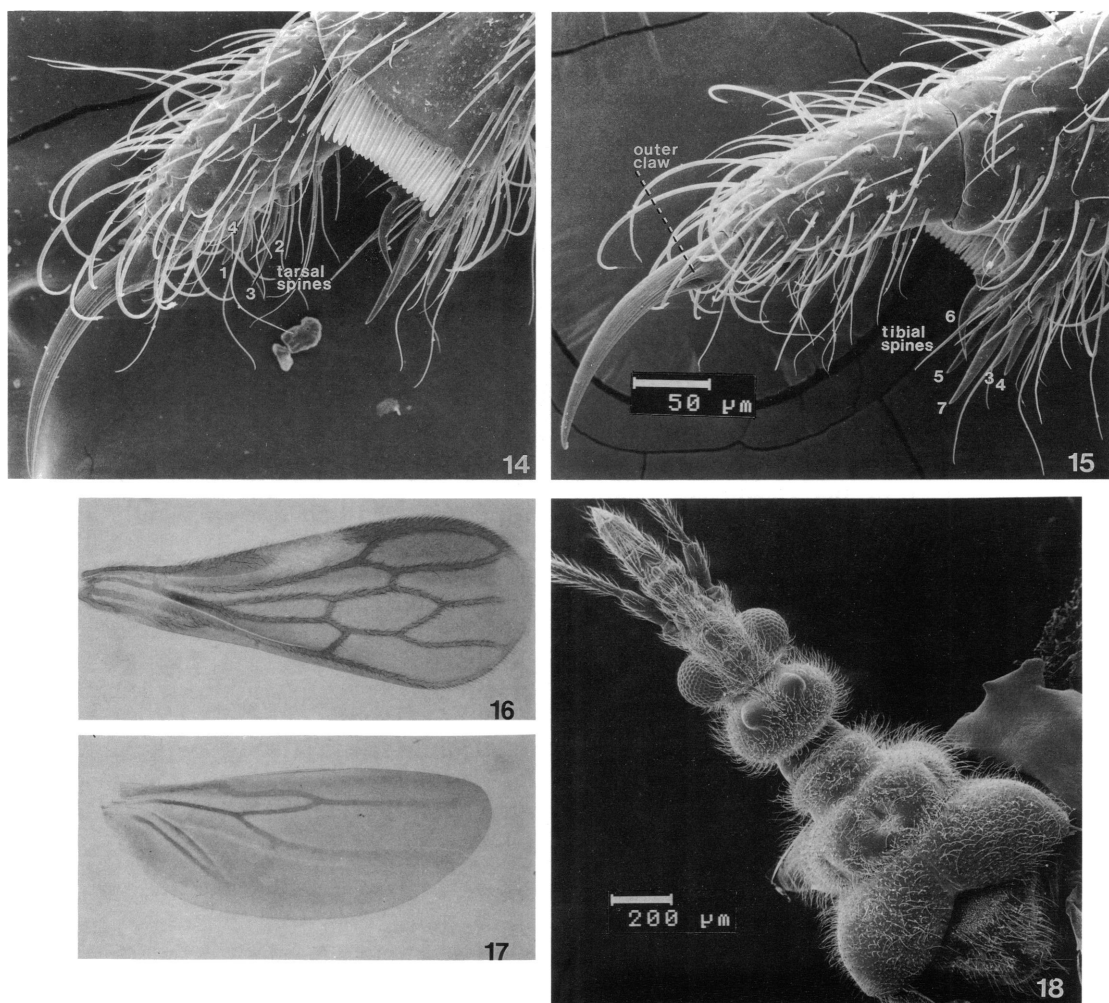
Figs. 14–18. *Enicocephalus almanzari* (extant species). 14, 15: SEMs of foretarsi and apices of tibiae, also showing numbering of spines. **14.** Mesal view. **15.** Lateral view. 16, 17. Light photographs of wings. **16.** Forewing. **17.** Hind wing (both to same scale). **18.** SEM of head and prothorax.

eight with same date and one with date of VII/91. In the AMNH.

ETYMOLOGY: Named for Victor Almanzar, resident naturalist and manager of the beautiful cloud forest atop Loma Quita Espuela. Victor diligently tended for months the Malaise trap in which these specimens were caught.

DISCUSSION: This species is undoubtedly closely related to *E. cubanus* based on the distinctive coloration of the wings. It is interesting to note that *E. cubanus* has the broadest distribution in the Caribbean (being throughout Cuba, on Jamaica, and Hispaniola) and yet the new species is endemic to the Dominican Republic. It is important to note differences in the localities within the Dominican Republic: *E. cubanus* is known from near Constanza (Cordillera Septentrional), the foothills of the Cordillera Central near Santiago, and now with a new record of it from the Sierra de Bahoruco in Pedernales province. The latter site is from a montane broadleaf forest isolated by extensive pine forests, "Las Abejas," and is the same locality and date of collection as recorded below for *E. bahorucensis. Enicocephalus almanzari* was found near the southernmost point of the Cordillera Central, in a very wet cloud forest (map, fig. 24). Only males were caught in the
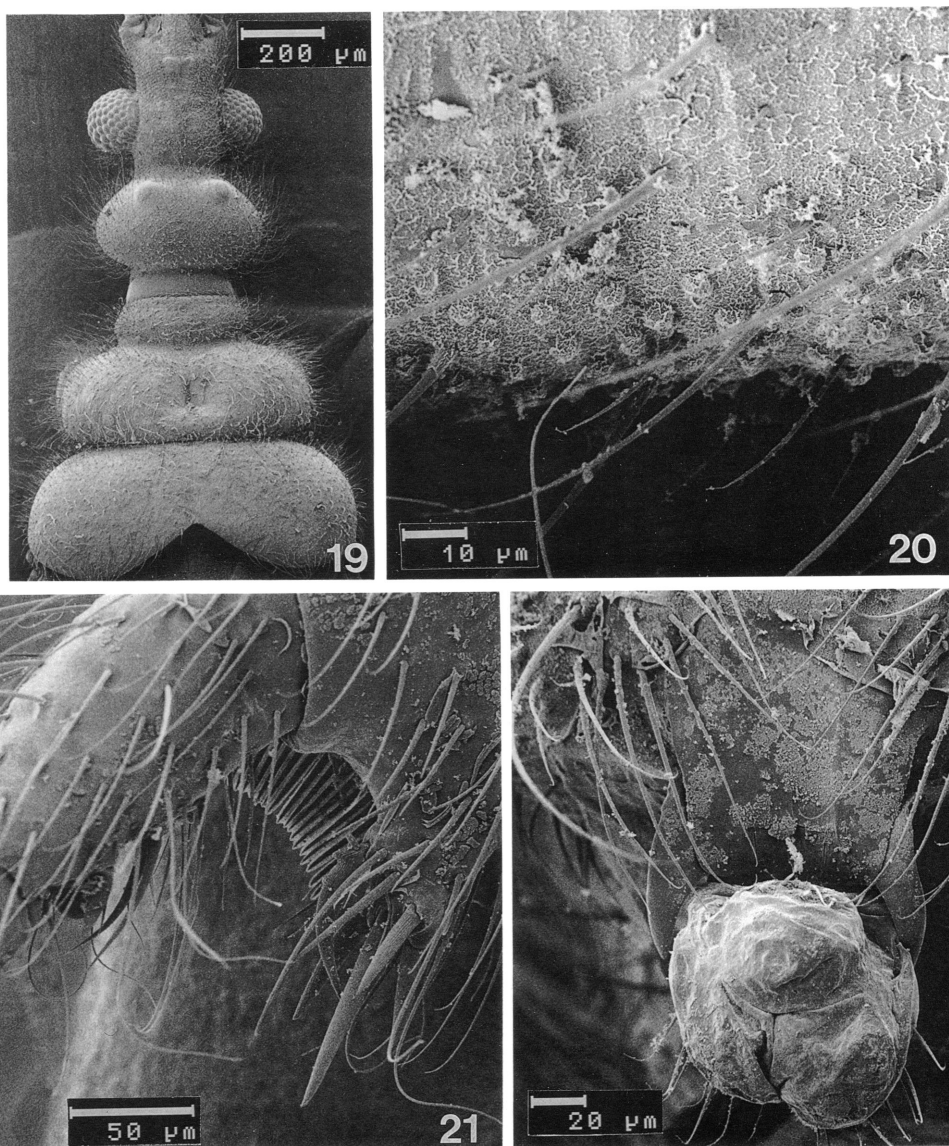
Figs. 19–22.   SEMs of *Enicocephalus bahorucensis*. **19**. Dorsal view of head and prothorax. **20**. Cuticular granules on ventral surface of forefemur. **21**. Lateral view of apex of foreleg. **22**. Male genitalia (dorsal view).

Malaise trap, presumably because they were swarming.

Enicocephalus bahorucensis, new species
Figures 19–23

DIAGNOSIS: Most of body dark brown: antennae, head, thorax, pleura, forelegs; scutellum and mid- and hind femora reddish brown; abdominal tergites barely sclerotized, light red; wing evenly dusky brown (tip not white), proximal third of C + Sc scarlet. Antennae longer than head + pronotum. Male genitalia very distinct, with huge guide and broad, sclerotized, knifelike parameres. Known only from mountains of the southwestern Dominican Republic.

