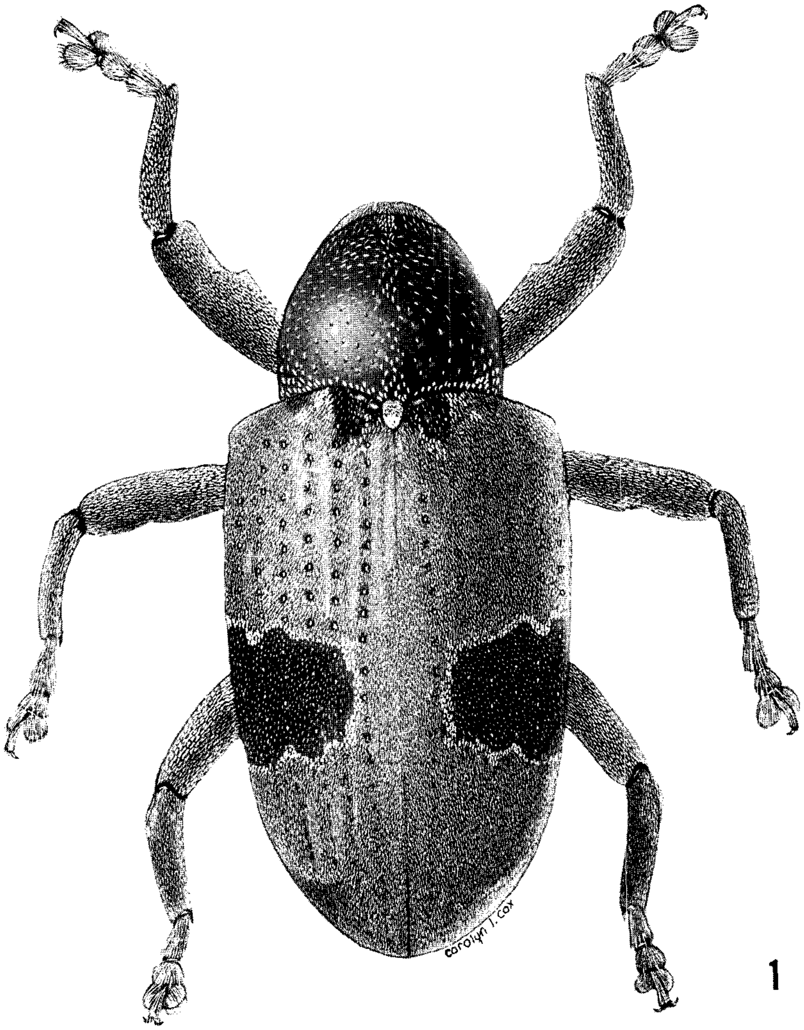

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Frontispiece and Fig. 1. *Rhinochenus transversalis,* habitus.

CLASSIFICATION AND EVOLUTION OF *RHINOCHENUS* LUCAS (COLEOPTERA: CURCULIONIDAE: CRYPTORHYNCHINAE), AND QUATERNARY MIDDLE AMERICAN ZOOGEOGRAPHY

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The genus Rhinochenus *is a compact, well defined group of some 18 species of Neotropical Cryptorhynchini, most of them seed predators of the caesalpiniaceous tree* Hymenaea courbaril. *The species are keyed, described, illustrated, and arrayed in five species groups. The following new species are described:* R. fiedleri *(type-locality "BRAZIL");* R. klagesi *(type-locality BRAZIL. Para: Santarem);* R. maculipes *(type-locality BRAZIL. Mato Grosso: Chapada dos Guimarães);* R. amapensis *(type-locality BRAZIL. Amapa: Serra do Navio);* R. chevrolati *(type-locality BRAZIL. Mato Grosso: Chapada dos Guimarães);* R. mangabeirensis *(type-locality BRAZIL. Para: Mangabeira, Mocajuba district);* R. chorrensis *(type-locality EL SALVADOR. La Libertad: Los Chorres);* R. janzeni *(type-locality COSTA RICA. Puntarenas: Rincon, Osa Peninsula);* R. thrombithorax *(type-locality PERU. Huanuco: Cachicoto);* R. caucensis *(type-locality COLOMBIA. Valle del Cauca);* R. pseudostigma *(type-locality BRAZIL. Para: Fazenda Taperinha, Santarem). The following new synonymies are proposed, junior names parenthetic:* R. stigma *Linnaeus (*R. sticticus *Lucas,* R. trilineatus *Chevrolat,* R. rougieri *Chevrolat);* R. transversalis *Chevrolat (*R. bahiensis *Chevrolat,* R. innotatus *Chevrolat);* R. x-rubra *Chevrolat (*R. subcruciatus *Chevrolat,* R. lucasi *Chevrolat).*

The evolutionary history of this genus is difficult to interpret, because of complex variation, feeble morphological differentiation, and apparent mimetic convergences. Recurring Pleistocene refugia appear to offer a plausible explanation for phylogenetic and zoogeographic relationships. All diversification within species groups probably is related to these phenomena, and probably is continuing today as suggested by sympatric occurrences of reproductively isolated or semi-isolated forms of R. stigma, *for example. Host plant associations seem also to point to a rapid phylogenetic diversification, since only* R. brevicollis *Chevrolat, a member of the complex* stigma *group, is known to attack a host genus other than* Hymenaea.

Briefly, the refugial hypothesis is one of alternating contraction and expansion of forested areas brought about by alternating dry and wet periods, accompanied by fragmentation of ranges, local isolation and differentiation, and subsequent expansion of ranges and reinforcement of differentiation. This hypothesis has recently been advanced by various authors to account for the unexpectedly complex lowland flora and fauna of the Amazon Basin. By incorporating observations on various other insect groups, I here extend the hypothesis as a significant factor in evolution of the lowland fauna of Middle America, and use it in an attempt to develop an initial synthesis of Pleistocene Middle American zoogeography.

El género Rhinochenus *se forma un grupo cerrado de como 18 especies de Cryptorhynchini en Centro y Sur América, principalmente comedores de frutas de la* Hymenaea courbaril *(Caesalpiniaceae). Yo reconozco cinco grupos de especies. Se han ofrecido claves, descripciones, y ilustraciones. Yo describo como nuevos los siguientes:* R. fiedleri *(localidad típica "BRAZIL");* R. klagesi *(localidad típica BRAZIL. Pará: Santarém);* R. maculipes *(localidad típica BRAZIL. Mato Grosso: Chapada dos Guimarães);* R. amapensis *(localidad típica BRAZIL. Amapá: Serra do Navio);* R. chevrolati *(localidad típica BRAZIL. Mato Grosso: Chapada dos Guimarães);* R. mangabeirensis *(localidad típica BRAZIL. Pará: Mangabeira, distrito de Mocajuba);* R. chorrensis *(localidad típica EL SALVADOR. La Libertad: Los Chorres);* R. janzeni *(localidad típica COSTA RICA. Puntarenas: Rincon, Península de Osa);* R. thrombithorax *(localidad típica PERU. Huánuco: Cachicoto);* R. caucensis *(localidad típica COLOMBIA. Valle del Cauca);* R. pseudostigma *(localidad típica BRAZIL Pará: Fazenda Taperinha, Santarém).*

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Son sinonimias nuevas, los nombres más jóvenes entre paréntesis: R. stigma *Linnaeus (* R. sticticus *Lucas,* R. trilineatus *Chevrolat,* R. rougieri *Chevrolat);* R. transversalis *Chevrolat (*R. bahiensis *Chevrolat,* R. innotatus *Chevrolat);* R. x-rubra *Chevrolat (*R. subcruciatus *Chevrolat,* R. lucasi *Chevrolat).*

La historia del desarollo de este género está complicada a causa de variación compleja, diferenciación pequeña, y convergencias mímicas. Los ciclos de los refugios en el Pleistoceno se forman una explanación para las afinidadas filéticas y geográficas. Toda de la diversificación en los limites de cada uno de los grupos de especies probablemente está aliado con estas fenóminas, y probablemente esta diversificación en nuestros dias se continua en los casos simpátricos de formas de R. stigma *que son isolados o semi-isolados reproductivomente. También, una diversificación filética muy rápida está indicado por las asociacionas con las plantas hospederas, porque solamente* R. brevicollis *Chevrolat, un miembro del grupo complejo del* R. stigma, *está conocido de un hospedero genérico otro que* Hymenaea.

Brevemente, la hipótesis de refugios es uno de ciclos alternativos de expansión y contracción de la selva causados por períodos alternativos de humedad y sequedad; así, las distribucionas geográficas son dividas y las poblacionas separadas y diferenciadas, entonces las distribucionas son unidas y las diferencias reforzadas. Esta hipótesis, aducido recentamente por autores varios, explica la flora y fauna compleja de las tierras bajas del Amazon. Con comentos sobre otros grupos de insectos, aquí yo extendo la hipóthesis como un factor significante en el desarollo de la fauna de tierras bajas en Centro América, y lo uso para descubrir una síntesis de la zoogeografía de Centro América en el Pleistoceno.

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INTRODUCTION

In a previous paper (Whitehead 1975) I discussed those members of two cryptorhynch weevil genera, *Conotrachelus* Schönherr and *Microscapus* Costa Lima, that are associated with fruits of the caesalpiniaceous tree *Hymenaea courbaril* L. However, the principal seed predators of this host plant belong to the genus *Rhinochenus* Lucas, treated herein. I recognize 18 species, all but one of which are known or suspected to attack fruits of *H. courbaril* or other *Hymenaea* species; the exception is *R. brevicollis* Chevrolat, which attacks fruits of various species of *Copaifera* L., a related host genus. Not much is known about the natural histories of most of the species, but those of southern Central America are being intensively studied by D. H. Janzen (cf. 1975). Previous major systematic treatments of *Rhinochenus* were by Chevrolat (1871), who described many forms as new species, and Fiedler (1951), who placed in synonymy some of Chevrolat's names. Despite these contributions it has not been possible to identify specimens satisfactorily, because the species were not adequately delimited, too many synonyms remained undeclared, and many species remained undescribed.

These weevils form a compact group both ecologically and morphologically, and the diagnoses given by Lucas (1857) and Chevrolat (1871) delimit the genus clearly. Adults are readily distinguished by size and habitus (Fig. 1-39) from most other weevils, and by the following combination from the comparatively few other forms that are superficially similar: Cryptorhynchini, rostrum short, flat, recessed in prosternum and part of mesosternum; body large, 7-18 mm; antenna inserted near apical 0.33 to 0.25 of rostrum, not conspicuously sexually dimorphic, funicle with 7 segments; interocular distance greater than minimum width of rostrum, eyes covered in repose by pronotal lobes; pronotum punctate, punctures not contiguous, disc with or without slight median elevation but otherwise without gross sculpture; scutellum conspicuous, oval or rounded, squamose; elytron with subapical swellings but otherwise without gross sculpture, without tubercles, intervals flat or convex, striae indicated by rows of punctures; legs with each femur unidentate, each tibia with apical comb of 2 rows of stout bristles, tarsal claws free, simple; and vestiture squamose, dorsum without erect scales or setae, at least posterior 0.33 of elytron densely squamose, scales tan to orange.

The development of taxonomic knowledge of *Rhinochenus* began with Linnaeus (1758, *R. stigma*), Fabricius (1798, *R. piger*), Illiger (1806, *R. nota*), and Boheman (1844, *R. reichei*), each of whom named one form placed in various generic combinations. Schönherr (1837) discussed variations of *R. stigma,* placing *R. piger* and *R. nota* in synonymy. Lucas (1857) defined *Rhinochenus* based on his *R. sticticus*. Chevrolat (1871) presented the first comprehensive review, assigned all previously described species, removed *R. piger* from synonymy, and described 14 new species; later (1880) he described 2 more new species, for a total of 20 recognized species. Champion (1905) regarded all Central American forms as variations of *R. stigma.* More recently, Fiedler (1951) reduced the number of recognized species to 13, placing in synonymy 7 names recognized as valid by Chevrolat.

I have examined type-material of 13 of the 21 previously named forms. C. W. O'Brien examined for me the type-material of 5 additional forms plus a paratype of *R. subcruciatus,* and I follow his interpretations herein. D. H. Janzen provided notes on the type of *R. stigma.* The types of *R. nota* and *R. subcruciatus* have not been located; I accept Fiedler's interpretation of *R. nota,* synonym of *R. stigma,* and O'Brien's interpretation of *R. subcruciatus,* synonym of *R. x-rubra.* Among the 18 species recognized herein are 11 that I describe as new; I recognize only 7 of the 21 previously available names as valid.

Phylogenetic relationships among species in the *transversalis* and *stigma* groups are not clear. Some of the widespread species are greatly varied geographically, and relationships of various populations treated as *R. stigma,* in particular, need additional study. However, relationships are clear enough to allow some preliminary zoogeographic and ecological comparisons.

Morphological differentiation at species level is slight, suggesting that the species are either recently evolved or under very similar ecological pressures. Differentiation within species groups probably was greatly augmented by repeated restrictions of habitat during dry phases of the Pleistocene. In this paper I have attempted to relate distributions of the species, and of geographic forms of some of the widely ranging, varied species, to circum-Amazonian Pleistocene forest refugia as summarized by Vuilleumier (1971); cf. Fig. 150. The *Rhinochenus* fauna of South America is much too poorly known to contribute new insights into this matter, the fauna of western and northwestern South America particularly so. However, I have reinterpreted certain Central American distributional patterns to at least in part reflect similar Pleistocene events.

All *Rhinochenus* except *R. brevicollis*, which apparently prefers various species of *Copaifera,* are known or suspected to attack fruits of *Hymenaea.* According to Janzen (1975) eggs are deposited on the *Hymenaea* fruits only during a brief period well after the fruits have reached full size, when they no longer ooze defensive resins if punctured but are still soft enough for larval penetration. Natural histories have been worked out by D. H. Janzen (pers. comm.) for Central American forms of *R. janzeni* new species, *R. stigma,* and *R. transversalis* Chevrolat. The most specialized species is *R. stigma,* adapted to forest conditions and dependent on such external agents as rodents, peccaries, or deer to free the adults from the seed pod; neither larva nor adult can drill its own exit hole. The other two species are able to drill their own exit holes but otherwise are quite different in behavior. It is probable that in those areas of South America where 5 or more species may attack a single fruit crop, each species has distinctive behavioral properties.

Certain color patterns, of integument and vestiture, recur throughout the genus and also in some other cryptorhynch genera. D. H. Janzen (pers. comm.) suggests that these are cryptic, with the deep reddish brown integumental coloration resembling that of the *Hymenaea* seeds and the yellow to beige to mottled vestiture coloration resembling that of the pulp surrounding the seeds. The pulp of fruits attacked by *R. stigma* in Central America is characteristically discolored and mottled, and Central American specimens of *R. stigma* are colored to match. The only other species that departs from the normal pattern of dense, pale vestiture broken by bold red or dark orange areas is *R. maculipes* which may, therefore, be another species causing pulp discoloration.