DESCRIPTION: Based entirely on males. Body length 2.95–3.55 (mean 3.27) mm. Body mostly dark brown, with some scarlet. Head entirely dark brown, with scarlet eyes and ocelli. Antennae dark brown, with apical half
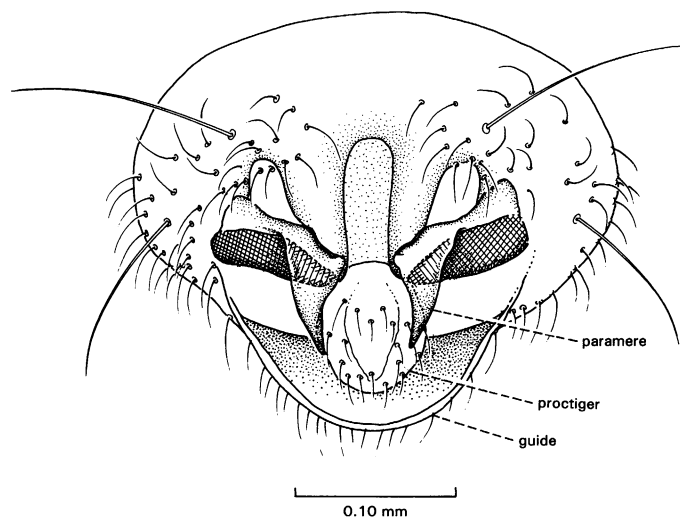
Fig. 23.   Drawing of male genitalia of *Enicocephalus bahorucensis*, labeled to show aedeagal guide, parameres, and proctiger.

to third of distal flagellomere lighter. Fore and hind lobe of pronotum dark brown. Pleura and forecoxae dark brown. Membrane of fore and hind wings a pale, even, dusky brown; veins same color as membrane; basal third of C + Sc scarlet. Tip of wing not white. Forefemur mostly dark brown; with diffuse, light red at apex; foretibia entirely dark brown; tarsus light brown. Mid and hind coxae with diffuse scarlet color. Mid and hind femora dark to pale brown, with diffuse scarlet color at apex; mid and hind tibiae and tarsi entirely light brown. Scutellum and metanotum brown to red-brown. Abdomen is a light, diffuse scarlet.

Head, pronotum, and scutellum with dense, even covering of fine setae. Postnotum bare. Ratio of HL to HW across eyes 1:0.67. Ratio width across eyes to synthlipsis 1:0.46. Ratio L:W of hind lobe of head 1:1.50. Eyes of medium size in lateral view, attaining level of ventral surface and not reaching dorsal margin. Antennal segments I–IV 1:3.58:3.85: 2.82.

Pronotum as in figure 19; with very deep incision on posterior margin; incision extends to 0.40 length of hind lobe of pronotum. Fore and hind wings fully developed and apparently not caducous. Setae on forewing veins in two rows, one row on each edge. Small patch of setae present on radial vein of hind wing where it departs from costal edge. Hind wing with row of two irregular

rows of ca. 15 setae on apex. Setae on forefemur of uniform length, not interspersed with smaller spines. Granular surface structures on forefemur limited to anterior portion of ventral surface. Tibial spine VI with distinct subbasal hump (fig. 21). Apex of tibia with standard arrangement of five spines. Tarsal spine VI crescentic. About 25 teeth in tibial comb.

Male genitalia large and distinctive: Parameres broad, heavily sclerotized; with apices knifelike, folded backward and then downward. Parameres flank a bulbous, membranous proctiger, which bears ca. 12 fine setae. Guide very broad and large. Genital capsule with numerous fine setae, but pair of very long setae on each side.

HOLOTYPE: Male. DOMINICAN REPUBLIC: Pedernales Province, ca. 23 km NE Pedernales, 1500 m, Oct. 5, 1992, D. Grimaldi and J. Stark. Caught in Malaise trap set up in montane rain forest isolated by extensive *Pinus caribbeana* forests. In the AMNH.

OTHER MATERIAL: Paratype series of six males with same label data as holotype. In the AMNH.

ETYMOLOGY: Pertaining to the Sierra de Bahoruco, on the Barahona Peninsula of the Dominican Republic, where the specimens were collected.

DISCUSSION: Closely related to the living species *E. wygodzinskyi* and the amber species *E. prius*, based on the combination of
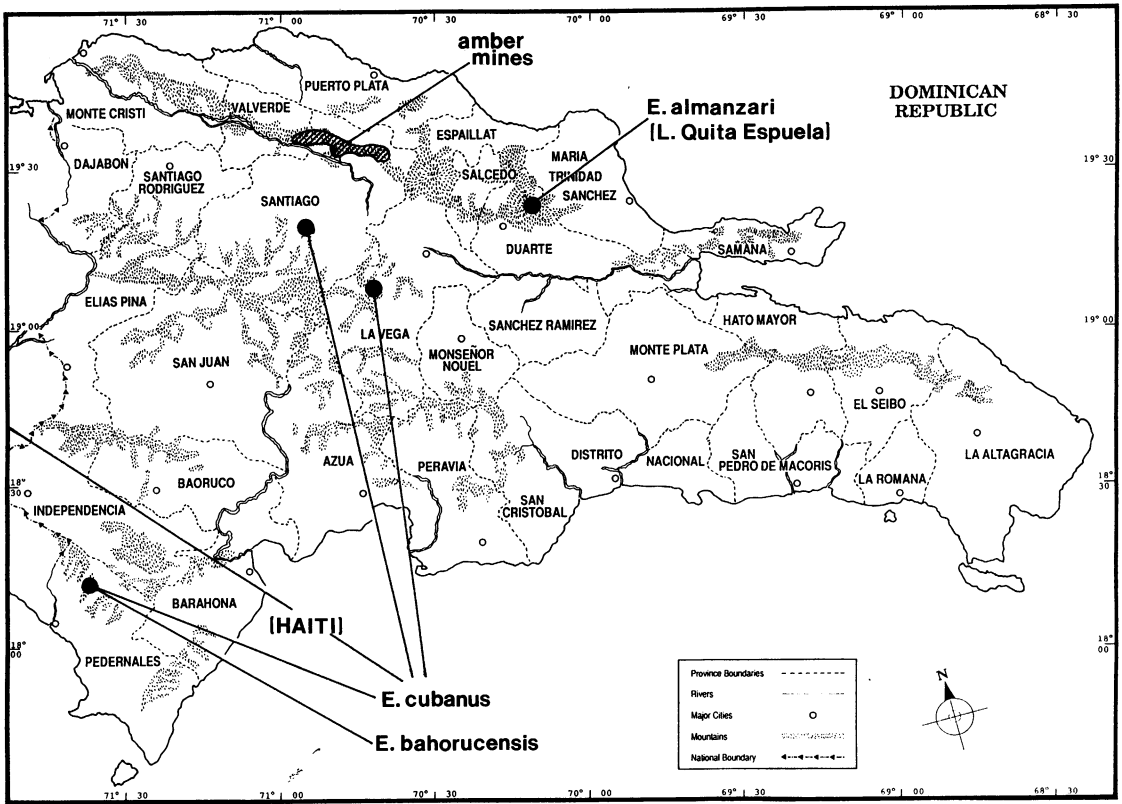
Fig. 24. Distribution map of fossil and living specimens of *Enicocephalus* collected from the Dominican Republic.

the fine granulations on the ventral surface of the forefemur (character 4) and the long humeral cell of the hind wing (character 13). *Enicocephalus bahorucensis* and *E. wygodzinskyi* also share the very distinctive feature of a large male genital capsule with elaborate genitalia and large, broad guide. Of the 10 species in the genus where the guide shape is known, the most common and also plesiomorphic shape is a truncate, tonguelike guide (*E. neblinensis* has a long, thin guide with rounded apex). Guide shapes were not incorporated into the matrix for the cladistic analysis, due to the many missing entries.

AMBER SPECIES

Enicocephalus seniculus, new species
Figures 25–28, 33–40, 46–47

DIAGNOSIS: Distinguished from other Dominican amber *Enicocephalus* species on basis of dark overall body color; pronotum being longer than the head; the relatively narrow

forewing and the forewing venation, especially the relatively smaller discal cell and narrow straight medial cell (see description for proportions).

DESCRIPTION: Length of male 3.7 mm (AMNH DR-10-67); female 3.42 mm (AMNH DR-10-81). General body color evenly dark brown overall, including head and rostrum, thorax, and legs. Antenna mostly dark brown; fourth segment slightly lighter, with slight dark rings near middle and at tip in holotype (without rings in other specimens). Forewings very light brown, with slightly darker veins; without white tip.

Pronotum longer than head: relative lengths of head to pronotum = 1:1.25 [DR-10-81]; 1:1.3 [DR-10-67]); 1:1.46 [11334]; 1:1.22 [DR-10-28]. Ratio head length to width across eyes 1:0.73 [11334], 1:0.56 [DR-10-81]. Ratio length to width of hind lobe of head 1:1.7 [11334], 1:1.3 [DR-10-81]. Ratio length of eyes to anteocular distance 1:1.68 [DR-10-67 and DR-10-28], 1:1.46 [DR-10-126], 1:1.1
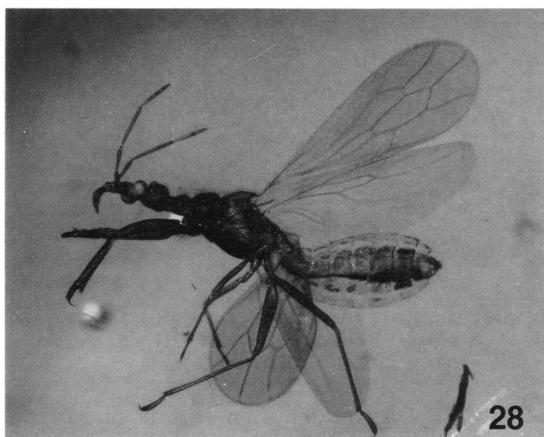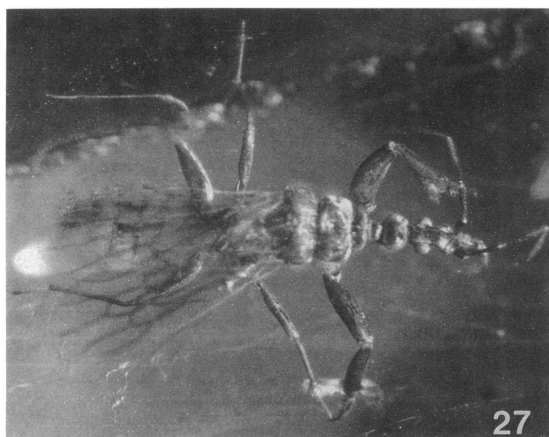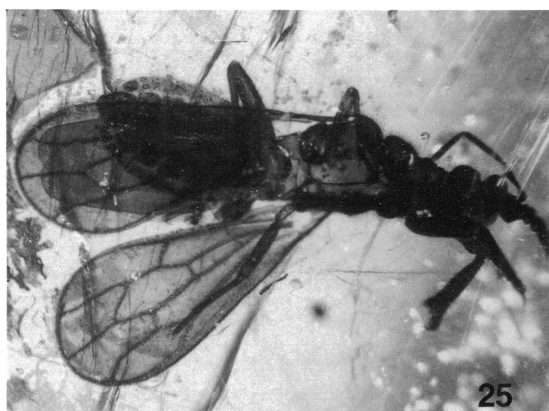
Figs. 25–28. *Enicocephalus seniculus*. **25.** AMNH DR-10-126 (paratype male). **26.** AMNH DR-8-380 (paratype male). **27.** AMNH DR-10-81 (paratype female). **28.** AMNH DR-10-67 (holotype male).

(DR-10-81). Ratio width of eyes to synthlipsis 1:1.6 [DR-10-81]. Eyes in side view projected below ventral margin and distant from dorsal margin (fig. 26) [DR-10-28; DR-10-67]. Antennal segments I-IV (with means, then ranges, of proportions): 1 : 2.1 (2.0-3.3) : 4.0 (2.9-5.1) : 3.5 (2.6-4.2).

Pronotum as shown in figure 34. Posterior lobe of head and all of pronotum with dense, long, fine pilosity. Incision on posterior margin deep, ratio depth of incision to length of posterior lobe of pronotum = 1.2.0 [DR-10-81]. Ratio width of mid to hind pronotal lobes 1:1.1 [11334], 1:1.2 [DR-10-81].

Forewings relatively narrow: ratio length to width 1:0.41 [DR-10-67], 1:0.38 [DR-10-81]. Venation as shown in figure 46 (for AMNH DR-10-81; very consistent for all six specimens). C + Sc with standard array of

setae, rather thick and setulose. Apex of Rs very slanted, in line with gradual curve of basal part of vein. Apical radial cell long and narrow (ca. $5\times$ longer than wide); vein M straight, with Rs and Cu1b diverged slightly away from M at apex; discal cell short (ca. $3\times$ longer than wide), with pointed apex (basal section of M and Cu1a of equal lengths); vein Cu1a almost perpendicular to vein M; apical cubital cell straight, not slightly curved (cf. *E. subvitreous* [DR-8-369]); basal cubital cell extended beyond basal cell. Hind wing with veins R and Cu incomplete, not meeting apically; humeral cell short, only ca. $0.45\times$ length of wing; apex of wing without setulae.

Forelegs as shown in figures 33, 39 (for DR-10-81 and DR-10-67, respectively). Ventral surface of forefemur with small granular surface. Tibial spine VI sharp, crescentic, with

distinct subbasal hump. Tibial spine VII distinctly longer than others, except in AMNH DR-10-81, where it is only slightly longer than spine V. Foretarsi as in figure 33. Tarsal spine III strongly crescentic, with 2 thin spines proximally. Outer tarsal claw well developed, about 0.3× length of inner claw.

Genitalia best observed in AMNH DR-10-67 (figs. 35–36); with standard, tongue-shaped guide (base not clearly seen); parameres projected and paddle-shaped, with apparently minutely hooked, sclerotized tips; tergite 10 large, with deep dorsal notch.

HOLOTYPE: Male, AMNH DR-10-67, in perfect condition, and fully displayed (fig. 28); in a dark yellow, oval piece, 20 × 11 mm. The piece also contains a male scatopsid fly. Specific amber mine source unknown.

OTHER MATERIAL: Five paratypes, as follows. AMNH 11334: Male, in a small (10 × 5 mm), oval, dark yellow piece; body slightly distorted by compression; slightly pyritized; distal half of abdomen and right wings lost at surface of amber. Presumably from the La Toca group of amber mines. AMNH DR-8-380 (fig. 26): Male, in a clear yellow piece of amber (16 × 26 mm), with bubbles and some fracture planes. Specimen is complete but partially obscured by fractures. AMNH DR-10-28: Male, in an orange piece with some swirls and fractures (13 × 22 mm), also containing a female dolichopodid fly. Specimen completely intact, but best observation is lateral view of head and thorax. AMNH DR-10-81 (fig. 27): Female, in a suboval piece of clear, dark yellow amber (28 × 14 mm), contains a few small pieces of debris and a minute worker ant. Specimen is completely intact and fully visible. AMNH DR-10-126 (fig. 25): Male, in a small (8 × 12 mm), drop-shaped, dark yellow piece, with some fine bubbles and fractures filled with brown substance. Specimen is hollowed out and missing dorsal surface of thorax, but all other structures fully visible.

ETYMOLOGY: From Latin, meaning "little old man."

DISCUSSION: The cladistic analysis, presented later, shows this species not to be closely related to the extant Caribbean and other fossil *Enicocephalus* species, but rather to a group of three extant species from Hylaean South America. This is an example of geographic extinction within the Dominican amber fauna.

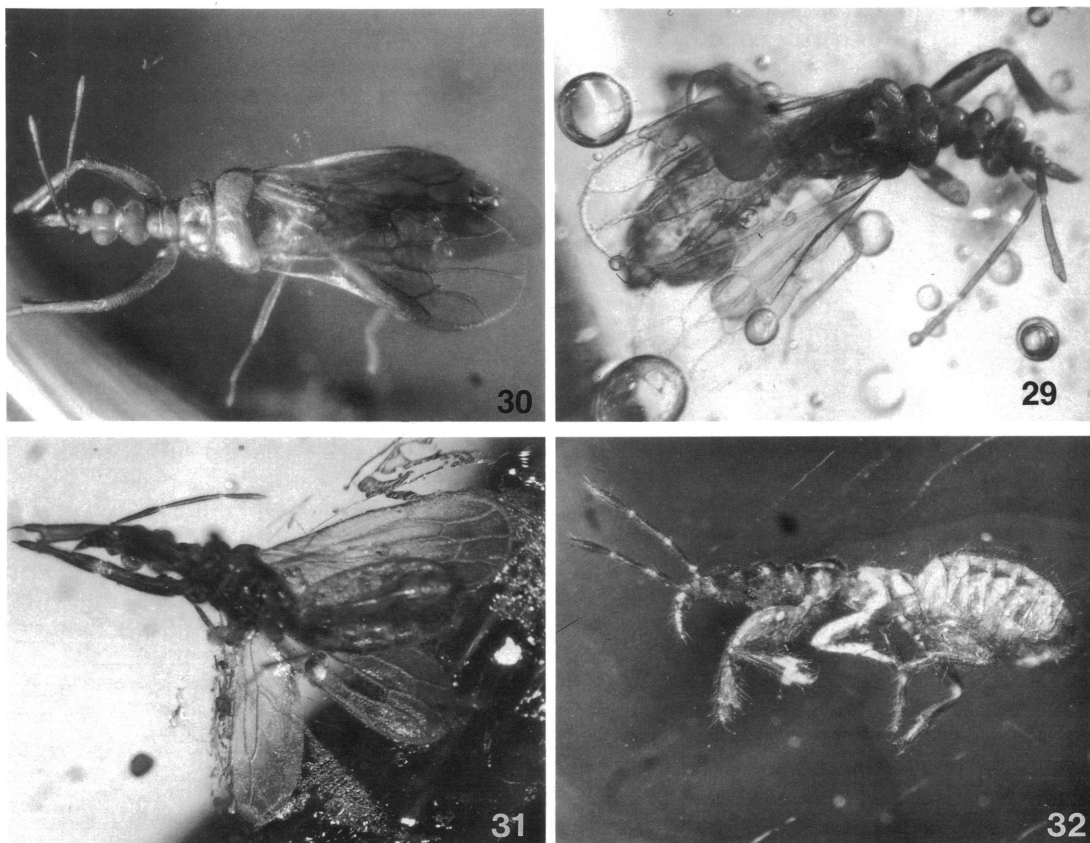### *Enicocephalus subvitreus,* new species
Figures 29, 41–42, 50

DIAGNOSIS: General body color light reddish brown (probably originally scarlet); head longer than pronotum, very short anteocular distance, eyes large relative to synthlipsis (see below for proportions); short, dense fine pilosity (fig. 41; compare with figs. 34 and 45). Wing with basal cell and basal-cubital cell nearly the same length (generally basal-cubital cell longer). Based on single male.