I suspect that the pattern of cryptic coloration is complicated by some form of mimicry. Certain color patterns are represented by two or more phyletically distant species in certain areas but are not represented elsewhere. Alternatively, populations of two or more unrelated, geographically varied species may nearly precisely resemble one another in some localities, to an extent that cryptic coloration alone seems an inadequate explanation for resemblance. Whether or not this is true mimicry is unknown, as the weevils are palatable to a wide spectrum of bird and mammal predators (Janzen, pers. comm.) and thus can only be mimics, yet no models are known. However, I assume mimicry exists and discuss such presumed mimetic convergences at length.

MATERIALS AND METHODS

Materials. – This study is based on examination of over 2200 pinned and labelled adult specimens, plus several hundred unpinned specimens of *R. stigma* from Costa Rica. Large series from Costa Rica and Cayenne were contributed by D. H. Janzen, for whose ecological studies this project was undertaken. The following acronyms represent collections and responsible curators from whom materials were borrowed; not all of these are cited in the text because depositories are not given for the abundant and widespread *R. stigma* and *R. transversalis*.

AMNH	American Museum of Natural History, New York, N. Y.; P. Vaurie.
BMNH	British Museum (Natural History), London, England; R. T. Thompson.
CAS	California Academy of Sciences, San Francisco, CA.; D. H. Kavanaugh.
CMPP	Carnegie Museum, Pittsburgh, PA.; G. Wallace.
CWOB	C. W. O'Brien, Florida A & M University, Tallahassee, FL.; C. W. O'Brien.
FMNH	Field Museum, Chicago, IL.; H. S. Dybas.
H&AH	H. & A. Howden, Carleton University, Ottawa, Ontario; A. T. Howden.
IRSB	Institut Royal des Sciences Naturelles, Brussels, Belgium; R. Damoiseau.
MCZ	Museum of Comparative Zoology, Cambridge, MA.; J. C. Scott.
MNHB	Museum für Naturkunde der Humboldt-Universität, Berlin, DDR; F. Hieke
MNHP	Muséum National d'Histoire Naturelle, Paris, France; H. Perrin.
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil; H. Reichardt.
NMSF	Natur-Museum Senckenberg, Frankfurt am Main, Germany; R. zur Strassen.
RMSS	Naturhistorisk Riksmuseet, Stockholm, Sweden; T. Nyholm.
UCV	Universidad Central de Venezuela, Maracay, Venezuela; F. Fernandez Yepez.
UPCB	Universidade Federal do Parana, Curitiba, Brazil; J. S. Moure & G. H. Rosado Neto.
USNM	United States National Museum of Natural History, Washington, D. C.; R. E. Warner.
UZMC	Universitetets Zoologiske Museum, Copenhagen, Denmark; N. Møller Andersen.

Criteria for species recognition. – I use standard criteria as described previously (Whitehead 1972). Because of the limited and geographically dispersed nature of materials examined, no statistical analysis was attempted for purposes of gene flow determination. In simple terms, I sorted specimens to distinguishable forms and then attempted to link up different geographic forms through intermediates. Thus, if allopatric forms were linked by intermediates they were considered conspecific; and if not so linked and if distinguished to a degree similar to differences between sympatric forms they were considered as distinct.

Morphological differences between species are slight, and the characteristics variable. Differences even in male and female genitalia at species level are subject to being nullified by variation and are not necessarily of crucial importance. In the male phallus and female eighth sternite of one species, *R. stigma,* I found both inter- and intrapopulational differences of a magnitude that might ordinarily be expected of distinct species, yet these differences do not correspond to other morphological variables.

Ranking. – In this study I use neither subgeneric nor subspecific ranks, as neither are necessary or desirable. Instead, for supraspecific ranking I use the informal "species group", and rather than attempt to define discrete infraspecific units I discuss infraspecific variation as such. I believe the species, species groups, and genus as treated herein are real evolutionary units, but the species groups are units of convenience rather than phylogenetic equivalents.

Measurements and definitions. – In general, I follow standard terminology as used in weevil studies (see also Whitehead 1975), but 4 morphological features (see Fig. 9-10) require definition here. The *metasternal sulcus* is a median, longitudinal impression extended as an elongate triangle from the base of the metasternum to or nearly to the apex; this sulcus is polished and impunctate, but in members of the *transversalis* group has dense, erect scales or setae in its apical 0.25 to 0.75; it is not part of the rostral canal of the prosternum and mesosternum. The *lateral processes* of the mesosternum surround the anterior edges of the middle coxal cavities. As used in this paper, the term "sternum 1", for example, refers to the first visible sternum. The female *eighth sternite,* or spiculum ventrale, is the sclerotized portion of morphological sternum 8; of taxonomic interest is the form of the pigmented area only, as the outer margins are membranous.

I use a set of relatively well defined measurements of a selected individual or individuals representative of each species, incorporated as a separate part of the species description, to indicate not only size but also to define proportions. Some of the measurements are admittedly imprecise, notably the antennal insertion because of variation in form of antennal scrobe or sulcus, and the various parts of the antenna because of variations in position. Thus, only a cursory attempt was made to determine variation; rather, these measurements form the basis for describing proportions characteristic of species groups, notably the relative position of the antennal insertion and the relative shape of the pronotum. I mean quite specific things when I refer to the length of the rostrum or the position of the antennal insertion; these are reference statements rather than true statements of length or position, however. I measure the rostrum laterally, from (a) base of mandible to (b) distal margin of antennal scrobe to (c) anterior margin of eye; the length of the rostrum is (a to b) + (b to c), and the antennal insertion is herein defined as (b). The measurements used are the following.

LE	length of longer elytron.
LP	length of pronotum along midline.
WPmax	maximum width of pronotum.
WPbase	width of pronotum at base.
WE	maximum width across elytra.
LR	length of rostrum = base of mandible to base of antennal sulcus + base of antennal sulcus to anteroventral margin of eye.

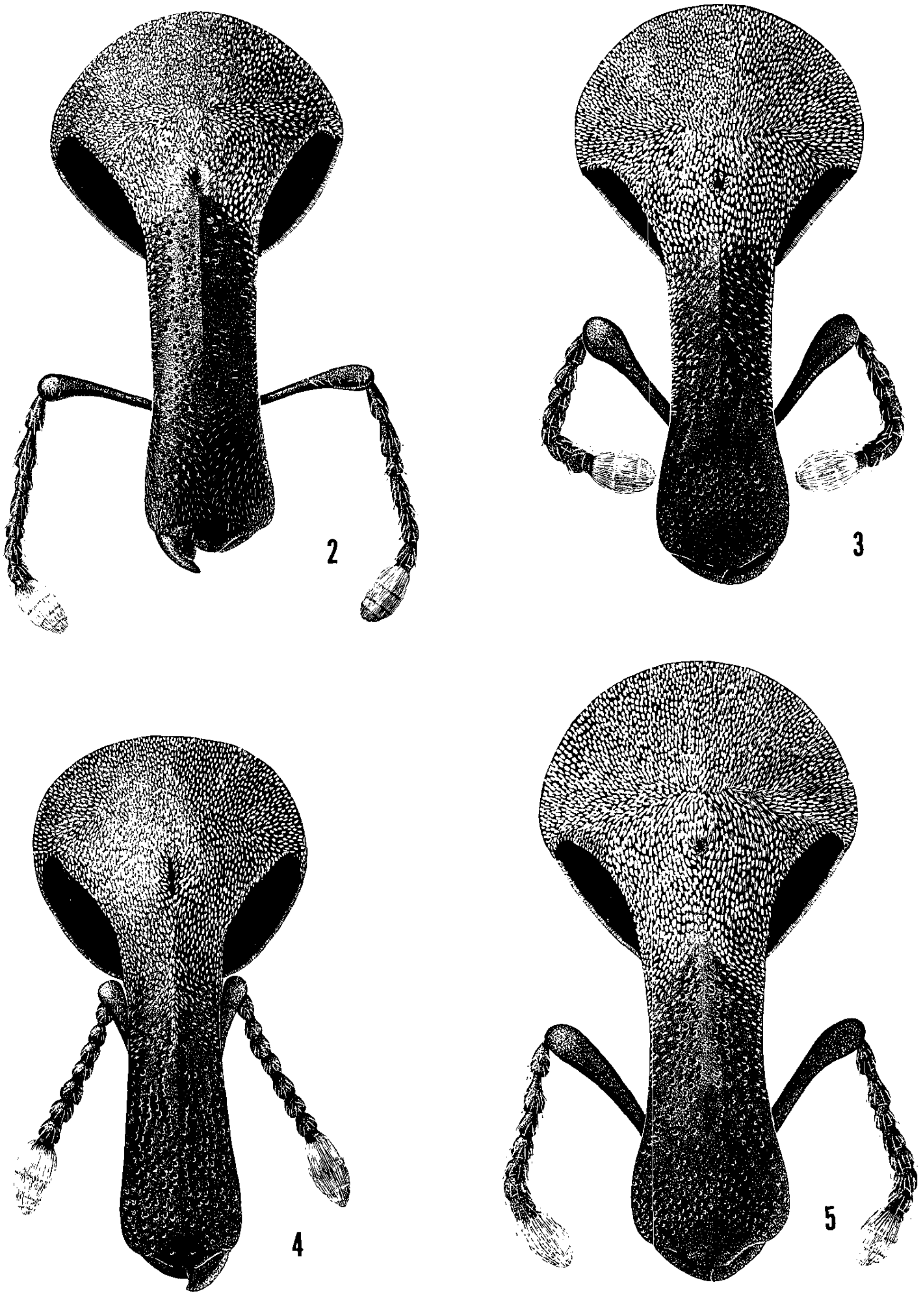


Fig. 2-5. *Rhinochenus* spp., head: 2, *R. transversalis;* 3, *R. chorrensis*; 4, *R. stigma*; 5, *R. janzeni.*

WRmin	minimum width of rostrum, near middle.
WRmax	maximum width of rostrum, near apex.
WFmin	width of frons between eyes.
WFmax	width of frons across eyes.
LA	length of antenna = length of scape measured from base of antennal sulcus + length of funicle + length of club.

Techniques. – Measurements and illustrations were made with a Spencer AO dissecting microscope, measurements with an ocular micrometer and drawings with an ocular grid. Genital dissections were made by relaxing the specimens in hot alcohol, extracting the genitalia through the anal aperture, clearing in hot KOH, and storing in glycerine. The female eighth sternite and spermatheca and the male phallus in ventral view were drawn from glycerine preparations; the phallus apex was drawn from specimens mounted on points and oriented to obtain the desired caudodorsal aspect. The genitalia were drawn by me, other morphological features by C. Cox, and charts and maps by I. Feller.

Descriptive format. – Under each species I give, as appropriate, literature and synonymic data, data on type-material, taxonomic notes, diagnostic combination, description including measurements of selected specimen(s), variation, material examined, etymological note, natural history, phylogenetic relationships, and geographic relationships. In the paragraphs on phylogenetic and geographic relationships I attempt to place the taxon in a relational frame of reference by using Hennig's (1966) methods, to discuss geographic relationships of related taxa, and to correlate distributions with postulated Pleistocene forest refugia as summarized by Vuilleumier (1971) and Vanzolini (1973).

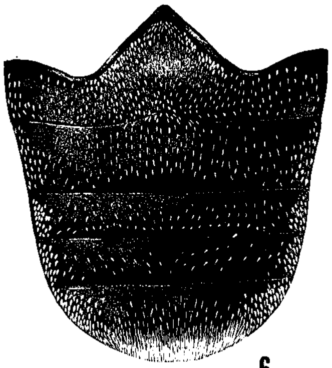
GENUS *Rhinochenus* LUCAS

Rhinochenus Lucas 1857: 171; Chevrolat 1871: 85; Champion 1905: 537; Fiedler 1951: 1102.
Type-species: *Rhinochenus sticticus* Lucas, by monotypy; synonym of *Curculio stigma* Linnaeus.

Diagnostic combination. – See introduction.

Description. – Cryptorhynchini; length of pronotum + elytron 7 - 18 mm. Integument rufous to rufopiceous above, darker beneath. Vestiture squamose; erect setae absent dorsally, variously distributed along midline and apex of abdomen, only. Head (Fig. 2-5) with rostrum broad, recessed in repose into deep rostral canal extended to middle of mesosternum, apex of canal arcuate; mandible acutely toothed on inner margin; surface of rostrum punctate above, with vague or fine median carina in basal 0.50, otherwise without dorsal macrosculpture; antennal insertion near apical 0.33 to 0.25 of rostrum, not or slightly sexually dimorphic; antennal scrobe slightly descendent toward base; antennal funicle 7-segmented; frons with deep, circular fovea, head otherwise without conspicuous macrosculpture; eyes widely separated, interocular distance greater than minimum width of rostrum, eyes in repose hidden by pronotal lobes. Pronotum (Fig. 11-39) not produced forward to entirely conceal head, conical or subconical, variously widest at base or near middle, distinctly transverse to about as long as wide; surface punctate, punctures not confused, separated by at least 0.50 diameters of each; disc with or without slight median swelling, surface otherwise without distinct macrosculpture. Scutellum conspicuous, ovate to circular, densely squamose. Elytron (Fig. 11-39) with subapical swelling and punctate striae but without costae, tubercles, or other macro-sculpture; intervals flat to moderately convex, sutural interval not raised; stria 10 extended beyond middle 0.33, interval 10 in middle 0.33 narrow but evident; humeral region squared. Hind wings fully developed. Legs with each femur unidentate beneath; each tibia with outer margin not serrate, each with apical comb of 2 rows of stout bristles; tarsal claws simple, free, equal. Venter of thorax with middle coxae separated by distance greater than maximum width of rostrum; metasternum long, distance between middle and hind coxae longer than antennal club, with polished, elongate median sulcus (Fig. 9-10); metepisternal suture distinct. Abdomen (Fig. 6-10) along midline with sternal ratio approximately 5:3:2:2:3, sternal sutures not angulate posterolaterally, suture between sterna 1 and 2 produced slightly forward at middle but other sutures transverse; sternum 1 slightly sexually, dimorphic in some species, more convex in female; sternum 5 slightly to strongly sexually dimorphic, generally convex in female and biconvex in male. Male genitalia with phallus (Fig. 40-79) not greatly varied, apex truncate to narrowly rounded, slightly to conspicuously lipped but not hooked; endophallus with or without conspicuous field of spicules or spines, without other sclerites. Female genitalia with eighth sternite and spermatheca (Fig. 80-136) various.

Natural history. – Of the 18 included species, 17 are known or inferred to attack fruits of *Hymenaea* spp., especially *H. courbaril* L.; this is a large caesalpiniaceous tree characteristic of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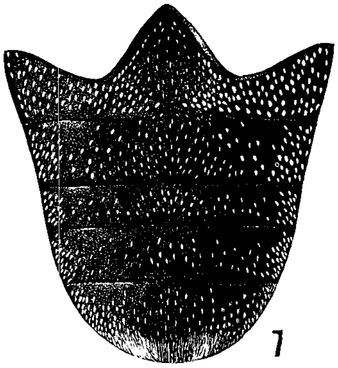
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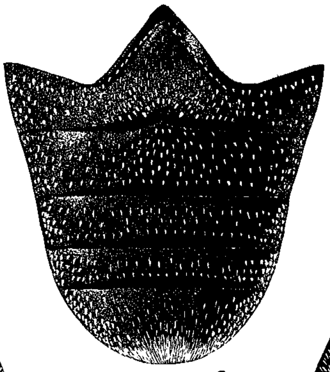
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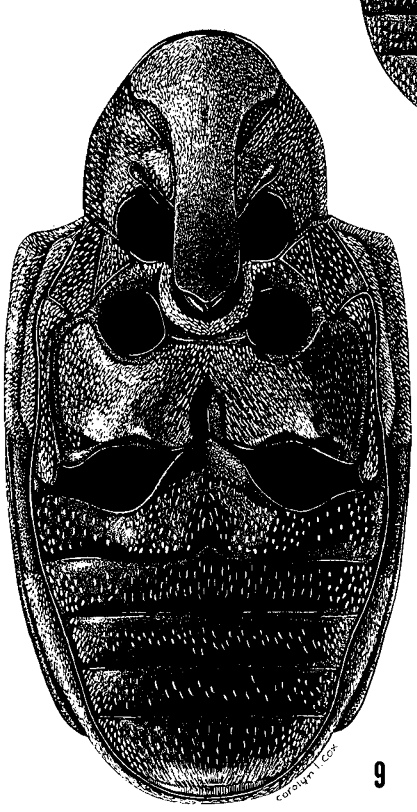

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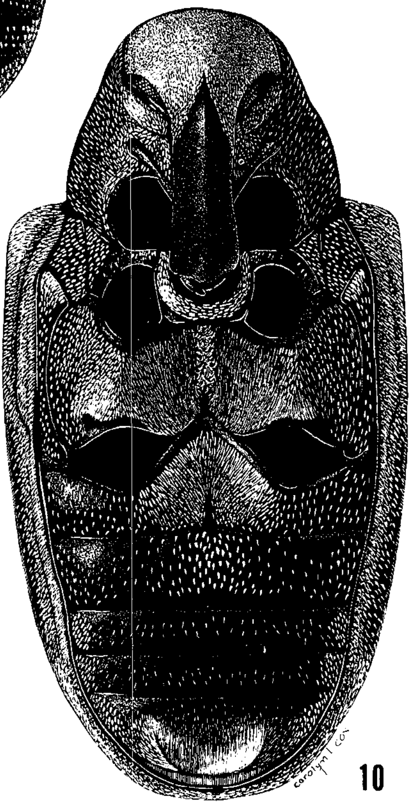

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Fig. 6-8. *Rhinochenus* spp., abdomen: 6, *R. transversalis,* female; 7, *R. chorrensis,* male; 8, *R. janzeni,* female. Fig. 9-10. *Rhinochenus* spp., venter: 9, *R. stigma,* female; 10, *R. transversalis,* male.

dry tropical American semideciduous forests. The exceptional species, *R. brevicollis*, is a South American species which is recorded from *Copaifera* spp., another caesalpiniaceous legume. Throughout the known range of *Rhinochenus*, the host *Hymenaea* trees are adapted as a response to weevil seed predation to produce large fruit crops only once in every 3-4 years but fruiting apparently is annual elsewhere (e.g., Greater Antilles) and the fruit crops smaller (Janzen pers. comm.). Hence there is reason to suppose that the apparent absence of *Rhinochenus* from the Grijalva Basin of Chiapas and northward is not an artifact of inadequate sampling, but real.

The natural histories of Central American *Rhinochenus* are under study by Janzen; his studies have produced some useful comparative data, summarized herein for *R. janzeni*, *R. stigma*, and *R. transversalis*. Currently, however, insufficient data are available for extensive systematic comparisons in characteristics other than structure and distribution. Flight dynamics and vagility; population dynamics; immature stages; ecological comparisons – all of these areas are in infant stages of knowledge and can only be touched briefly in this paper.

Distribution. – Representatives of this genus are known to occur from the Pacific slopes of southern Mexico (Chiapas) to "Paraguay" and southern Brazil (Santa Catarina). Most of the species seem to have relatively restricted ranges, but *R. stigma* occupies nearly the entire range of the genus. Distributions of most of the South American species are readily correlated at least approximately with Pleistocene forest refugia which have been postulated to have ringed the Amazon Basin (see Vuilleumier 1971 and Vanzolini 1973, and Fig. 150). Similarly, geographic forms of some of the more widespread species correspond readily to these refugia, but some species have been too rarely collected for comparative analysis of geographic variation. Most of the range has been inadequately sampled, but the species probably are reasonably well represented from all areas except the western and northwestern parts of South America.

Key to Species

Many of the species of *Rhinochenus* are morphologically similar and/or geographically varied, and consequently difficult to distinguish. This key should therefore be used in conjunction with descriptions and distributions. Couplet 12, especially, is difficult to use without comparative material. Body size is normally nearly uniform, but in a few species there is conspicuous geographic variation, and in all species occasional dwarf individuals occur; hence size is used sparingly and must be interpreted with caution.

1 Metasternal sulcus with erect scales or setae in apical 0.5 to 0.75 (Fig. 10) 2

1′ Metasternal sulcus without erect scales or setae (Fig. 9) 5

2 (1) Elytra and femora variegated with dark gray scales, lateral macula indistinct or feebly defined; (habitus, Fig. 18); Brazil (Mato Grosso, Para) .... 3. *R. maculipes* n. sp., p. 131

2′ Elytra and femora not variegated, lateral macula sharply defined or reduced to small spots or absent 3

3 (2′) Rostrum punctate-squamose immediately in front of frontal fovea, midline punctate distad to basal 0.75; abdominal sterna 3-4, with punctations scattered, not in narrow transverse bands; Brazil .... 1. *R. fiedleri* n. sp., (habitus, Fig. 11); p. 130

3′ Rostrum (Fig. 2) impunctate immediately in front of frontal fovea, or nearly so; abdominal sterna 3-4 each with transverse band of punctures 4

4 (3′) Pronotum conical, widest at base; larger, LP + LE normally over 11.5 mm; elytral macula if present irregular in outline, macula reduced or obsolete in specimens from northeastern South America; (habitus, Fig. 1); Honduras to Cayenne and "Brazil" .... 4. *R. transversalis* Chevrolat, p. 132

4′ Pronotum subconical, widest near middle; smaller, LP + LE under 11.5 mm; elytral macula large, transversely oval, regular in outline; (habitus, Fig. 12); Brazil (Para) . . . . 2. *R. klagesi* n. sp., p. 130

5 (1′) Pronotum conical and transverse, widest at base and LP/WP = 0.88-0.92; antennal insertion at or behind distal 0.33 of rostrum; LP + LE normally over 15 mm; South America 6

5′ Pronotum subconical and/or about as long as wide, in most specimens widest near middle and in most species LP/WP = 0.98-1.02; antennal insertion at or in front of distal 0.33 of rostrum; LP + LE normally under 16 mm and in most species under 15 mm; Central and South America 9

6 (5) Elytra (Fig. 15) with complete transverse band of dense vestiture in basal 0.33; northern South America 7

6′ Elytra (Fig. 14, 16) with at most a small sutural shield of dense vestiture in basal 0.33; southern Brazil 8

7 (6) Elytra with basal glabrous band complete; (habitus, Fig. 15), Cayenne and Brazil (Amapa) . . . . 5. *R. amapensis* n. sp., p. 137

7′ Elytra with basal glabrous band interrupted laterally, intervals 6, 9, and 10 with dense basal vestiture; Colombia . . . . 6. *R. hercules* Chevrolat, p. 138

8 (6′) Head glabrous except across frontal fovea and around eye margin, femora with large glabrous areas; (habitus, Fig. 16); Brazil (Bahia, Mato Grosso, Minas Gerais) . . . . 7. *R. reichei* (Boheman), p. 139

8′ Head densely squamose behind frontal fovea, legs uniformly squamose; (habitus, Fig. 14); Brazil (Mato Grosso) . . . . 8. *R. chevrolati* n. sp., p. 141

9 (5′) Pronotum transverse, LP/WP = 0.84-0.92. 10

9′ Pronotum about as long as wide, LP/WP = 0.98-1.02 11

10 (9) Pronotum not strongly gibbous; sterna 3-4 with vestiture subrecumbent; (habitus, Fig. 25); Costa Rica and Panama . . . . 12. *R. janzeni* n. sp., p. 148

10′ Pronotum strongly gibbous; sterna 3-4 with vestiture erect; (habitus, Fig. 22); Peru . . . . 13. *R. thrombithorax* n. sp., p. 149

11 (9′) Elytral vestiture (Fig. 21) uniformly dense, tan, broken by lateral macula extended to suture, forward to base, and completely encircling basal area of dense vestiture; (habitus, Fig. 21); northeastern South America . . . . 10. *R. x-rubra* Chevrolat, p. 146

11′ Elytral vestiture not in pattern described above, either lateral macula not extended forward along suture or pattern not sharply defined 12

12 (11′) Strial punctures relatively fine, punctures at anterior 0.33 of striae 5 and 6 with diameters equal to or less than width of interval 5 13

12′ Strial punctures relatively coarse, punctures at anterior 0.33 of striae 5 and 6 with diameters greater than width of interval 5 17

13 (12) Distal comb of tibia orange; (habitus, Fig. 26); El Salvador . . . . 11. *R. chorrensis* n. sp., p. 147

13′ Distal comb of tibia dark brown to black; South America 14

14 (13′) Elytral maculation (Figs. 23-24) reduced, at most with narrow, irregular transverse band; (habitus, Fig. 23-24); Colombia to Trinidad . . . . 14. *R. caucensis* n. sp., p. 150

14′ Elytral maculation (Fig. 29) normal, with large circular or oval transverse spot 15

15 (14′) Rostrum with fine, narrow, inconspicuous median carina in basal 0.50; sternum 1 without apical fringe of scales 16

15′ Rostrum with broad, flat, alutaceous area in basal 0.50, not carinate; sternum 1 with apical fringe of scales; Brazil (Para) . . . . 9. *R. mangabeirensis* n. sp., p. 142

16 (15) LP + LE under 10 mm, generally under 9 mm except in Venezuela; phallus (Fig. 65) with apex narrowly rounded but not distinctly lipped; (habitus, Fig. 29); Venezuela to southern Brazil (Santa Catarina) . . . . 16. *R. brevicollis* Chevrolat, p. 153

16′ LP + LE normally over 10 mm, not known from Venezuela; phallus (Fig. 66-67) with apex narrowly rounded and distinctly lipped; (habitus, Fig. 30); northeastern South America . . . . 17. *R. pseudostigma* n. sp., p. 155

17 (12′) Rostrum with median carina conspicuous, convex, polished; elytral vestiture uniform, tan, if lateral macula conspicuous then strial punctures squamose; (habitus, Fig. 27-28); South America south of Amazon River . . . . 15. *R. cinereopunctatus* Chevrolat, p. 151

17′ Rostrum with median carina fine to obsolete, alutaceous; elytral vestiture not as described above, various; (habitus, Fig. 31); southern Mexico (Chiapas) to southern Brazil . . . . 18. *R. stigma* (Linnaeus), p. 156

The species groups and species

THE *transversalis* GROUP

Included species. – *R. fiedleri* n. sp., *R. klagesi* n. sp., *R. maculipes* n. sp., and *R. transversalis* Chevrolat.

Diagnostic combination. – Adults of this group are distinguished from those of other *Rhinochenus* by having erect scales in the metasternal sulcus; male genitalia with phallus short, broad, truncate apically, and endophallus without spine field; and female genitalia with eighth sternite slender, stem proportionately long and with narrow base, and with dense fringe of apical setae.

Description. – Size moderate for genus. Integument above rufous, below rufopiceous. Head with or without vestiture along midline in front of frontal fovea, densely squamose behind fovea; antenna inserted at or slightly behind anterior 0.33 of rostrum, LRapex/LRbase 0.47 - 0.55 in male and 0.53 - 0.63 in female, WRmin/WRmax 0.74 - 0.80, LR/LA 0.61 - 0.71, LR/LP 0.60 - 0.66; second funicular segment about 0.4 - 0.5 as wide as long and about as long as first funicular segment; interocular ratio 0.41 - 0.48. Prothorax conical or subconical, 0.90 - 0.94 as long as wide; punctures near middle of disc separated by average distances less than diameters of each. Scutellum ovate to circular, about 0.7 - 1.0 as wide as long. Elytron with strial punctures fine to coarse; intervals flat, uniform in width; WE/LE 0.56 - 0.60. Lateral processes of mesosternum glabrous or sparsely to densely squamose. Ventral sulcus of metasternum with slender, erect scales in apical 0.25 to 0.75. Sternum 5 strongly biconvex in male. Distal comb of tibia black. Male genitalia with phallus short, wide, parallel-sided or swollen at middle, broadly truncate at apex; endophallus without evident field of spines or spicules. Female eighth sternite slender, stem long and with narrow base, apex with dense fringe of setae or at least with more than single row of setae, hyaline area not acuminate basally; spermatheca with nodulus not produced.

Natural history. – The host plant, *Hymenaea courbaril,* is known for *R. transversalis,* deduced for *R. klagesi* and *R. maculipes* by association with long series of other *Rhinochenus* specimens bearing identical label data, and assumed for *R. fiedleri.* See discussion of natural history of *R. transversalis.* The type of cryptic coloration of *R. maculipes* is a departure from that of the other species in the genus, probably indicative of a behavioral difference. The pattern of maculation of *R. klagesi* is nearly identical to that of some sympatric members of other groups, suggesting a mimetic relationship.

Geographic relationships. – The aggregate range is from southern Central America to southern Brazil, sympatric with all other groups. At least *R. klagesi* and *R. maculipes* are sympatric in northern Brazil.

Phylogenetic relationships. – The *transversalis* group is clearly monophyletic, defined by the synapotypic squamose metasternal sulcus, truncate phallus, and bare endophallus. It most probably is the sister group of all other *Rhinochenus*, as suggested both by cladistic analysis (cf. Willis 1971, Whitehead 1972) and by relatively great morphological discontinuity, but the other *Rhinochenus* share no known unreversed synapotypic character state.

1. *Rhinochenus fiedleri* Whitehead, new species

Type-material. – Holotype: male labelled "Brazil" and "W. G. Dietz Coll.". Type-locality: Brazil, no precise designation. Type-depository: MCZ.

Diagnostic combination. – The holotype of this species is distinguished from other members of the *transversalis* group by having punctations and vestiture along the midline of the head in front of the frontal fovea.