DESCRIPTION: Length of male 2.4 mm. General body color light reddish brown, original color probably scarlet. Head slightly darker than pronotum, especially in anteocular space. Tip of rostrum darker than rest; antennal segments I and II darker than others, segment IV not noticeably lighter than III. Sides of hind lobes of pronotum darker than rest of pronotum. Forewings very light, perhaps hyaline; without white tip. Legs same light red-brown as pronotum, except foretibia and tarsi, which are darker. Abdomen very pale.

Head longer than pronotum, ratio of head to pronotal lengths 1:0.73. Ratio head length to width across eyes 1:0.56. Ratio length to width of hind lobe of head 1:1.9. Very short anteocular distance; ratio length of eyes to anteocular distance 1:0.3. Eyes rather large, but not bulging as in *E. exophthalmus* Wygodzinsky and Schmidt; ratio width of eyes to synthlipsis 1:0.77. Eyes not observable in side view. Antennal segments I–IV: 1:1.6:3.6:2.6.

Pronotum as shown in figure 41. Hind lobe of head and entire pronotum covered with short, dense, fine pilosity. Incision on posterior margin deep, ratio depth of incision to length of posterior lobe of pronotum = 1:1.8. Proportional width of mid to hind pronotal lobes 1:1.2.

Forewings relatively broad, ratio length to width = 1:0.44. Venation in figure 50. C + Sc with standard array of setae, not especially thick or setulose. Apex of Rs slanted, but not in line with gradual curve of basal part of

Figs. 29–32. Amber *Enicocephalus* spp. **29.** *E. subvitreus*, holotype male (AMNH DR-8-369). **30.** *E. omen*, holotype male (AMNH DR-10-74). **31.** *E. prius*, holotype male (AMNH 11835). **32.** Nymph, species indeterminate (AMNH DR-10-132).

vein. Apical radial cell deep (only 2.7× longer than width); veins M and Rs strongly curved and divergent; vein Cu1b diverged slightly away from M; discal cell of intermediate size, 3× longer than wide), with blunt apex (basal section of M longer than Cu1a); vein Cu1a almost perpendicular to vein M and Cu1b; apical cubital cell slightly curved; basal cubital cell barely extended beyond basal cell. Hind wing with veins R and Cu incomplete, not meeting apically; humeral cell long, ca. 0.73× length of wing. Hind wing with setae on apical margin, entirely around apex (not limited to tip).

Foretibia and tarsi at odd angles, difficult to view (require various angles). Ventral surface of forefemur with granular surface, limited to ventral surface (not on medial surface). Tibial spine VI with distinct subbasal hump, crescentic spine VII very long. Tarsal

spine III strongly crescentic. Outer tarsal claw very small, barely observable.

Genitalia (male) observable (figure 42), with paramere lobes apparent and median structure with apparently minutely bifid apex (guide and support structure? This is possibly an artifact of looking down on the rim of a tubular guide). Details not observable.

HOLOTYPE: Male, AMNH DR-8-369, in dark yellow, irregular oval piece of amber, 14 × 24 mm. Piece also contains a female dolichopodid fly and a male cecidomyiid midge. Exact provenance within the eastern group of Dominican amber mines is unknown.

ETYMOLOGY: Latin, meaning "under glass."

DISCUSSION: This species is most closely related to the Puerto Rican species, *E. usingeri*, as based on the exophthalmic eyes (character 2). The eyes do not bulge as much as
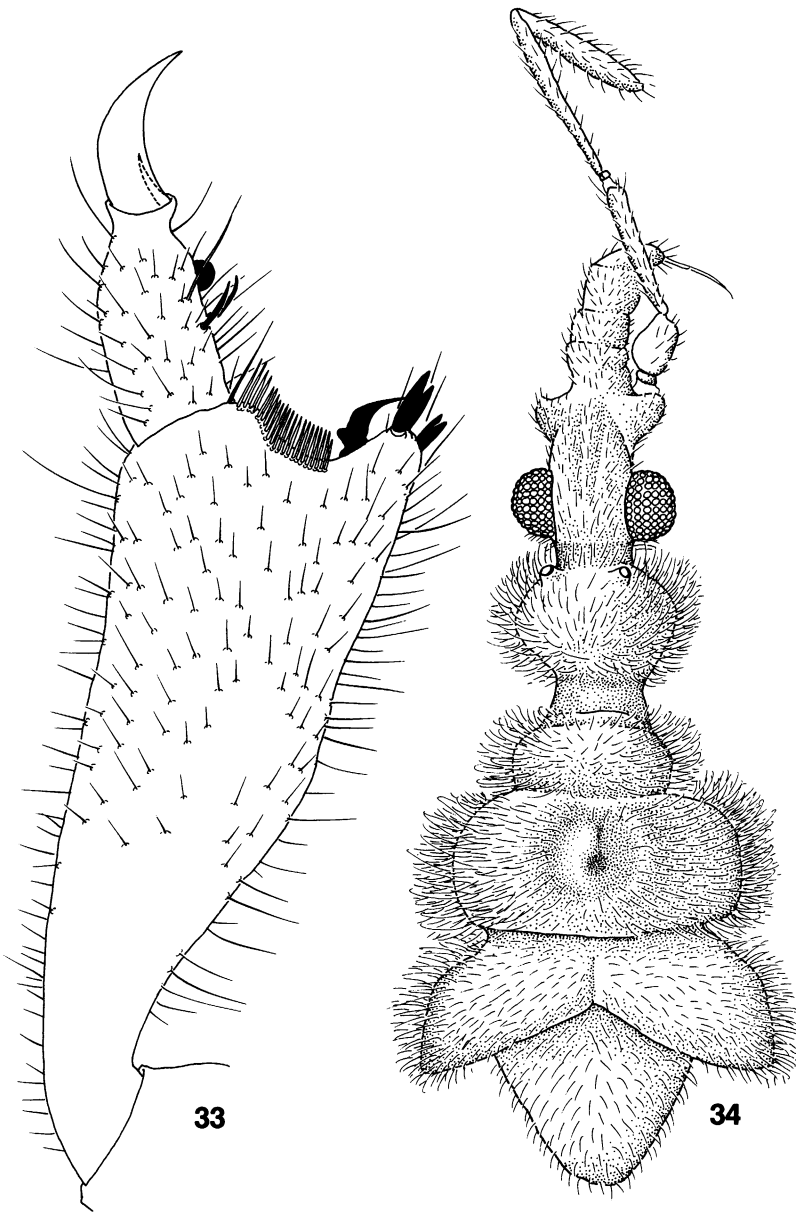
Figs. 33, 34. *Enicocephalus seniculus*, paratype male (AMNH DR-10-81). **33.** Mesal view of foretibia and tarsus. **34.** Dorsal view of head and thorax.

in *E. usingeri*. It is interesting to note that *E. subvitreus* slightly extends the distribution of the clade composed of *semirufus* and *usingeri*, both restricted to Puerto Rico. Grimaldi never found these species in the Dominican Republic. As reported in the section on cladistic analyses, inclusion of *E. subvitreus* affects phylogenetic hypotheses of a Caribbean

clade which includes these Puerto Rican species.