Description of male. – Length, pronotum + elytron, 11.5 mm. Vestiture squamose, light tan, concolorous except for minute dark scales in bare areas of elytron. Head densely squamose from behind basal 0.25 of rostrum laterally and from base of rostrum dorsally, area immediately in front of frontal fovea squamose. Rostrum with fine carina in postmedian 0.25, impunctate along midline near carina but punctate behind carina, elsewhere finely and nearly uniformly punctate; microsculpture with meshes slightly stretched longitudinally, flattened, obsolete near carina. Pronotum (Fig. 11) about as wide at middle as at base, disc with slight median elevation; punctures fine, moderately dense, near middle of disc separated by average distances equal to slightly less than diameters of each; punctures each with small, inconspicuous scale except for broad scales in anterior and posterior ventropleural corners and in divided prescutellar spot; microsculpture granulose. Elytron (Fig. 11) with lateral macula large, nearly circular, irregular, extended to about stria 1, faintly rimmed; scutellar area bare; strial punctures each with slightly enlarged scale, punctures not surrounded by glabrous spots, inconspicuous in apical 0.33, at basal 0.33 about as wide as interval 5; interval 10 in middle 0.33 narrow, convex, stria 10 feeble; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum with 3-4 fine scales, microsculpture granulose; middle 0.33 of metepisternum with about 1 irregular row of scales mesally, microsculpture granulose; sides of metasternum moderately densely squamose except for granulose margin. Abdomen with sternum 1 flattened mesally, densely squamose mesally but sparsely so laterally, scales slender and subrecumbent, no apical marginal band of scales; sterna 2-4 with scales slender and subrecumbent except laterally where broad and recumbent, sterna 3-4 each uniformly densely punctate. Legs densely squamose, ventral pads of tarsi tan. Male genitalia with phallus (Fig. 40) short and broad, apex truncate; endophallus without conspicuous spicules.

Measurements, holotype male: length, LE, 8.6 mm + LP, 2.9 mm = 11.5 mm; WPmax = WPbase, 3.2 mm; WE, 5.2 mm; LR, 0.64 mm + 1.22 mm = 1.86 mm; WRmin, 0.71 mm; WRmax, 0.96 mm; WFmin, 0.82 mm; WFmax, 1.84 mm; LA, 1.11 mm + 1.33 mm + 0.53 mm = 2.97 mm.

Material examined. – I examined only the holotype, from an unspecified locality in Brazil.

Etymological note. – This species is dedicated to Carl Fiedler, in recognition of his studies of cryptorhynch weevils.

Natural history. – No data are available, but I assume this species attacks *Hymenaea courbaril* as does *R. transversalis,* and that its feeding behavior is similar.

Geographic relationships. – Whether or not this species is sympatric with other members of the *transversalis* group is unknown.

Phylogenetic relationships. – I regard *R. fiedleri* as sister to the common ancestor of the other members of the *transversalis* group, plesiotypic in having punctures in front of the frontal fovea but apotypic in having visible sterna 3-4 more completely punctate.

2. *Rhinochenus klagesi* Whitehead, new species

Type-material. – Holotype: male labelled "Santarem. July, 1919. S. M. Klages. Acc. 6324.". Type-locality: Santarem, Para, Brazil. Type-depository: CMPP. Allotype: female, same label data as holotype (CMPP). Paratypes: 9 specimens with same label data as holotype (CMPP, USNM).

Diagnostic combination. – Specimens of this species are distinguished from other members of the *transversalis* group by having the pronotum distinctly wider at middle than at base.

Description. – Length, pronotum + elytron, 10.0 - 11.1 mm. Vestiture squamose, light tan, scales of pronotum and elytral macula orange. Head densely squamose from behind basal 0.25 of rostrum laterally and from frontal fovea dorsally, area immediately in front of frontal fovea bare or nearly so. Rostrum with fine carina in basal 0.50, impunctate along midline near carina, elsewhere finely and nearly uniformly punctate; microsculpture with meshes longitudinally stretched, flattened, obsolete near carina. Pronotum (Fig. 12) wider at middle than at base, disc with slight median elevation; punctures coarse, dense, near middle of disc separated by average distances equal to about 0.50 diameters of each; punctures each with conspicuous orange scale except for broad pale scales in anterior and posterior ventropleural corners and in divided prescutellar spot; microsculpture granulose. Elytron (Fig. 12) with lateral macula large, transverse, rectangular, regular, extended to about middle of sutural interval, not or faintly rimmed; scutellar area of orange scales absent or small; strial punctures each with slightly enlarged scale, punctures not surrounded by glabrous spots, inconspicuous in apical 0.33, at basal 0.33 much narrower than interval 5; interval 10 in middle 0.33 narrow, convex, stria 10 feeble; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum bare or sparsely squamose, microsculpture granulose; middle 0.33 of metepisternum with about 1 - 2 irregular rows of scales mesally, microsculpture flattened and longitudinally stretched; sides of metasternum moderately densely squamose except along margin where microsculpture flattened. Abdomen with sternum 1 flattened mesally in male, convex in female, densely squamose mesally but sparsely so laterally, scales slender and subrecumbent, no apical marginal band of scales; sterna 2 - 4 with scales slender and subrecumbent except laterally where broad and recumbent, sterna 3 - 4 each with transverse band of 1 - 2 rows of punctures. Legs densely squamose, ventral pads of tarsi tan. Male genitalia with phallus (Fig. 41) relatively slender, parallel-sided, apex (Fig. 48) truncate; endophallus without conspicuous spicules. Female genitalia with spermatheca (Fig. 86); eighth sternite (Fig. 80) with apical setae less dense than in related species.

Measurements, holotype male: length, LE, 7.5 mm + LP, 2.4 mm = 9.9 mm; WPmax, 2.7 mm; WPbase, 2.6 mm; WE, 4.3 mm; LR, 0.38 mm + 0.91 mm = 1.29 mm; WRmin, 0.71 mm; WRmax, 0.84 mm; WFmin, 0.80 mm; WFmax, 1.69 mm; LA, 0.82 mm + 1.11 mm + 0.44 mm = 2.37 mm.

Material examined. – I examined 11 specimens from the type-locality (Fig. 137).

BRAZIL. Para: Santarem (11; CMPP, USNM).

Etymological note. – This species is dedicated to S. M. Klages, collector of the type-series of this species and large quantities of other South American beetles.

Natural history. – Specimens of *R. pseudostigma, R. stigma,* and *R. cinereopunctatus* bear the same label data as does the holotype of *R. klagesi*, hence all 4 species probably were found in association with fruits of *Hymenaea courbaril.* Santarem specimens of *R. pseudostigma* almost exactly match those of *R. klagesi* in external appearance, thereby suggesting the existence of a mimetic complex; see discussion of *R. pseudostigma.*

Geographic relationships. – Among members of the *transversalis* group, *R. klagesi* is sympatric with at least *R. maculipes,* and among other *Rhinochenus* with at least *R. brevicollis, R. pseudostigma, R. stigma,* and *R. cinereopunctatus.* In terms of postulated Pleistocene refugia, relationships are unclear because Santarem, the only known locality, is intermediate between the Guyana and Madeira-Tapajoz refugia and is represented by elements of both.

Phylogenetic relationships. – This species is plesiotypic in pronotal form and therefore is regarded as sister to the common ancestor of *R. transversalis* and *R. maculipes* with which it shares the synapotypic condition of reduced punctation in front of the frontal fovea. The limited available distributional data preclude a definite statement that this form is a distinct species; it could be conspecific with *R. fiedleri, R. transversalis,* or both. It is distinguished, however, by numerous details, is more modest in body size than is normal for other members of the group, and if not sympatric is probably at least sufficiently proximal in distribution as to make genetic continuity unlikely in face of the differences.

3. *Rhinochenus maculipes* Whitehead, new species

Type-material. – Holotype: female labelled "Cent. Brazil. Chapada. 2600. ft. Nov. 1902. A. Robert. 1903-96.". Type locality: Chapada dos Guimarães, Mato Grosso, Brazil. Type-depository: BMNH. Allotype: male labelled "Chapada Brazil Acc. No. 2966" and "Sept." (CMPP). Paratypes: female labelled "maculipes mihi Dup", etc. (BMNH); male with same label data as allotype except "Oct." (USNM); and female from Santarem, Para, Brazil (CMPP).

Diagnostic combination. – Specimens of this species are distinguished from other members of the *transversalis* group by having glabrous strial punctures and by having variegated femora and elytra.

Description. – Length, pronotum + elytron, 13.2 - 13.9 mm. Vestiture squamose, scales mostly small, pale yellow, elytra and femora variegated with dark gray scales. Head densely squamose from behind anterior eye margin laterally and from behind frontal fovea dorsally, rostrum without conspicuous scales except at extreme base. Rostrum with fine median carina in basal 0.50, impunctate on carina and in small area along and in front of apical 0.50 of carina, elsewhere finely and nearly uniformly punctate; microsculpture with meshes strongly stretched longitudinally, flattened or obsolete near carina. Pronotum (Fig. 13) conical, widest at base; disc with slight median elevation; punctures coarse and dense, near middle of disc separated by average distances equal to about 0.50 diameters of each; punctures each with small, conspicuous or inconspicuous scale except for broad scales in complete ventropleural band and few broad scales along midline and in paralateral longitudinal stripes; microsculpture evident but flattened, surface shiny. Elytron (Fig. 13) conspicuously glabrous around strial punctures and nearly glabrous in middle 0.33 of intervals 9 - 10, without definite lateral macula or bare scutellar area; vestiture pale yellow except for longitudinally arranged dark gray variegation; holotype with broad gray scales on most of sutural interval, small spot near basal 0.17 of interval 2, small spot near base of interval 3, short stripe near base and on middle 0.33 of interval 4, short stripe near basal 0.40 of interval 5, spots near apical 0.33 and basal 0.33 of interval 6, and spots near apical 0.33 and middle of interval 7; strial punctures with scales fine, inconspicuous; punctures coarse and deep, conspicuous throughout; interval 10 in middle 0.33 narrow, vaguely defined; microsculpture flattened. Venter of thorax densely squamose; lateral processes of mesosternum with few scales, longitudinally microsculptured; middle 0.33 of metepisternum with about 1 - 2 irregular rows of scales mesally, polished; sides of metasternum moderately densely squamose except for polished margin. Abdomen with visible sternum 1 of female convex mesally and moderately squamose, in male concave mesally and with dense erect setiform scales, no apical marginal band of scales, in lateral 0.33 with scales less dense and surface shinier; sterna 2 - 4 with scales narrow and moderately dense except laterally where slightly or much broader, sterna 3 - 4 each with transverse band of about 2 -3 rows of punctures. Legs densely squamose except femora with much of anterior and posterior faces sparsely squamose and with mixture of dark and pale scales, ventral pads of tarsi pale yellow. Male genitalia with phallus (Fig. 42) swollen at middle, apex (Fig. 46) and endophallus as in *R. transversalis.* Female genitalia with spermatheca (Fig. 87) and eighth sternite (Fig. 81) similar to those of *R. transversalis.*

Measurements, holotype female: length, LE, 10.4 mm +LP, 3.5 mm = 13.9 mm; WPmax = WPbase, 3.8 mm; WE, 5.9 mm; LR, 0.80 mm + 1.51 mm = 2.31.mm; WRmin, 0.80 mm; WRmax, 1.02 mm; WFmin, 0.98 mm; WFmax, 2.13 mm; LA, 1.42 mm + 1.77 mm + 0.62 mm = 3.81 mm.

Variation. – In a female paratype, scales in the gray maculated areas of the elytra are relatively minute. In some specimens the maculated areas are more extensive, with several small spots on interval 2, apical spots on intervals 4 and 5, and complete lateral macula on intervals 4-8 which is indefinite in outline, formed of stripes of gray maculation on each interval rather than a discrete area.

Material examined. – I examined 5 specimens from central and northern Brazil (Fig. 137).

BRAZIL (1; BMNH). Mato Grosso: Chapada dos Guimarães (3, BMNH, CMPP, USNM). Para: Santarem (1; CMPP).

Etymological note. – The holotype was placed under the manuscript name "*R. maculipes*" in the British Museum, and I here validate that name.

Natural history. – The holotype specimen was among a uniformly labelled series including *R. chevrolati, R. cinereopunctatus,* and *R. stigma;* none of these specimens bore natural history data, but both *R. cinereopunctatus* and *R. stigma* are known to attack *Hymenaea courbaril,* and I conclude by inference that *R. maculipes* does also. Phylogenetic relationships suggest that it is likely to be behaviorly similar to *R. transversalis.* The elytral maculation, however, suggests otherwise; the disrupted pattern is unlike that of other *Rhinochenus* but may, like the mottled pattern of some forms of *R. stigma,* be cryptic in resembling discolored pulp, suggesting that larval or adult *R. maculipes* may in some way cause pulp discoloration. Thus, comparisons of the natural histories of *R. maculipes* and *R. transversalis* are needed.

Geographic relationships. – *Rhinochenus maculipes* is known to be sympatric with several other *Rhinochenus* species including at least one other member of the *transversalis* group, *R. klagesi.* Available distributional data suggest that it is a component of the Madeira-Tapajoz Pleistocene refugium.

Phylogenetic relationships. – This species differs greatly from *R. transversalis* in vestiture pattern but is morphologically similar and perhaps geographically proximal but allopatric. I regard *R. maculipes* and *R. transversalis* as sister species.

4. *Rhinochenus transversalis* Chevrolat

Rhinochenus transversalis Chevrolat 1871: 91; Fiedler 1951: 1108. Lectotype: here designated, male labelled "p 91 Çay.", "TYPUS", "Rhinochenus transversalis Chev", etc. Type-locality: "Cayenna", here restricted to Kourou-Tonate rd. 1 km E jct. of Kourou and coastal roads, Cayenne. Type-depository: RMSS.

Rhinochenus bahiensis Chevrolat 1871: 92; Fiedler 1951: 1107. Holotype: male labelled "Bahiensis Chev. Bahia Type", "Museum Paris ex. Coll. Oberthur", "HOLOTYPE", etc. Type-locality: Bahia, Bahia, Brazil; this locality is far south of other reported localities and may represent an incorrect original citation. Type-depository: MNHP. NEW SYNONYMY.

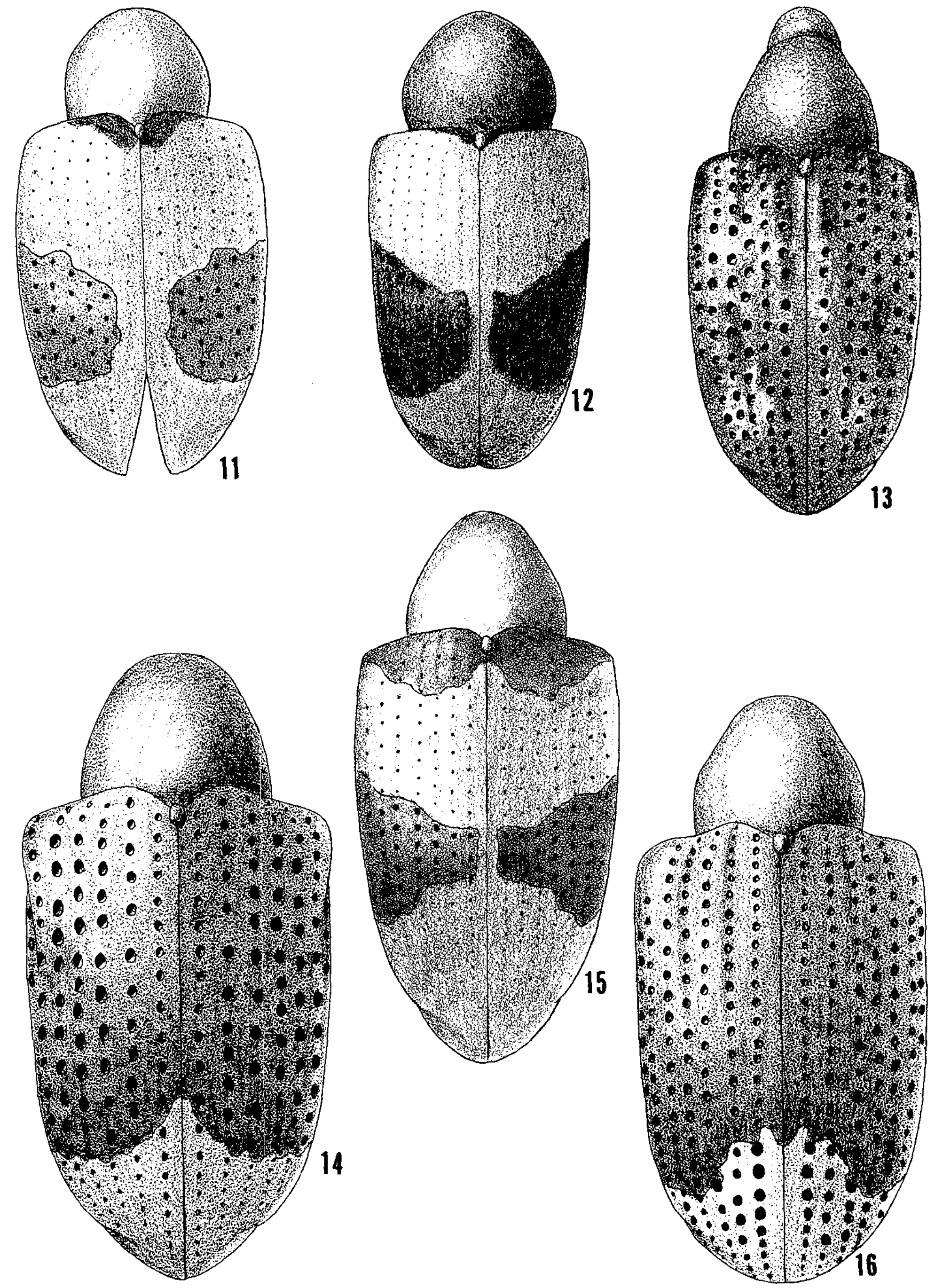

Fig. 11-16. *Rhinochenus* spp., habitus: 11, *R. fiedleri;* 12, *R. klagesi;* 13, *R. maculipes;* 14, *R. chevrolati;* 15, *R. amapensis;* 16, *R. reichei.*

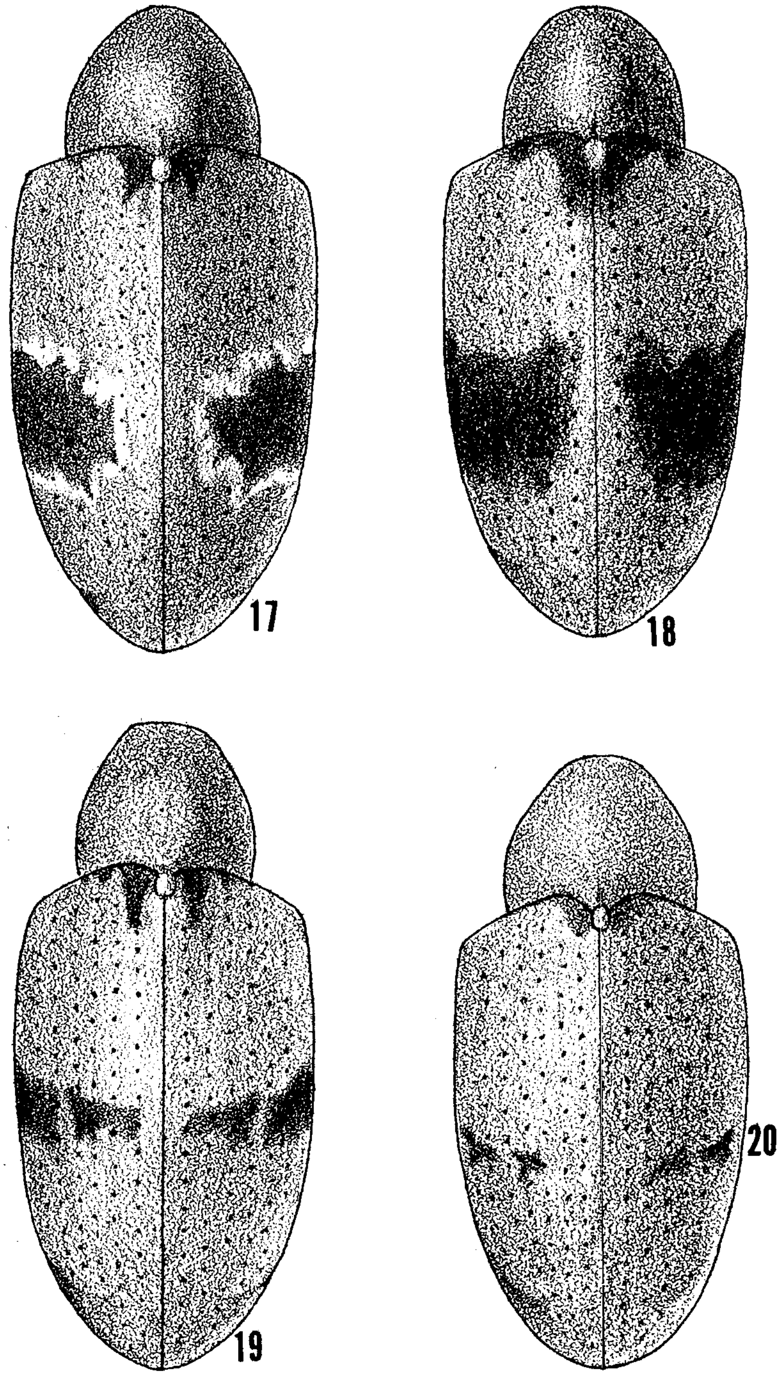

Fig. 17-20. *Rhinochenus transversalis*, chromatic variation: 17, Bagaces, Costa Rica; 18, Osa Peninsula, Costa Rica; 19, Trinidad; 20, Kourou, Cayenne.

Rhinochenus innotatus Chevrolat 1871: 92; Fiedler 1951: 1108 (placed in synonymy with *R. bahiensis*). Lectotype: here designated, male labelled "420" (pink). "TYPUS", "Rhinochenus innotatus Chev.", etc. Type locality: "Colombia". Type-depository: RMSS. NEW SYNONYMY.

Taxonomic notes. – The name *R. transversalis* has page priority over *R. bahiensis* and *R. innotatus.* In addition to lectotypes for *R. transversalis* and *R. innotatus,* the Riksmuseum has a paratype male of *R. bahiensis* labelled "fulvicollis", "Jekel 13" (pink), "TYPUS", "Rhinochenus Bahiensis Ch Var Bahia", " = innotatus Chevr. (Fiedler)", etc.; this specimen represents Chevrolat's variety γ.

Champion (1905) treated this species as *R. stigma,* varieties β and γ; these varieties are infrapopulational variations found within samples from Guanacaste and San Jose, Costa Rica. Similarly, Chevrolat's (1871) varieties α, β, and γ of *R. bahiensis* are infrapopulational variations found within the Kourou sample of *R. transversalis* listed below.

Diagnostic combination. – Among members of the *transversalis* group, specimens of *R. transversalis* are distinguished from specimens of *R. maculipes* by lacking conspicuous glabrous areas around the strial punctures, from specimens of *R. fiedleri* by lacking punctures and scales in front.of the frontal fovea, and from *R. klagesi* by the conical pronotum.

Description. – Length, pronotum + elytron, 11.8 - 14.9 mm. Vestiture squamose, light tan to ochraceous, concolorous except in some specimens with minute dark scales in bare areas of elytron. Head densely squamose from behind base of rostrum laterally and from behind frontal fovea dorsally, rostrum without conspicuous scales except at extreme base. Rostrum (Fig. 2) and pronotum (Fig. 1) as in *R. maculipes.* Elytron (Fig. 17-20) with pattern varied: disc nearly uniformly ochraceous. with 1-3 small spots near middle, with complete or nearly complete transverse band at middle, or with large irregular lateral spot; in most specimens intervals 9-10 bare at middle, in some specimens humeral region bare; scuteller region bare or nearly bare in some specimens; discal macula with scales varied from sparse, fine, and slender to barely differentiated from scales elsewhere on disc, with or without rim of enlarged scales; strial punctures each with slightly to conspicuously enlarged scale, punctures not surrounded by glabrous spots, inconspicuous in apical 0.33; interval 10 in middle 0.33 feebly defined, not carinate; microsculpture flattened, surface shiny. Venter of thorax (Fig. 10) densely squamose, scales slender mesally and broad laterally; lateral processes of mesosternum with few scattered scales to densely squamose, microsculpture longitudinally arranged; middle 0.33 of metepisternum with punctations increasingly dense toward apex, not arranged in longitudinal rows; sides of metasternum densely squamose except at margins where bare or with few scales and with microsculpture flattened but evident in most specimens. Abdomen (Fig. 6, 10) with sternum 1 convex mesally in female and with scales recumbent and slightly narrower than laterally, in male concave and with scales hairlike and erect, no posterior marginal scales; sterna 2-4 with outer scales dense and broad, inner scales slender and suberect, sterna 3-4 each with transverse band of about 3-4 rows of punctures. Legs densely squamose, ventral pads of tarsi orange. Male genitalia with phallus (Fig. 43) short and broad, apex (Fig. 47) broadly truncate; endophallus without conspicuous spicules. Female genitalia with spermatheca (Fig. 88); eighth sternite (Fig. 82-84) slender, base slender, apical setae normally dense.

Measurements, male from Villa Colon, Costa Rica: length, LE, 9.9 mm + LP, 3.1 mm = 13.0 mm; WPmax = WPbase, 3.7 mm; WE, 5.5 mm; LR, 0.76 mm + 1.29 mm = 2.05 mm; WRmin, 0.76 mm; WRmax, 0.96 mm; WFmin, 0.84 mm; WFmax, 1.80 mm; LA, 1.11 mm + 1.35 mm + 0.58 mm = 3.04 mm.

Measurements, male from Kourou, Cayenne: length, LE, 9.1 mm + LP, 3.1 mm = 12.2 mm; WPmax = WPbase, 3.4 mm; WE, 5.5 mm; LR, 0.64 mm + 1.24 mm = 1.88 mm; WRmin, 0.76 mm; WRmax, 0.93 mm; WFmin, 0.84 mm; WFmax, 2.00 mm; LA, 1.16 mm + 1.38 mm + 0.49 mm = 3.03 mm.

Variation. – One female from 9 mi. E Esparta, Costa Rica (USNM) is aberrant in having the dorsal punctation notably sparse and irregular, vestiture sparse, and apex of eighth sternite (Fig. 84) sparsely setose. Another female from Bagaces, Costa Rica (USNM) is a dwarf, measuring 8.6 mm in length in contrast to the normal 11.8-14.9 mm.

In central and western Costa Rica, most specimens have an irregular elytral spot extending from near the lateral margin to somewhere between striae 1 and 3, and the spot has moderately dense, wide scales and a pale border; interval 2 from its base to slightly behind the scutellum has sparse, fine scales; and the pronotal scales are large. Most specimens from Panama are similar except that the scutellar area is not differentiated. One specimen from the Osa Peninsula in southeastern Costa Rica has the elytral spot greatly enlarged, without the pale border, and with notably fine, sparse, short, hairlike scales; interval 2 is nearly bare half way to spot; and the pronotal scales are fine. In one specimen from Venezuela, the elytral spot is small and distant from the lateral margin, has a pale border, and has sparse, fine scales; interval 2 is nearly bare half way to spot; and the pronotal scales are fine. Most specimens from Trinidad and Guyana have the spot developed as a broken or complete transverse band, no pale margin, scales sparse, fine, and slender; interval 2 is nearly glabrous from base to about 0.33 distance to band; and the pronotal scales are slender. Specimens from Brazil and Cayenne have the elytra nearly uniformly squamose, with or without 1-3 minute spots in area of band, no pale margins, and the scales of the scutellar region are not or only slightly reduced; and the pronotal scales are fine. See Fig. 17-20.

Material examined. – I examined more than 396 specimens of *R. transversalis,* from Honduras southward through Central America and across northern South America to Brazil (Fig. 137).

HONDURAS. Comayagua: 6 km. N Comayagua. NICARAGUA. Chontales. COSTA RICA. Alajuela: 3.5 mi. W. Rio Prendas, nr. Alajuela. Cartago: Turrialba. Guanacaste: Bagaces; Comelco, Bagaces; 4-5 mi. N. Bagaces; Cañas; La Pacifica, Cañas; 2-4 mi. E Cañas; 8 mi. N Cañas. Puntarenas: 9 mi. E Esparta; Monteverde road, 10 mi. N 24th de Noviembre; Rincon, Osa Peninsula. San Jose: Escazu; Sabanilla; San Jose; Villa Colon. PANAMA. Cocle: Rio Hato. VENEZUELA . Barinas: Campo Alegre.TRINIDAD. Port of Spain; St. Augustine. GUYANA. Bartica District: Kartabo. CAYENNE. Kourou-Tonate road; Roches de Kourou. BRAZIL. Bahia: Bahia (?).

Natural history. – So far as known, larvae of *R. transversalis* develop exclusively in fruits of *Hymenaea courbaril,* and adults have been taken in association with these fruits from October through April. According to D. H. Janzen (pers. comm.), one larva develops in each fruit. The larva eats a portion of each of the several seeds in the pod, and in so doing will kill any other larvae of *Rhinochenus* present. Janzen names this species the "holedriller", since the adult is capable of escaping through an exit hole drilled through the thick pod wall by the larva before pupation. In Costa Rica, this species is relatively rare in undisturbed forest but in disturbed areas tends to replace *R. stigma* because of its lack of dependence on external agents for emergence from the pod. Specimens are rarely collected except in association with the host fruits.

In Central America, the elytral pattern of *R. transversalis* is distinctive from those of other species. However, in northern South America, where the pattern is reduced to a narrow transverse band or row of spots or is evanescent, the patterns of the distantly related *R. transversalis* and *R. caucensis* are strikingly similar (cf. Fig. 19-20, 23-24). These species are not known to be syntopic, but as this type of maculation is not repeated elsewhere in the range of *Rhinochenus* I suspect that *R. caucensis* and *R. transversalis* may form part of a mimetic complex. Elsewhere in South America, the elytral macula of *R. cinereopunctatus* also tends to be evanescent, but through decreased differentiation of scale size rather than through reduction in size of macula.