***Enicocephalus omen*, new species**
Figures 30, 45, 51

DIAGNOSIS: Also a light color, like *E. sub-vitreus*, but without any dark markings on
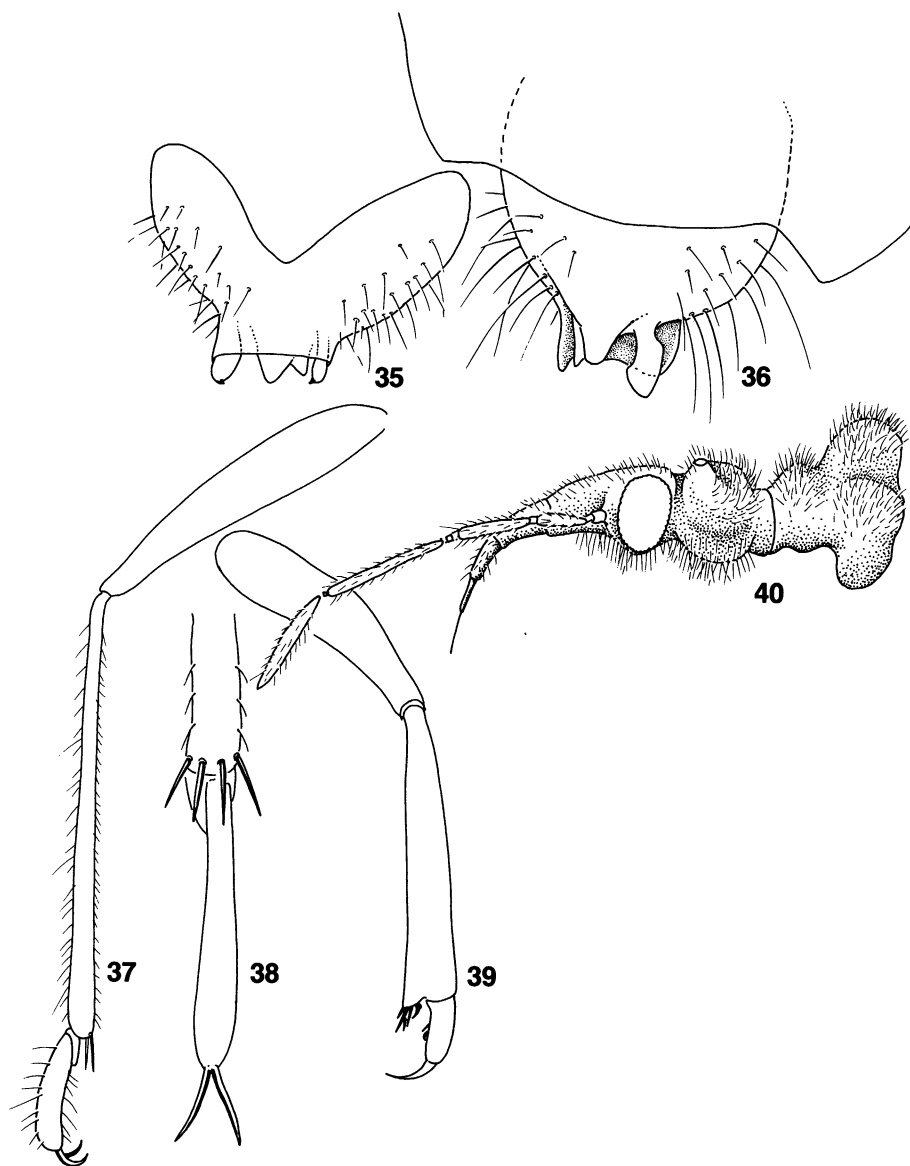
Figs. 35–40. *Enicocephalus seniculus*. 35, 36. Male genitalia, holotype (AMNH DR-10-67). **35.** Dorsal view. **36.** ventral view. 37–39: legs of holotype. **37.** Hind leg. **38.** Detail of midtarsus and apex of midtibia. **39.** Foreleg. **40.** Lateral view of head of paratype male (AMNH DR-10-28).

body and also distinguishable on the basis of the dusky wing with white tips and light base. Incision on posterior margin of posterior pronotal lobe shallow. Ventral surface of forefemur without cuticular granules. Antennal segment III relatively long (5.3× length of segment I, vs. 2.9–4.6 × the length in other amber species). Vein Cu1a very strongly slanted; see description for other wing characters.

DESCRIPTION: Length of male 3.38 mm. General body color even, pale orange; presumably scarlet in life. Entire head and rostrum pale orange, no dark areas. First and second antennal segments slightly darker than others; apical half of fourth segment lighter. All lobes of pronotum homogeneously pale orange. Forewings lightly dusky, with veins darker; base of wing light, tip white. White tips of forewings include most apical parts of
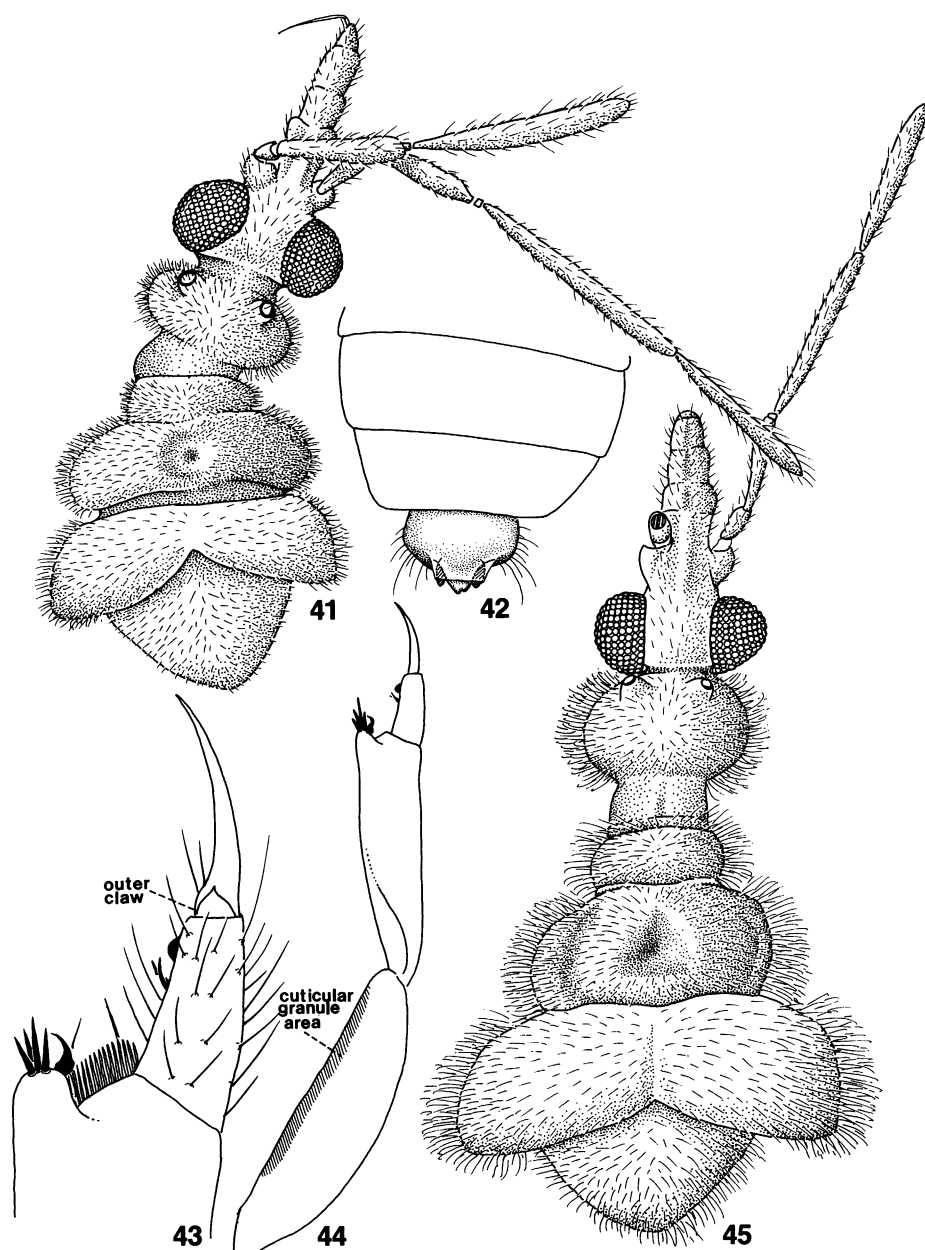
Figs. 41–45.   Amber *Enicocephalus* spp. 41, 42. *E. subvitreus*, male holotype (AMNH DR-8-369). **41.** Head and thorax, dorsal view. **42.** Genital capsule, dorsal view. 43, 44. *E. prius*, male holotype (AMNH 11835). **43.** Detail of foretarsus and apex of tibia. **44.** Entire foreleg. **45.** *E. omen*, holotype male (AMNH DR-10-74), dorsal view of head and thorax.

veins Rs, M, and Cu1b, and the stretch of costal vein between them. No light areas on C + Sc, as in *E. almanzari*. Legs and abdomen pale orange.

Ratio head length to pronotum: 1:1.43. Ratio head length to width across eyes 1:0.74.

Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular distance 1:0.6. Ratio width of eyes to synthlipsis 1:1.3. Eyes in side view not observable. Ratios antennal segments I–IV: 1:2.8:5.3:4.6.
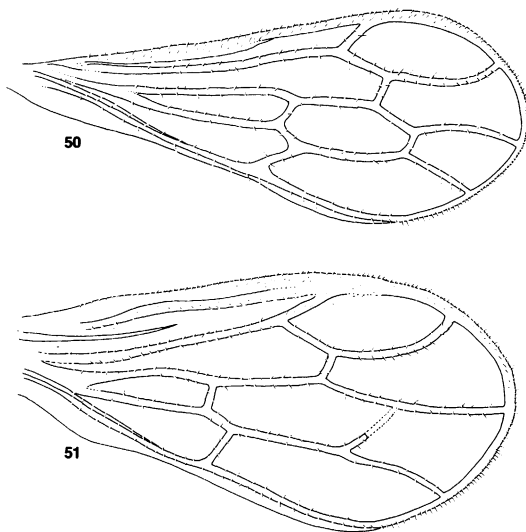
Pronotum as shown in figure 45. Hind lobe
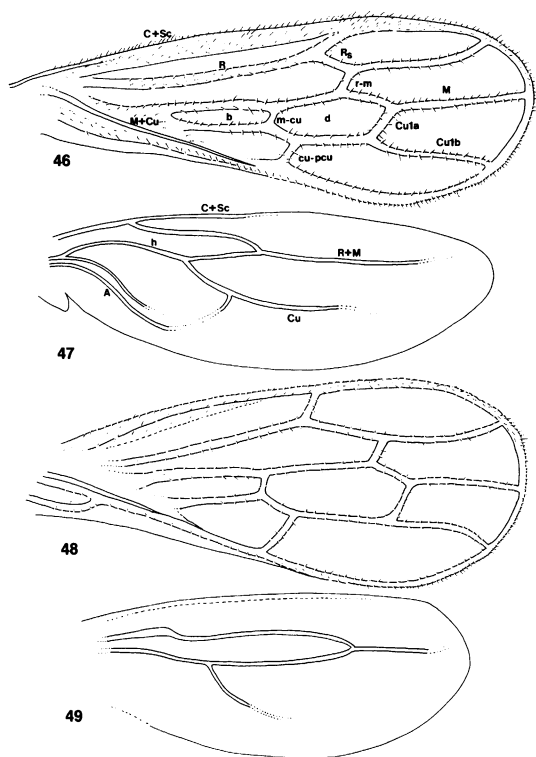
Figs. 46–49. Wings of amber *Enicocephalus* spp. 46, 47. *E. seniculus*, paratype male (AMNH DR-10-81). **46**. Forewing. **47**. Hindwing (same scale). 48, 49. *E. prius*, holotype male (AMNH 11835). **48**. Forewing. **49**. Hindwing.

Figs. 50, 51. Forewings of amber *Enicocephalus* spp. **50**. *E. subvitreus*, holotype male (AMNH DR-8-369). **51**. *E. omen*, holotype male (AMNH DR-10-74).

of head and pronotum covered with long, fine, dense pile. Incision on posterior margin shallow; ratio of depth of incision to length of posterior lobe of pronotum = 1:1.27. Ratio width of mid to hind lobes of pronotum = 1:1.6.

Forewings quite broad, ratio length to width 1:0.5. Venation as shown in figure 51. C + Sc with standard array of setae, not especially thick or setulose. Apex of Rs slanted, perfectly in line with gradual curve of basal part of vein. Apical radial cell deep (only 2.7× longer than depth), oval in shape; veins M very slightly curved; Rs very strongly curved away from M; vein Cu1b diverged slightly away from M; discal cell very large, nearly the size of apical cubital cell; discal cell with pointed apex (basal section of M and length of Cu1a nearly equal)[one wing with Cu1a teratologically incomplete]; vein Cu1a very strongly slanted against veins M and Cu; api-

cal cubital cell slightly flared at apex; basal cubital cell extended beyond basal cell. Hind wing barely visible, but apex without setae on apical margin.

Minute structures on foretarsi and tibia not easily seen without different views. Ventral surface of forefemur smooth, completely without any granular surface. Tibial spine VI with distinct subbasal hump. Tarsal spine III strongly crescentic. Outer tarsal claw well developed, not vestigial.

Genitalia obscured by black substance.

HOLOTYPE: Male, AMNH DR-10-74, in a clear yellow, oval piece of amber 18 × 24 mm. The piece contains a few fractures but is otherwise very clear. A tiny proctotrupoid wasp is also in the piece. Exact provenance within the western group of Dominican amber mines is unknown.

ETYMOLOGY: Latin; meaning "portent, sign, prophecy," in reference to the early appearance of the species and its obvious relationships with extant Caribbean species.

DISCUSSION: Appears equally related to the living species *E. almanzari* (from the Dominican Republic) and *E. cubanus* (widespread throughout the Greater Antilles, except for Puerto Rico). This relationship is based on the unique feature of having dusky

forewings with the tip white (character 10). Presence of *E. omen* in Dominican amber establishes the Caribbean endemism of this clade to at least the Oligo-Miocene boundary.

Enicocephalus prius, new species
Figures 31, 43–44, 48–49

DIAGNOSIS: Second antennal segment relatively long, ca. 4 times the length of first segment (vs. 2–3× as long in other amber species); wing vein Rs nearly perpendicular to vein C + Sc; humeral cell in hind wing very long (ca. 0.7× length of wing); ventral surface of forefemur with cuticular granules; outer tarsal claw vestigial.

DESCRIPTION: Length of male 2.8 mm. General body color brown, including head, rostrum, pronotum, and legs. Antennal segments I and II darker than other segments; segment IV with light apex. Hind lobe of head slightly darker than pronotum. Forewings hyaline, with slightly darker veins. Abdomen very compressed, coloration obscured.

Head and pronotal length measurements obscured by odd angle of specimen. Ratio antennal segments I–IV = 1:4.0:4.6:3.6. Posterior lobe of head and pronotum with dense covering of fine, short hairs. Posterior margin of posterior pronotal lobe with deep incision. Wing venation as shown in figures 48–49. Rs vein almost perpendicular to C + Sc, not in line with vein R. Forewings of intermediate width, ratio length to width 1:0.43. C + Sc with standard array of setae, not especially thick or setulose. Apical radial cell rather large, almost half the length of wing and extended to nearly tip of wing; length is 3.7× the depth. Vein M nearly straight; Rs very strongly curved away from M; vein Cu1b diverged strongly away from M at its apex. Discal cell large, with truncate apex (Cu1a slightly longer than basal section of M); vein Cu1a almost perpendicular to veins M and Cu1b. Basal cubital cell extended beyond basal cell. Hind wing with very short Cu vein; vein R + M incomplete, not reaching wing tip; humeral cell very long, nearly 0.7× length of wing. Apex of hind wing without setae.

Forelegs as shown in figures 43–44. Ventral surface of forefemur with granular surface, but not extended to sides of femur (fig. 44). Tibial spine VI with distinct subbasal hump,

strongly crescentic. Foretarsi as in figure 44. Tarsal spine III strongly crescentic. Outer tarsal claw vestigial (fig. 43), best seen in anterior view of claw.

Genitalia preserved but obscured by layer of air.

HOLOTYPE: Male, AMNH 11835, in a flat piece of clear, dark yellow amber 24 × 22 mm. The piece also contains a very small adult cicadellid, portion of a leg of a large insect, and some fine bubbles and debris. Piece supposedly originates from the La Vega group of amber mines.

ETYMOLOGY: Latin, meaning "prior, beforehand."

DISCUSSION: This species is most closely related to the living species *E. bahorucensis*, known only from the Barahona Peninsula of southwestern Dominican Republic. Relationship is based on the extremely reduced outer claw of the forelegs (character 1).

CLADISTICS AND BIOGEOGRAPHY

Analyses of *Alienates* biogeography are seriously limited by the lack of data. Most of the living species are not known for adult males, which is the stage preserved in amber. Since there is very little sexual dimorphism in *Enicocephalus*, and all species are known as adults, it is possible to closely compare the amber specimens with the living species. In fact, there are several living species with more missing entries for character states in the matrix than occur for the fossil species! (Some of the living species shed their wings, and the winged stage is not known for two of these.)

Table 1 presents a matrix of 17 characters for four fossil and 19 living species of *Enicocephalus*. *Neoncylocotis* was used as the outgroup taxon to polarize characters, since Wygodinzky and Schmidt (1991) indicated this as the sister genus to *Enicocephalus* (it is possible that only a clade of New World *Neoncylocotis* is the sister group of *Enicocephalus* [Pavel Štys, personal commun.]). Below is a description of each character (0 is plesiomorphic, 1 is apomorphic).

0. Body coloration: 0: entirely brownish, small portions sometimes with tinges of scarlet; abdomen whitish (but not scarlet). 1: Abdomen scarlet; body brown or scarlet.

1. Outer claw of the forelegs: 0: smaller

TABLE 1

Matrix of Characters for Living and Fossil*
Enicocephalus

	1111111 01234567890123456
almanzari	10011000001000110
bahorucensis	11011001000001010
boraceianus	0001001???01??000
cubanus	10010000001000110
dominicus	10010101000001110
exophthalmus	10110100000010110
flavicollis	0001000?00000?000
guarani	0001000???00??000
lenkoi	00001010100100001
neblinensis	0001000?00000?000
ningulus	00001010100000001
pilosus	00010001000100000
schuhi	0001001101000?000
semirufus	11000100000001110
sturmi	00010001010100001
taeuberi	0000100100010?000
tupi	00010011000100000
usingeri	1111010100000?110
wygodzinskyi	10011001000001010
seniculus	00001000010100000
subvitreous	11110101000001110
prius	?1011000000011010
omen	10010000001000110

*Last four species, out of alphabetical sequence with the prior ones, are the fossil taxa.

than inner claw, about ½–⅓ the size. 1: extremely reduced, about ¹⁄₁₀ the size.