Geographic relationships. – *Rhinochenus transversalis* may be allopatric to other members of the *transversalis* group; Brazilian records need confirmation and clarification (I think the supposed type-locality of *R. bahiensis* is in error, but have seen various specimens labelled "Brazil"). Throughout its range it occurs in the same fruit crops with *R. stigma*; in southeastern Costa Rica and western Panama with *R. janzeni*; and in Trinidad and Cayenne with at least *R. x-rubra.* Pleistocene refugial relationships are unclear because of the wide geographic distribution, but it seems likely from a consideration of geographic variation that several refugia were occupied. The Central American form probably is associated with a refugium or refugia in the area surrounding the Costa Rica-Chiriqui highlands; specimens from Venezuela, Trinidad, and Guyana, which tend to have the narrow, transverse elytral fascia, may be associated with one or more of the refugia of northwestern South American drainage systems; and specimens from Cayenne and "Brazil", with the elytral macula greatly reduced or vestigial, probably derive from the Guyana refugium.

Phylogenetic relationships. – I regard *R. transversalis* as the sister species of *R. maculipes.* These 2 forms could be geographic variations of one species, but the differences between them are so much greater than is the known variation within *R. transversalis* that I treat them as reproductive isolates.

THE *hercules* GROUP

Included species. – *R. amapensis* n. sp. and *R. hercules* Chevrolat.

Diagnostic combination. – Adults of this group are distinguished from other *Rhinochenus* by the combination of lacking erect scales in the metasternal sulcus, having the antennal insertion behind the anterior 0.33 of the rostrum, and having a complete anterior band of dense elytral vestiture; male genitalia not known; female genitalia with eighth sternite broad, stem proportionately short and with broad base, and with dense fringe of apical setae.

Description. – Size large for genus. Integument rufous above, rufopiceous below. Head with vestiture along midline in front of frontal fovea, densely squamose behind fovea; antenna inserted behind anterior 0.33 of rostrum, LRapex/LRbase 0.67 - 0.69 in female, WRmin/WRmax 0.71 - 0.74, WRmin/LR 0.34 - 0.38, LR/LA 0.65 - 0.67, LR/LP 0.65 - 0.67; second funicular segment about 0.50 as wide as long and about as long as first funicular segment; interocular ratio 0.41 - 0.46. Prothorax conical, widest at base, 0.89 - 0.94 as long as wide; punctures near middle of disc separated by average distances nearly twice diameters of each. Scutellum ovate, about 0.7 as wide as long. Elytron with strial punctures coarse, at anterior 0.33 as wide or wider than interval 5, in posterior 0.33 inconspicuous and not surrounded by glabrous areas; intervals flat, uniform in width; WE/LE 0.61 - 0.66. Lateral processes of mesosternum not or sparsely squamose. Ventral sulcus of metasternum without erect scales in apical 0.50. Distal comb of tibia black. Female eighth sternite broad, stem short and with broad base, apex with dense fringe of setae, hyaline area acuminate basally. Male genitalia and secondary sex characters not known.

Natural history. – Whether conspecific, or reproductive isolates as treated here, these 2 forms probably are biological equivalents and may be behaviorly similar to members of the *reichei* group. The host plant is unknown, probably *Hymenaea courbaril.*

Geographic relationships. – The included species so far as known are allopatric, closely related, and perhaps not reproductively isolated from each other. The aggregate range is across northern South America north of the Amazon, from Colombia to northeastern Brazil, in contrast to the more southern distributions of members of the *reichei* group.

Phylogenetic relationships. – The *hercules* group is clearly monophyletic, defined by the synapotypic placement of the antennal insertion well behind the anterior 0.33 of the rostrum. It probably is sister to the *reichei* group as suggested by the large body size characteristic of members of both groups and by possession of numerous symplesiotypic characteristics, but I have not discovered any definitive synapotypic characteristics to define the *hercules-reichei* lineage. Differences between the groups are relatively minor in an evolutionary sense but are sufficiently conspicuous to merit emphasis by placement in separate groups. Perhaps the bare elytral base in members of the *hercules* group reflects a general trend toward loss of elytral vestiture as in the *reichei* group.

5. *Rhinochenus amapensis* Whitehead, new species

Type-material. – Holotype: female labelled "Colecao J. Lane" and "SERRA do NAVIO Terr. Amapa BRAZIL 25 IX - 1957 J. Lane leg.". Type-locality: Serra do Navio, Amapa, Brazil. Type depository: MZSP. Paratypes: 2 females from Cayenne (MNHP).

Diagnostic combination. – In having the antennal insertion near the apical 0.40 of the rostrum, lacking erect scales in the metasternal sulcus, and having the anterior elytral band of vestiture complete, specimens of this species resemble only those of *R. hercules* from which they differ by being much smaller and by having the wide basal glabrous band of the elytra complete to lateral margins.

Description of female. – Length, pronotum + elytron, 15.1 - 15.6 mm. Vestiture squamose, light tan, concolorous. Head densely squamose from behind middle of rostrum laterally and from near base of rostrum dorsally. Rostrum with fine median carina in basal 0.50, elsewhere nearly uniformly punctate; surface dull from longitudinally oriented microsculpture. Pronotum (Fig. 15) widest at base, disc without pronounced median elevation; punctures fine and sparse; punctures with broad scales in complete ventropleural band, prescutellar spot, and paramedian basal spots, scales otherwise small and slender; microsculpture granulose. Elytron (Fig. 15) with lateral macula transverse, extended at least to middle of interval 1 or to suture, jagged in outline, without conspicuous rim; base of elytron with complete, wide, transverse glabrous band from lateral margin to suture;

strial punctures each with broad scale; interval 10 in middle 0.33 narrow, flat, stria 10 feeble; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum bare, microsculpture granulose; middle 0.33 of metepisternum densely squamose, microsculpture granulose; sides of metasternum densely squamose except for granulose margin. Abdomen with sternum 1 convex or slightly flattened and with slender recumbent scales mesally, scales elsewhere broad; sterna 2-4 with scales broad and dense laterally, elsewhere slender and sparse, sterna 3-4 each with transverse band of about 1-3 rows of punctures; sternum 5 flattened apically, densely squamose, scales most dense lateroapically, broad laterally but elsewhere slender. Legs densely squamose, ventral pads of tarsi tan. Female genitalia with spermatheca (Fig. 98) proportionately large; eighth sternite (Fig. 95) broad, base broad, apical setae dense.

Measurements, holotype female: length, LE, 11.2 mm + LP, 3.8 mm = 15.0 mm; WPmax = WPbase, 4.2 mm; WE, 7.2 mm; LR, 1.02 mm + 1.47 mm = 2.49 mm; WRmin, 0.96 mm; WRmax, 1.29 mm; WFmin, 1.13 mm; WFmax, 2.51 mm; LA, 1.42 mm + 1.77 mm + 0.62 mm = 3.81 mm.

Material examined. – I examined 3 female specimens from Cayenne and northeastern Brazil (Fig. 138).

BRAZIL. Amapa: Serra do Navio (1; MZSP). CAYENNE. St. Jean du Maroni (1; MNHP); St. Laurent du Maroni (1; MNHP).

Etymological note. – This species is named for the type-locality, Territory of Amapa, Brazil.

Natural history. – No data are available, but specimens of *R. pseudostigma* and *R. x-rubra* from St. Jean du Maroni were collected in association with fruits of *Hymenaea courbaril.* However, label data are not identical and specimens evidently were collected over a period of some years so no direct inference may be drawn, but there is no reason to suggest that the host is other than *H. courbaril.*

Geographic relationships. – Several other species have been found within the probable range of *R. amapensis*; at least *R. pseudostigma* and *R. x-rubra* occur in the same Cayenne localities, and at least *R. stigma* in the Amapa locality. *Rhinochenus amapensis* is not known or suspected to be sympatric with the other member of the *hercules* group, *R. hercules.* Known localities correlate well with environs of the postulated Guyana Pleistocene forest refugium.

Phylogenetic relationships. – *Rhinochenus amapensis* and *R. hercules* are sister species. They obviously are closely related and perhaps even conspecific, but among the few specimens available of each the numerous differences are constant.

6. *Rhinochenus hercules* Chevrolat

Rhinochenus hercules Chevrolat 1871: 86; Fiedler 1951: 1107. Holotype: female (?) labelled "Colombia Coll. Jek", "typus 1871", "Hercules (Jekel) Chevr.", "R. hercules Chevrol. typus!". Type-locality: "Colombia". Type-depository: Societa Entomologica Italiana, Genova.

Taxonomic notes. – The holotype was examined by C. W. O'Brien, and compared with material described herein: slightly smaller, rostrum without distinct carina, and venter with vestiture more dense. Chevrolat (1871) described the elytral maculae as joined at suture; in O'Brien's notes, they do not meet on suture but appear to do so under low magnification because the surfaces are somewhat abraded.

Diagnostic combination. – Specimens of this species are readily distinguished by their combination of large size, lack of erect scales in metasternal sulcus, insertion of antenna near apical 0.40 of rostrum, anterior elytral vestiture band complete, and basal glabrous band of elytra not extended to side margins.

Description. – As in *R. amapensis* except as follows. Length, pronotum + elytron, 18.0 - 18.6 mm. Elytral intervals 6, 9, 10 squamose basally, basal glabrous band thus incomplete. Lateral processes of mesosternum with few, scattered scales, microsculpture flattened and longitudinally stretched. Microsculpture of metepisternum flattened, inconspicuous, longitudinally stretched. Female genitalia with spermatheca (Fig. 97) proportionately smaller than in *R. amapensis*; eighth sternite (Fig. 94).

Measurements, female from Colombia: length, LE, 13.8 mm + LP, 4.8 mm = 18.6 mm; WPmax = WPbase, 5.2 mm; WE, 9.2 mm; LR, 1.29 mm + 1.91 mm = 3.20 mm; WRmin, 1.09 mm; WRmax, 1.53 mm; WFmin, 1.27 mm; WFmax, 3.11 mm; LA, 1.73 mm + 2.40 mm + 0.67 mm = 4.80 mm.

Material examined. – I examined 2 female specimens with imprecise label data, probably both from Colombia (Fig. 138).

No locality (1; USNM). COLOMBIA (1; BMNH).

Natural history. –No data are available, but the host plant presumably is *Hymenaea courbaril.*

Geographic relationships. – As no precise localities are known, no precise comparisons may be made concerning sympatric species or putative refugial relationships. The only other member of the *hercules* group, *R. amapensis*, is evidently allopatric.

Phylogenetic relationships. – *Rhinochenus hercules* and *R. amapensis* are either sister species or geographic forms of the same species.

THE *reichei* GROUP

Included species. – *R. chevrolati* n. sp. and *R. reichei* (Boheman).

Diagnostic combination. – Adults of this group are distinguished from other *Rhinochenus* by the combination of lacking erect scales in the metasternal sulcus, having the antennal insertion behind the anterior 0.33 of the rostrum, and having the anterior band of dense elytral vestiture reduced to at most a small sutural shield or absent; male genitalia with phallus swollen at middle, apex narrowly rounded and lipped, endophallus with basal field of large spines; and female genitalia as described for *hercules* group.

Description. – Size large for genus. Integument rufous or castaneous above, rufopiceous below. Head either with vestiture along midline in front of frontal fovea and densely squamose behind fovea, or nearly completely glabrous except around eye and across base of rostrum; antenna inserted behind anterior 0.33 of rostrum, LRapex/LRbase 0.51 - 0.57, WRmin/WRmax 0.71 - 0.76, WRmin/LR 0.36 - 0.48, LR/LA 0.57 - 0.63, LR/LP 0.55 - 0.67; second funicular segment about 0.5 as wide as long and about as long as first funicular segment; interocular ratio 0.42 - 0.52. Prothorax conical, widest at base, 0.88 - 0.92 as long as wide; punctures near middle of disc separated by average distances of 0.50 to 1.50 times diameters of each. Scutellum ovate, about 0.6 - 0.8 as wide as long. Elytron with strial punctures coarse, at anterior 0.33 wider than interval 5, in posterior 0.33 conspicuous and surrounded by glabrous spots; intervals convex, costate, odd intervals slightly to conspicuously wider and more strongly raised than even intervals; WE/LE 0.60 - 0.62. Lateral processes of mesosternum bare. Ventral sulcus of metasternum without erect scales in apical 0.50. Sternum 5 feebly biconvex in male, feebly differentiated from female. Distal comb of tibia black. Male genitalia with phallus long, swollen at middle, narrowly rounded and lipped at apex; endophallus with basal field of large spines. Female eighth sternite broad, stem short and with broad base, apex with dense fringe of setae, hyaline area acuminate basally.

Natural history. – The host plant of *R. reichei* is known to be *Hymenaea courbaril.* It is probably the same for *R. chevrolati* since specimens were in a long series containing also *R. stigma* and *R. cinereopunctatus* which are known to attack *H. courbaril.* The natural histories of these species are probably similar but must be differentiated to some degree to allow sympatry to exist.

Geographic relationships. – The included species are partially sympatric and syntopic, and therefore certainly are reproductive isolates. The aggregate range may be restricted to southern Brazil south of the Amazon, though one specimen of *R. reichei* is labelled as from "Colombia". If indeed southern, then the *reichei* group is not sympatric with its sister lineage, the *hercules* group. The common ancestor of these groups probably was widespread in the Amazon Basin in pre-Pleistocene time, became fragmented into northern and southern isolates during an early dry phase of the Pleistocene, and subsequently was subdivided into existing components during a later dry phase.

Phylogenetic relationships. – The *reichei* group is clearly monophyletic, defined by the synapotypic reduction in anterior elytral vestiture and the alternately costate elytral intervals. It agrees with the *hercules* group in the possibly synapotypic large body size, and probably the *hercules* and *reichei* groups share a relatively recent common ancestry. If the components of this lineage are recent, however, the lineage itself is probably much older; it is sister to the lineage containing the monobasic *mangabeirensis* group and the much more diverse *stigma* group.

7. *Rhinochenus reichei* (Boheman)

Cryptorhynchus reichei Boheman 1844: 303. *Rhinochenus reichei*, Chevrolat 1871: 86; Fiedler 1951: 1106. Lectotype: here designated, male (?) labelled "TYPUS", "Dupont", "*Cr. Reichei* c Bahia. Mannerheim", "Rhinochenus Luc.", etc. Type-locality: Bahia, Bahia, Brazil. Type-depository: RMSS.

Diagnostic combination. – Members of *R. reichei* differ from all other *Rhinochenus* by having the frons and anterior surfaces of the femora largely glabrous rather than covered with uniformly dense vestiture.

Description. – Length, pronotum + elytron, 11.1 - 16.2 mm, normally over 14 mm. Vestiture squamose, nearly white, concolorous. Head with squamose vestiture limited to narrow, complete or incomplete band across frontal fovea and around eye. Rostrum with fine median carina in basal 0.50, nearly uniformly punctate; microsculpture flattened, meshes longitudinally stretched. Pronotum (Fig. 16) widest at base, disc without pronounced median elevation; punctation uneven, punctures near middle of disc relatively coarse and separated by average distances of 0.50 to 1.50 times diameter of each but laterally much finer and sparser; punctures with scales minute and setiform except for broad scales in anterior and posterior ventropleural corners, some specimens with few scales along base and midline; microsculpture obsolete. Elytron (Fig. 16) with squamose vestiture limited to apical 0.33 with each strial puncture surrounded by large glabrous spot, some specimens with small squamose spot between striae 1 and 2 near basal 0.25; strial punctures without conspicuous scales, coarse and deep, in most specimens as wide as or wider than alternate narrow intervals; intervals convex, subcostate, alternate odd-numbered intervals conspicuously wider and more raised than even-numbered intervals; interval 10 in middle 0.33 narrow, not carinate, microsculpture obsolete. Venter of thorax densely squamose mesally; lateral processes of mesosternum glabrous, longitudinally microsculptured; middle 0.33 of metepisternum with about 1-2 irregular rows of scales externally, polished internally; sides of metasternum bare, nearly or wholly impunctate, polished. Abdomen with sternum 1 slightly more convex mesally in female than in male, with or without partial apical band of scales, slightly opaque and with dense, fine, subrecumbent setiform scales mesally, polished and nearly impunctate laterally except along anterior and posterior margins; sternum 2 opaque mesally and polished laterally, setiform scales sparse mesally and nearly absent laterally, broad scales absent or present only in small area at hind angle; sterna 3-4 opaque, each with lateral 0.13 densely squamose and with transverse median band of about 2-3 rows of punctures; sternum 5 slightly concave mesally in male, lateral 0.33 of margin with dense broad scales, median 0.33 of margin with dense long scales, elsewhere densely punctate. Legs densely squamose except femora with anterior and posterior faces largely bare, ventral pads of tarsi orange. Male genitalia as in *R. chevrolati* except sclerotized margin narrower apically (Fig. 45), endophallus with spines proportionately smaller, slenderer, and more numerous. Female genitalia with spermatheca (Fig. 93); eighth sternite (Fig. 92) broad, base broad, sclerotization condensed apically, apical setae dense.

Measurements, male from Bahia, Brazil: length, LE, 12.1 mm + LP, 4.1 mm = 16.2 mm; WPmax = WPbase, 4.5 mm; WE, 7.5 mm; LR, 0.89 mm + 1.56 mm = 2.45 mm; WRmin, 1.02 mm; WRmax, 1.36 mm; WRmin, 1.16 mm; WFmax, 2.33 mm; LA, 1.47 mm + 1.87 mm + 0.53 mm = 3.87 mm.

Variation. – Specimens of this species are normally large, length 14-16 mm, but I have seen 1 dwarf female. A specimen from "Colombia" differs from Brazilian specimens by having a small patch of scales near the basal 0.50 of each elytron.

Material examined. – I examined 19 specimens from Colombia and Brazil (Fig. 138), but the Colombian record is probably the result of a labelling error.

COLOMBIA (1; MCZ). BRAZIL (1; USNM). Bahia: Bahia (= Salvador) (15; BMNH, IRSB, MNHP, RMSS, UPCB, USNM, including reared series from *Hymenaea courbaril*). Mato Grosso: Barra do Tapirape (1; CWOB); Chapada dos Guimarães (2; CMPP). Minas Gerais: Vicosa (1; USMN).

Natural history. – Adults have been collected in April and September, and a series was reared by G. Bondar from fruits of *Hymenaea courbaril* at Bahia. No behavioral data are available, but it is likely that the feeding behavior of this species and other members of the *hercules* and *reichei* groups is similar to that of *R. transversalis* as judged from phylogenetic relationships.

Geographic relationships. – Assuming that the Chapada record of *R. reichei* is correct, and there is no reason to assume otherwise, then this species is at least partially sympatric with its nearest relative, *R. chevrolati,* but probably not with members of the more distantly related *hercules* group. Several other species are sympatric with *R. reichei*: Bondar's reared series from Bahia included specimens of *R. stigma* and *R. cinereopunctatus* as well as *R. reichei,* and one undated Chapada series contained specimens of *R. brevicollis, R. maculipes, R. stigma, R. cinereopunctatus,* and *R. chevrolati* as well as *R. reichei.* Known locality records suggest recent dispersal from the Mato Grosso de Goias Pleistocene refugium and secondary contact with *R. chevrolati.*

Phylogenetic relationships. – This species and *R. chevrolati* are obvious sister species; differences between them are constant and conspicuous, yet sufficiently minor that only the known sympatry removes doubt that they are reproductive isolates.

8. *Rhinochenus chevrolati* Whitehead, new species

Type-material. – Holotype: male labelled "Cent. Brazil. Chapada. 2600. ft. Nov. 1902. A. Robert. 1903-96". Type-locality: Chapada dos Guimarães, Mato Grosso, Brazil. Type-depository: BMNH. Allotype: female, same label data as holotype (BMNH). Paratypes: 16 specimens, all from type-locality (BMNH, CMPP, USNM).

Diagnostic combination. – Members of *R. chevrolati* differ from all other *Rhinochenus* except *R. reichei* by the combination of conical pronotum, large strial punctures and narrow, convex intervals, and basal elytral vestiture limited to at most a small sutural shield. Members of *R. chevrolati* differ from those of *R. reichei* by having the frons, vertex, and femora uniformly densely squamose.

Description. – As in *R. reichei* except as follows. Length, pronotum + elytron, 16.5 - 17.8 mm. Head densely squamose behind anterior margin of eye and on lateral basal 0.33 of rostrum. Pronotum (Fig. 14) with punctures slightly coarser, near middle of disc separated by average distances equal to about 0.50 diameter of each, each with conspicuous slender scale rather than fine setae; microsculpture conspicuous and granulose dorsally, surface polished laterally; dense scales in complete band on ventropleural margin. Elytron (Fig. 14), vestiture in apical 0.33 more dense, strial punctures each surrounded by small glabrous spot; basal vestiture varied from absent to present in sutural shield extended laterad across interval 3; strial punctures with distinct scales; alternate odd-numbered intervals not or slightly wider and more raised than even-numbered intervals; microsculpture weak but evident. Venter of thorax more densely squamose, sides of metasternum with sparse, narrow scales; subrecumbent vestiture of abdominal sterna narrowly squamiform rather than setiform. Femora uniformly squamose. Male genitalia with phallus (Fig. 44) broad and swollen at middle, apex (Fig. 49) narrowly rounded, lipped, and with wide sclerotized margin; endophallus with large, broad spines, in dorsal aspect spine field dense and extended 0.50 way to apical orifice of phallus. Female genitalia with spermatheca (Fig. 92); eighth sternite (Fig. 90) with apical sclerotization broad and apical setae more dense than in *R. reichei.*

Measurements, holotype male: length; LE, 12.8 mm + LP, 4.2 mm = 17.0 mm; WPmax = WPbase, 4.8 mm; WE, 7.8 mm; LR, 0.84 mm + 1.47 mm = 2.31 mm; WRmin, 1.02 mm; WRmax, 1.38 mm; WFmin, 1.24 mm; WFmax, 2.40 mm; LA, 1.38 mm + 2.04 mm + 0.62 mm = 4.04 mm.

Variation. – The squamose vestiture on the basal 0.25 of the elytron ranges from absent through small spots near interval 2 to a complete sutural shield, as infrapopulational variation.

Material examined. – I examined only the 18 specimens in the type-series, from south-central Brazil (Fig. 138).
BRAZIL. Mato Grosso: Chapada dos Guimarães (18; BMNH, CMPP, USNM).

Etymological note. – I dedicate the name *R. chevrolati* to A. Chevrolat, for his contributions to knowledge of the genus.

Natural history. – I assume that *R. chevrolati* attacks fruits of *Hymenaea courbaril,* partly because the related *R. reichei* does and partly because in the BMNH series identical label data are associated with specimens of *R. stigma* and *R. cinereopunctatus* which are known to attack *H. courbaril.*

Geographic relationships. – Several other species are sympatric: one long series with uniform label data includes specimens of *R. maculipes, R. stigma,* and *R. cinereopunctatus* as well as *R. chevrolati*, and another long series contains specimens of all of these and also of *R. brevicollis* and *R. reichei.* The type-locality, Chapada, probably is most easily correlated with the Madeira-Tapajoz Pleistocene forest refugium.

Phylogenetic relationships. – This species and *R. reichei* clearly are sister species.

THE *mangabeirensis* GROUP

Included species. – *R. mangabeirensis* n. sp.

Diagnostic combination. – The single known representative of this group has the external characteristics of the *stigma* group but distinctive female genitalia: metasternal sulcus without erect scales, antenna inserted slightly in front of anterior 0.33 of rostrum, and elytral vestiture uniformly dense except in lateral macula; female genitalia with eighth sternite broad, stem proportionately short and with narrow base, apical margin with dense fringe of setae, and hyaline area broadly notched basally.

Description. – Size moderate for genus. Integument rufous above, slightly darker beneath. Head with vestiture along midline in front of frontal fovea, densely squamose behind fovea; antenna inserted slightly in front of anterior 0.33 of rostrum, LRapex/LRbase 0.45, WRmin/WRmax 0.78, WRmin/LR 0.51, LR/LA 0.57, LR/LP 0.49; second funicular segment about 0.7 as wide as long and about 0.7 as long as first funicular segment; interocular ratio 0.44. Prothorax subconical, widest near middle, about as long as wide; punctures near middle of disc coarse and dense, separated by average distances much less than diameters of each. Scutellum ovate, about 0.7 as wide as long. Elytron with strial punctures fine, at anterior 0.33 much narrower than interval 5, in posterior 0.33 inconspicuous and not surrounded by glabrous areas; intervals flat, uniform in width; WE/LE 0.63. Lateral processes of mesosternum glabrous. Ventral sulcus of metasternum without erect scales in apical 0.50. Distal comb of tibia black. Female eighth sternite broad, stem short and with narrow base, apex with dense fringe of setae, hyaline area broadly lobate basally. Male genitalia and secondary sex characters not known.

Natural history. – It is probable that *R. mangabeirensis,* like most other *Rhinochenus,* attacks fruits of *Hymenaea courbaril.* It may form an element of a mimetic complex involving several members of the *transversalis* and *stigma* groups, and in particular it closely resembles in external features the Santarem forms of *R. klagesi* and *R. pseudostigma.*

Geographic relationships. – No other *Rhinochenus* are known from the type-locality of *R. mangabeirensis.* However, this group probably is sympatric with at least the *transversalis, hercules,* and *stigma* groups.

Phylogenetic relationships. – I regard the *mangabeirensis* group as sister to the *stigma* group, distinguished by retention of plesiotypic features of the female genitalia. These two groups share the synapomorphous condition of antennal insertion distad of anterior 0.33 of rostrum, though the insertion is not as far forward in *R. mangabeirensis* as in most members of the *stigma* group. The ancestor of the *mangabeirensis-stigma* lineage probably was also characterized by having the relatively narrow pronotum, apparently secondarily broadened in certain members of the *stigma* group.

9. *Rhinochenus mangabeirensis* Whitehead, new species

Type-material. – Holotype: female labelled "Mangabeira MOCAJUBA PARA BRASIL XI-1952 Orlando Rego" and "Colecao M. Alvarenga", etc. Type-locality: Mangabeira, Mocajuba district, Para, Brazil. Type-depository: UPCB.

Diagnostic combination. – The only known specimen of this species is superficially similar to 4 other species known to occur in northern Brazil, but is very different in structure of the female eighth sternite from all of them. In addition, it differs from specimens of *R. klagesi* by lacking erect scales in the metasternal sulcus, from *R. stigma* by having small strial punctures, and from both *R. brevicollis* and *R. pseudostigma* by having a conspicuous impunctate area near the middle of the rostrum and a conspicuous row of apical marginal scales on sternum 1. It is notably similar to Santarem specimens of *R. klagesi* and *R. pseudostigma* in size and maculation, though the lateral elytral macula extends only to the middle of interval 2 rather than to the middle of interval 1.

Description of female. – Length, pronotum + elytron, 11.1 mm. Vestiture recumbent; scales stramineous, orange on pronotum and elytral macula, otherwise concolorous. Head densely squamose from behind middle of rostrum; rostrum without median carina but with median, flat, alutaceous area in postmedian 0.25, otherwise nearly uniformly densely punctate; microsculpture flattened, longitudinally stretched. Pronotum wider near middle than at base, disc with slight median elevation; punctures coarse and dense, near middle of disc separated by average distance much less than diameters of each; punctures with broad, pale scales in complete ventropleural band, scales elsewhere slender and dark. Elytron with large, transversely oval macula extended to middle of interval 2, macula without conspicuous rim; strial punctures each with slightly enlarged scale, not surrounded by glabrous spot, inconspicuous except in macula; interval 10 in middle 0.33 narrow, carinate; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous, with granulose microsculpture; middle 0.33 of metepisternum with irregular row of scales, microsculpture flattened. Abdomen with visible sternum 1 convex mesally, with conspicuous row of broad scales in middle 0.33 of apical margin, elsewhere scales mostly slender, closely spaced in middle 0.33, recumbent; sterna 2 - 4 with scales slender and recumbent except on lateral margins where broad and dense, sterna 3 - 4 each with transverse median band of about 2 rows of punctures; sternum 5 with scales slender and subrecumbent except along lateral margins where broad and recumbent, scales notably dense and setiform apically. Legs densely squamose, ventral pads of tarsi yellow. Female genitalia with spermatheca (Fig. 89); eighth sternite (Fig. 85) broad, with slender base and dense apical setae.

Measurements, holotype female: length, LE, 8.2 mm + LP, 2.9 mm = 11.1 mm; WPmax, 2.9 mm; WPbase, 2.8 mm; WE, 5.2 mm; LR, 0.44 mm + 0.98 mm = 1.42 mm; WRmin, 0.73 mm; WRmax, 0.93 mm; WFmin, 0.84 mm; WFmax, 1.91 mm; LA, 0.93 mm + 1.16 mm + 0.40 mm = 2.49 mm.

Material examined. – Only the holotype from northern Brazil (Fig. 140) was examined.

BRAZIL. Para: Mangabeira, Mocajuba district (1; UPCB).

Etymological note. – This species is named for the type-locality.

Natural history. – The host plant is not known, probably *Hymenaea courbaril*; *R. mangabeirensis* probably is part of a mimetic complex including also *R. klagesi* and *R. pseudostigma.*

Geographic relationships. – The type-locality of *R. mangabeirensis* corresponds approximately to the Belem refugium postulated for Amazonian lowlands during dry phases of the Pleistocene, and no other *Rhinochenus* are yet known from there. However, probably some members of the *transversalis, hercules,* and *stigma* groups occur in this region, and clearly at least *R. stigma* must occur there. Moreover, I assume that *R. mangabeirensis* is involved in a mimetic complex with at least *R. klagesi* and *R. pseudostigma* – each representing a different species group – and therefore predict that all 3 species are sympatric. Thus, *R. mangabeirensis* may really be an element of the Guyana refugium.

Phylogenetic relationships. – As the sole known representative of the *mangabeirensis* group *R. mangabeirensis* is regarded as sister to the stem species of the *stigma* group.