2. Eyes: 0: Not bulging. Ratio width of eye to synthlipsis generally greater than 1.3. 1: Large, exophthalmic, eye:synthlipsis ratio 0.7 to slightly less than 1.0.

3. Emargination on hind border of posterior lobe of pronotum: 0: shallow, extended to ca. ⅓ or less the length of posterior lobe of pronotum. 1: deep, extended to ½ or more the pronotal length.

4. Legs: 0: Fine granular, cuticular structures present on the ventromedial surface of the forefemur. 1: Structures lost.

5. Shape of tibial spine VI. 0: Strongly crescentic. 1: With subbasal hump, but not crescentic: tip is almost directly above base. Outgroup comparison was not useful for polarizing this character, since other genera are without this distinctive tibial spine. Polarization was done on the basis of internal consistency with other characters (e.g., presence of scarlet coloration).

6. Pronotal and head color. 0: Head and hind lobe of pronotum brown. 1: Fore and midlobes of prontoum bright orange, strongly contrasting with brown segments of head.

7. Apical setulae on the hind wing: 0: Absence appears plesiomorphic, based on several genera besides *Neoncylocotis*. 1: Present, as short fringe of hairs. The wings of two species, *E. flavicollis* and *E. guarani* are not known.

8. Hind wing venation: 0: Veins Cu and R + M not joined. 1: These veins joined into an apical loop (usually the apical portion of these veins not as well formed as the more proximal parts).

9. Forewing venation: 0: Veins C + Sc and R similar to other veins in thickness and setation. 1: These veins thickened and with dense, short, fine setulae.

10. Wing coloration: 0: Wings hyaline, or only slightly dusky, and without white tip. 1: Fore and hind wings dark, dusky brown, with the tip of the forewing white.

11. Shape of tibial spine VI. 0: Crescentic or only slightly curved; without long, fine tapered apex. 1: Crescentic, with long, fine, tapered apex.

12. Apex of discal cell (forewing). 0: Pointed. 1: Truncate; vein Cu1a hardly oblique, or almost perpendicular to other veins.

13. Humeral cell of hind wing. 0: Short, 0.46–0.51 wing length. 1: Long, 0.58–0.70 wing length.

14. Coloration of body. 0: Head and thorax brown, even if abdomen is scarlet. 1: Almost entire body scarlet, including head and thorax.

15. Coloration of vein C + Sc. 0: dusky brown, slightly darker than membranous parts of wing, like other veins. 1: with at least base red, sometimes more extensive.

16. Wing. 0: not caducous. 1: caducous. This might seem a difficult character to score, since winged individuals of presumably caducous species might not yet have lost their wings. However, this character is congruent with other characters in the cladistic analysis (e.g., 6 and 8). Also, termite alates in amber are frequently found with their wings detached; the same would presumably happen to individuals of enicocephalid species capable of shedding their wings.

Two living species, *E. boraceianus* and *E. guarani*, shed their wings and, thus, are missing characters 7, 8, 9, 12, and 13 in the ma-
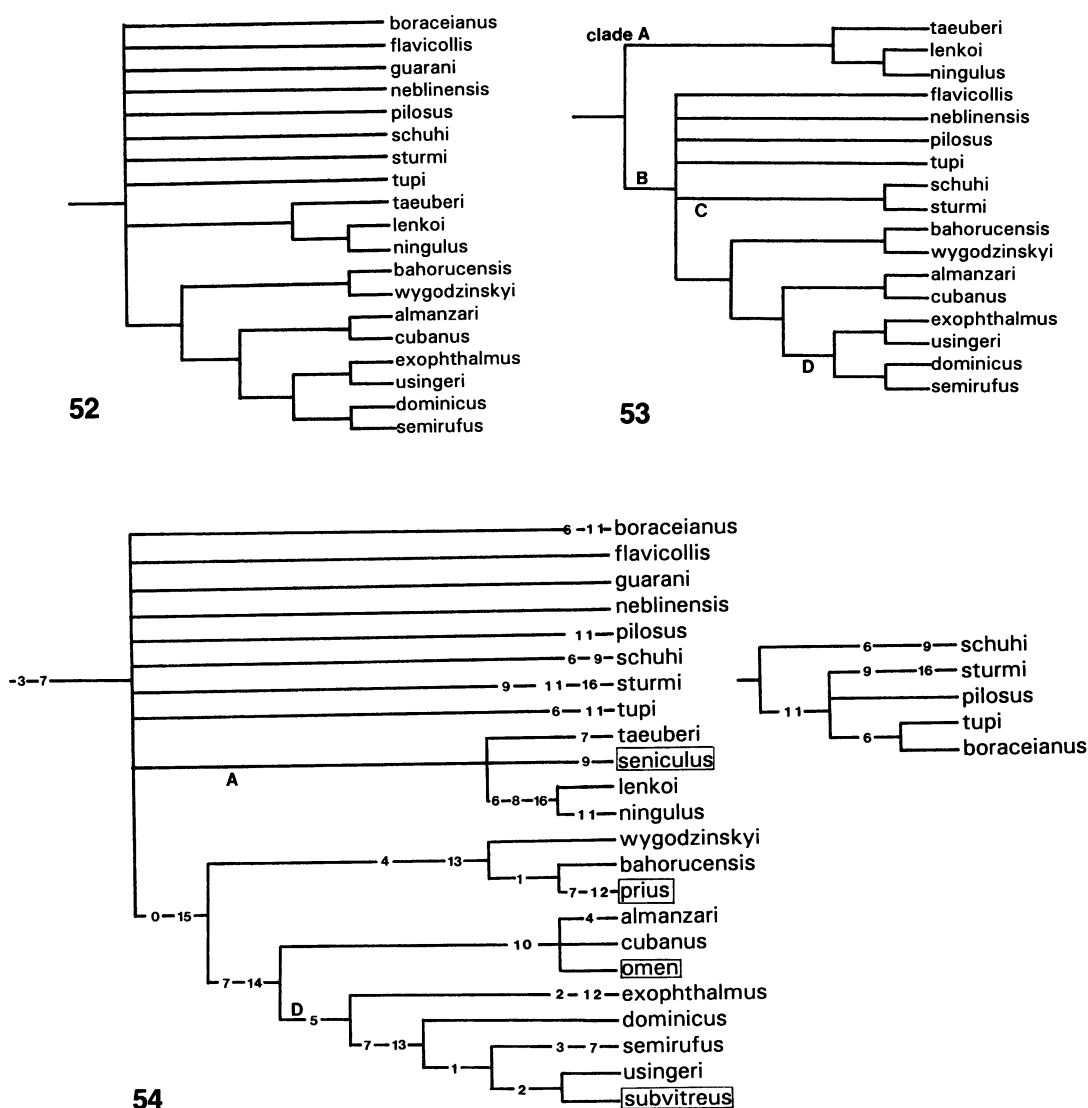
Figs. 52–54.   Nelsen consensus cladograms of living and amber fossil species of *Enicocephalus*. **52.** All living species, derived from 36 successively weighted trees. **53.** Living species, minus *E. boraceianus* and *guarani*, derived from two successively weighted trees. **54.** All living and amber fossil species, derived from four successively weighted trees; a more parsimonious arrangement is shown for the basal polytomy. Species names in boxes are Dominican amber fossils.

trix, which pertain to the wings. Due to the dramatic effects that missing characters impose upon cladistic analyses (Nixon and Davis, 1991; Platnick et al., 1991), it seemed appropriate to analyze the matrix with and without these two species. Analyses were done with the cladistic program Hennig86 using the m*bb* option (the implicit enumeration option was too exhaustive for a 486 MHz

computer to analyze). Between 3768 and 4901 most parsimonious trees resulted from analyses of various combinations of the matrix; from these trees successive weighting was done. Successive weighting dramatically reduced the number of trees, from which a nelsen consensus tree was derived. It was from these nelsen trees that comparisons were made among matrices that: (1) included only living

55

56
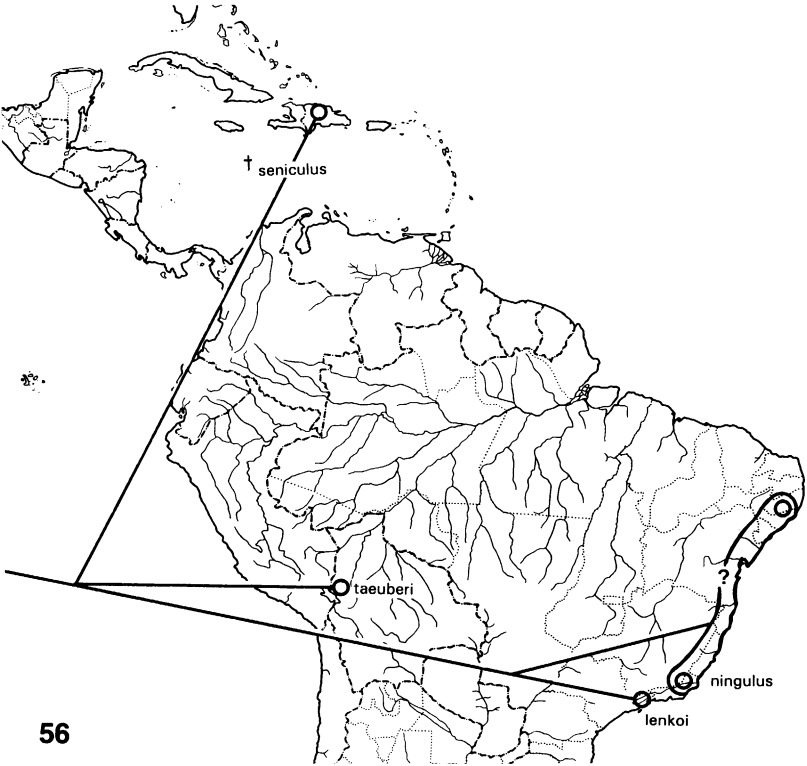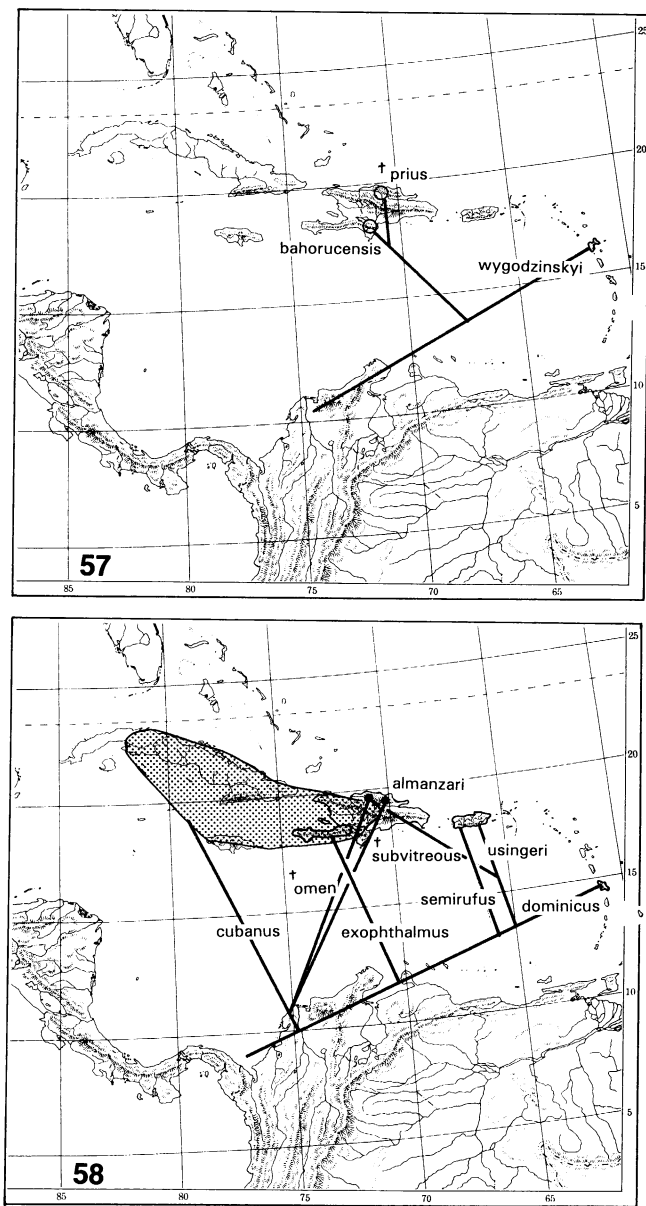
Figs. 55–58. Distribution maps of living and fossil *Enicocephalus*, with relationships of species superimposed.

Enicocephalus species; (2) the living species minus *boraceianus* and *guarani*; (3) included all living and Dominican amber fossil species; and (4) included living and amber fossil species, minus *boraceianus* and *guarani*. The lengths, consistency indices, and retention indices of the nelsen trees for the four versions of the matrix varied only between 34 and 42 steps, 0.40 and 0.44, and 0.68 and 0.74, respectively.

The effect of omitting *boraceianus* and *guarani* was substantial when the fossil species were not included: clade A was formed (see fig. 53), and this became the sister group to all the other species (clade B). Also, a clade C was formed by *E. schuhi* and *E. sturmi*. If

the fossils are included in the matrix, there curiously is no effect by omitting *boraceianus* and *guarani*: these species fall out in the basal polytomy, as in figure 54.

The effect of adding the four Dominican amber fossil species varied with the inclusion of *E. boraceianus* and *guarani* in the analysis. With *boraceianus* and *guarani* included, the part of the cladogram most distant from them was oddly effected whether or not the fossils were also included. Specifically, relationships of four species in apical nodes of a Caribbean clade (clade D) were rearranged. This is due entirely to the amber species *E. subvitreous*; the other three amber species do not affect cladogram topology. When *boraceianus* and *guarani* are not in the matrix, clade C is nonexistent, and clade A is not the sister group to all other species (i.e., there is no clade B). A basal polytomy of eight species occurs in three of the four nelsen trees (the exception being the analysis of living species, minus *boraceianus* and *guarani*). However, a more resolved scheme of four fewer steps was selected from among the four weighted trees derived from the most complete matrix (see fig. 54). This feature was restricted to the basal polytomy, and a more parsimonious solution could not be derived from the resolved, apical portions of the cladogram.

Several things must be kept in mind when discussing *Enicocephalus* biogeography. First, four undescribed species (based on nymphs and females) were reported by Wygodzinsky and Schmidt (1991), which were not included in these analyses. This is to be expected, for the incomplete sampling of this genus is also demonstrated by the discovery of two new living *Enicocephalus* species from the Dominican Republic. No *Enicocephalus* are known from the Venezuelan Andes, for example; they undoubtedly occur there. Secondly, *Enicocephalus* seems rather habitat specific, requiring the kind of wet, mature forests that are found only at higher altitudes on the larger Antillean islands. They appear absent from the smaller islands that lack mountains high enough for wet montane forests to grow; a notable exception to this is Dominica, which, although quite small compared to the Greater Antilles, is also very mountainous and lush. Discussions of biogeography must thus be tempered by short-

comings of incomplete sampling and an ecological specificity that may complicate the historical picture. However, several very coarse biogeographic patterns resulted from the cladistic analyses, which probably won't be affected much by additional new species and records.

One, Hylaean South America is an important area for the basal radiation of the genus. Basal clades with five species endemic to southern Brazil occur here, which have sister-group relationships with Andean species (*E. sturmi, taeuberi*) and a Dominican amber species (*E. seniculus*). *Enicocephalus seniculus*, thus, has no immediate relationship with the living and other Dominican amber species; it is a good example of a geographic extinction in the Dominican amber fauna. A discussion of geographic extinctions is given elsewhere (Grimaldi, 1992).

Secondly, with eight species endemic to the Caribbean, forming a consistently monophyletic group and with relationships being fairly well resolved, there are some interesting insular patterns. Two of the Dominican amber species, *E. omen* and *E. prius*, have their closest relatives living today in the Dominican Republic (*cubanus + almanzari*, and *bahorucensis*, respectively). This establishes the Hispaniolan endemism of these clades to at least the Oligo-Miocene boundary. The Hispaniolan endemics have the closest relationships with either Lesser Antillean species (*dominicus, wygodzinskyi*) or to a clade of Lesser Antillean + Puerto Rican species (including also *semirufus* and *usingeri*). In fact, there is a rather well-defined west-to-east progression of taxa, from Cuba to the Lesser Antilles. The clade composed of *E. cubanus + subvitreous + almanzari* is the most basal clade and also most westerly; then *exophthalmus* (on the Haitian peninsula); then *semirufus* and *usingeri* (on Puerto Rico); and *dominicus*, on Dominica. The fossil species *E. subvitreous* muddies this pattern somewhat, by extending the distribution of an otherwise Puerto Rican clade. *Enicocephalus subvitreous* actually affects the cladistic hypothesis based on just the living species closely related to it, which in turn greatly affects biogeographic hypotheses. With *subvitreous* in the analysis, the two species endemic to Puerto Rico become more closely related.

The enicocephalids fossilized in amber, in conclusion, form a valuable comparison between the oldest amber containing insect fossils, and a much younger amber biota. As might be expected, the Lebanese amber species is quite plesiomorphic; the Dominican amber species very closely resemble modern species. Very modernlike species apparently 30 million years old, and another record approximately 120 milion years old, substantiate an early Mesozoic origin for the Enicocephalomorpha. More exhaustive study of the Lebanese amber species may prove revealing for higher-level studies of subfamilies. The Dominican fossils, by contrast, are of minor importance phylogenetically; their value lies in illuminating the biogeography of a perplexing region.

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