THE *stigma* GROUP

Included species. – *R. brevicollis* Chevrolat, *R. caucensis* n. sp., *R. cinereopunctatus* Chevrolat, *R. chorrensis* n. sp., *R. janzeni* n. sp., *R. pseudostigma* n. sp., *R. stigma* (Linnaeus), *R. thrombithorax* n. sp., and *R. x-rubra* Chevrolat.

Diagnostic combination. – Adults of this group are distinguished from other *Rhinochenus* by having in combination the lack of erect scales in the metasternal sulcus and the antenna inserted apicad of the anterior 0.33 of the rostrum; male genitalia various in form but with apex narrowly to broadly rounded, angulate and/or lipped or not, endophallus with apical field of small spines; and female genitalia with eighth sternite slender and with sparse apical setae. Members of the *mangabeirensis* group agree in external characteristics but the female eighth sternite is broad and densely setose apically.

Description. – Size small to moderate for genus. Integument rufous to rufopiceous, darkened beneath. Head with vestiture along midline in front of frontal fovea, densely squamose behind fovea; antenna inserted at or in front of anterior 0.33 of rostrum, LRapex/LRbase 0.27 - 0.48, WRmin/WRmax 0.70 - 0.84, WRmin/LR 0.35 - 0.53, LR/LA 0.52 - 0.76, LR/LP 0.47 - 0.58; second funicular segment about 0.4 - 0.7 as wide as long and about 0.8 - 1.0 as long as first funicular segment; interocular ratio 0.39 - 0.44. Prothorax subconical in most specimens but widest near base in some, about as long as wide in most species but strongly transverse in some; punctures near middle of disc separated by average distances varying from about 0.5 to 1.5 times diameters of each. Scutellum ovate to nearly circular, about 0.7 to 1.0 as wide as long. Elytron with strial punctures fine to coarse, at anterior 0.33 varied from much finer to much wider than interval 5, in posterior 0.33 generally inconspicuous but in some forms conspicuous and surrounded by glabrous areas; intervals flat, uniform in width; WE/LE 0.57 - 0.69. Lateral processes of mesosternum glabrous or squamose. Ventral sulcus of metasternum without erect scales in apical 0.50. Distal comb of tibia black or orange. Male genitalia with phallus long, narrow to wide, parallel-sided or swollen near middle, narrowly rounded to angulate at apex; endophallus with apical field of small or moderate spines. Female eighth sternite slender, stem short and with narrow to broad base, apex with single row of apical setae, hyaline area acuminate to rounded basally; spermatheca with nodulus produced.

Natural history. – The host plant genus of *R. brevicollis* is *Copaifera*; *R. chorrensis, R. cinereopunctatus, R. janzeni, R. pseudostigma, R. stigma, R. x-rubra,* and probably *R. caucensis* and *R. thrombithorax* are seed predators of *Hymenaea* species. Some forms, including at least the dark, mottled Central American and Mato Grosso forms of *R. stigma,* are "non-holedrillers" dependent on external agents for release from *Hymenaea* fruits; these 2 forms are cryptic for discolored interstitial pulp. I suspect there are at least 2 mimetic complexes, one with *R. caucensis* convergent on *R. transversalis* (*transversalis* group) and the other with *R. pseudostigma*

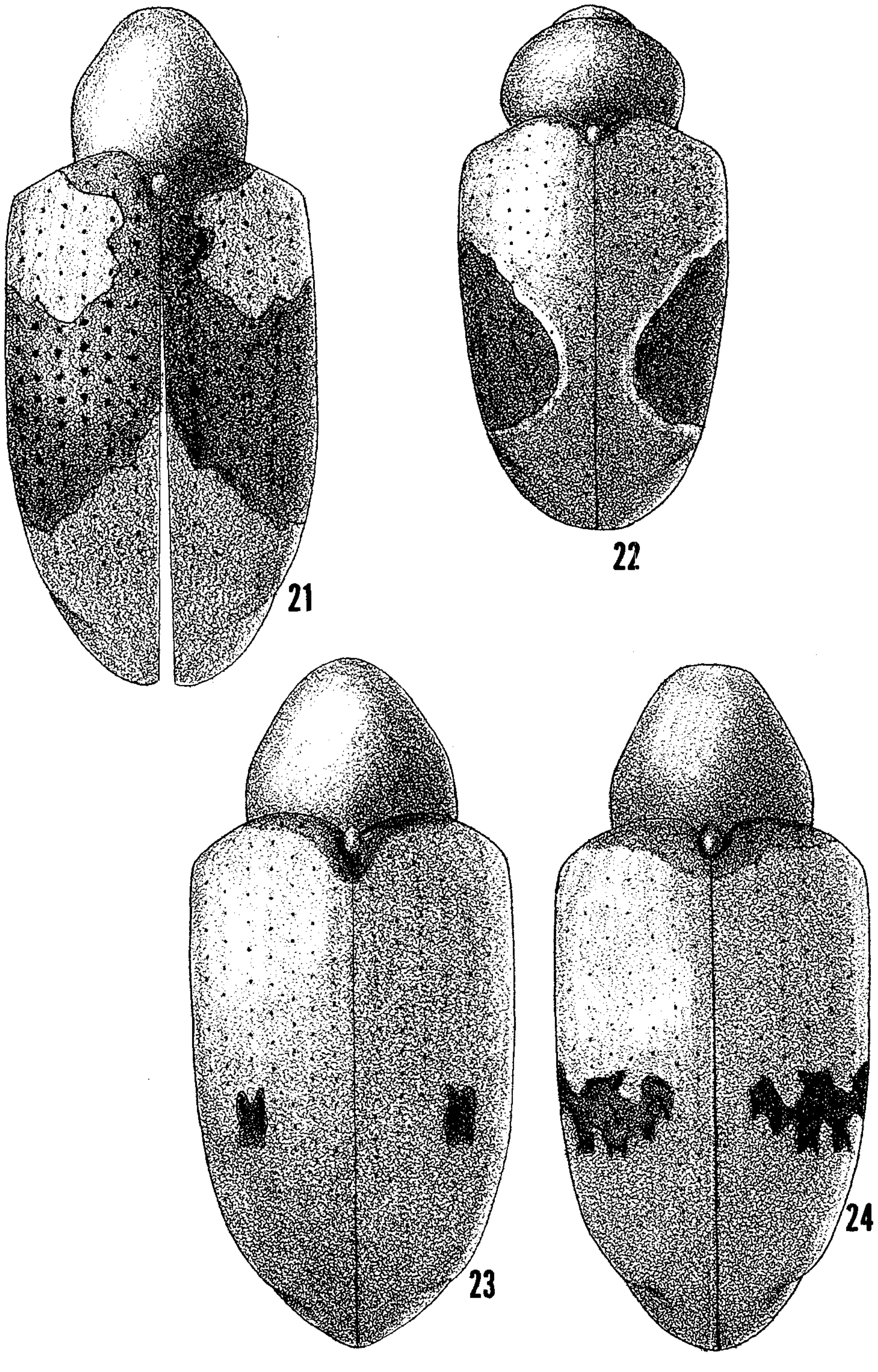

Fig. 21-24. *Rhinochenus* spp., habitus: 21, *R. x-rubra;* 22, *R. thrombithorax;* 23-24, *R. caucensis,* Valle del Cauca, Colombia, variation.

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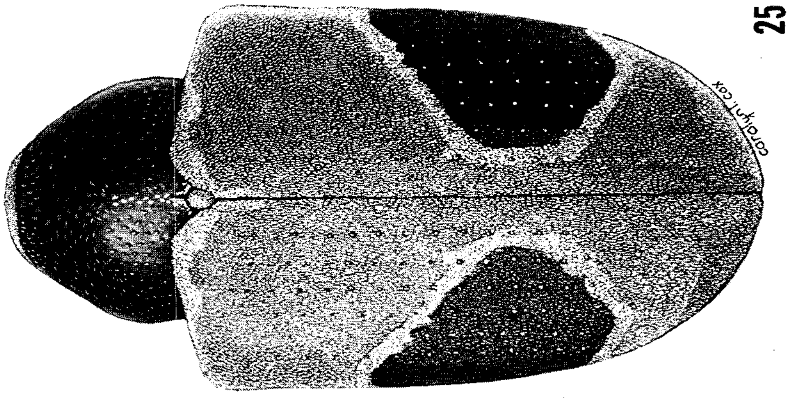

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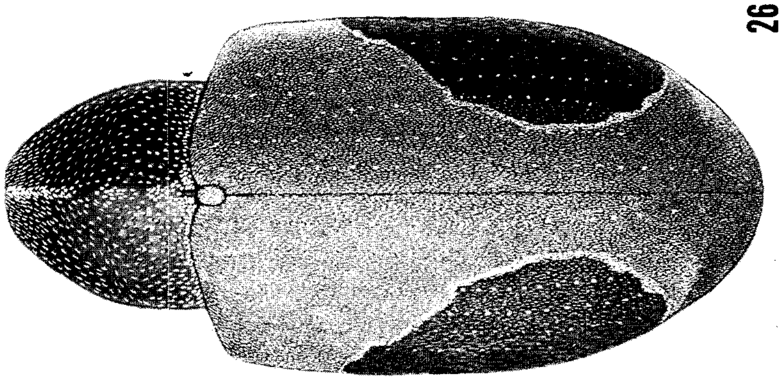

Fig. 25-26. *Rhinochenus* spp., habitus: 25, *R. janzeni*; 26, *R. chorrensis*.

convergent on *R. klagesi* and *R. mangabeirensis* (*transversalis* and *mangabeirensis* groups).

Phylogenetic relationships. – It seems clear that this group is monophyletic, defined by synapotypic female genital characteristics, and that it is sister to the *mangabeirensis* group, their relationship defined by synapotypic position of antennal insertion. Relationships within the group need additional study.

10. *Rhinochenus x-rubra* Chevrolat

Rhinochenus x-rubra Chevrolat 1871: 87. *Rhinochenus x-rubrum,* Fiedler 1951: 1106. Holotype: female labelled "Rubra Chev. Cayenne Type", "Museum Paris ex. Coll. Oberthur", "HOLOTYPE", etc. Type-locality: "Cayenna", here restricted to St. Jean du Maroni, Cayenne. Type-depository: MNHP.

Rhinochenus subcruciatus Chevrolat 1871: 87; Fiedler 1951: 1107. Holotype: not seen Type-locality: "Brasilia". Type-depository: not known. NEW SYNONYMY.

Rhinochenus lucasi Chevrolat 1871: 88; Fiedler 1951: 1107. Holotype: male labelled "Amazoni Coll. Jekel", "Typus 1871", "Rhinochenus Lucasi Chvl Amazona", "R. Lucasi Chev. typus!". Type-locality: "Amazona". Type-depository: Societa Entomologica Italiana, Genova. NEW SYNONYMY.

Taxonomic notes. – Although the name *R. subcruciatus* has line priority, I select *R. x-rubra* as senior synonym because I was personally able to examine the holotype of this named form only; in the Genova collection, the holotype of *R. lucasi* and paratype ("variety") of *R. subcruciatus* were examined by C. W. O'Brien. The *R. subcruciatus* paratype is labelled "Cayenna Coll. Jekel", "Typus 1871", "subcruciatus var. Chevrol." (on underside of preceeding), "subcruciatus Chev. Cayen", "R. subcruciatus Chevr. typus!". It probably is a male, with apical 0.33 of sternum 5 destroyed by dermestids.

O'Brien (pers. comm.) noted that the type of *R. lucasi* differs by being narrower, etc., perhaps varietal; the proposed synonymy is tentative. I have insufficient knowledge of Brazilian representatives of *R. x-rubra* to interpret variation.

Diagnostic combination. – Members of this species are distinguished by their distinctive elytral vestiture pattern, with the bare macula extended to suture and then forward to nearly or completely encircle the anterior field of dense vestiture.

Description. – Length, pronotum + elytron, 12.3 - 14.0 mm. Vestiture squamose, tan, concolorous. Head densely squamose from behind middle of rostrum laterally and from near base of rostrum dorsally. Rostrum with conspicuous median carina in basal 0.50, elsewhere nearly uniformly punctate; microsculpture flattened, conspicuous, meshes longitudinally stretched; second funicular segment about 0.6 - 0.7 as wide as long and 0.9 - 1.0 as long as first funicular segment. Pronotum (Fig. 21) conical or subconical, slightly wider to slightly narrower at middle than at base; LP/WP, 0.96 - 1.04; punctures fine, near middle of disc separated by average distances about 1.0 - 1.5 diameters of each; broad scales in complete ventropleural band and broken or complete basal band, scales otherwise small and slender; microsculpture granulose. Elytron (Fig. 21) with macula extended to suture, along suture to base, and around base to form complete or nearly complete ring around isolated anterior field of dense vestiture, macula irregular in outline and without conspicuous rim; strial punctures each with broad scale, not surrounded by glabrous spot, inconspicuous in apical 0.33; punctures at basal 0.33 coarse, punctures of striae 5 and 6 about 2.0 as wide as interval 5; interval 10 in middle 0.33 narrow, flat, stria 10 feeble; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum squamose in most specimens, microsculpture granulose; middle 0.33 of metepisternum densely squamose, microsculpture varied from granulose to flattened and longitudinally stretched; sides of metasternum densely squamose except for granulose margin. Abdomen with visible sternum 1 convex or slightly flattened mesally in female and strongly flattened mesally in male, with slender recumbent to subrecumbent scales mesally in female and with erect setae mesally in male, scales otherwise broad and recumbent; sterna 2 - 4 with scales slender and subrecumbent except laterally where broad and recumbent, sterna 3 - 4 each with transverse band of about 2 - 3 rows of punctures; sternum 5 flattened apically in female and biconvex apically in male, scales slender except laterally, most dense apicomesally in female and paramesally in male. Legs with ventral pads of tarsi tan; distal comb of tibia black. Male genitalia with phallus (Fig. 50) broad, swollen at middle, apex (Fig. 55) narrowly rounded and conspicuously lipped; endophallus with large field of long spicules. Female genitalia with spermatheca (Fig. 99); eighth sternite (Fig. 96) slender, base of stem broad, apical setae sparse.

Measurements, male from "Bresil": length, LE, 9.8 mm + LP, 3.5 mm = 13.3 mm; WPmax, 3.4 mm; WE, 5.8 mm; LR, 0.58 mm

+ 1.33 mm = 1.91 mm; WRmin, 0.84 mm; WRmax, 1.16 mm; WFmin; 1.02 mm; WFmax, 2.36 mm; LA, 1.47 mm + 1.42 mm + 0.53 mm = 3.42 mm.

Variation. – One specimen from Trinidad is paler in integument and slightly smaller than any of the other specimens, has the macula much narrower than in average specimens, and has the mesosternal lobes bare rather than squamose as in all except one other specimen. These differences are slight, and attributable to geographic or perhaps even infrapopulational variation.

Material examined. – I examined 21 specimens from various localities in Brazil, Cayenne, and Trinidad (Fig. 140).

No locality (1; BMNH). BRAZIL (2; BMNH, USNM). CAYENNE (12; BMNH, IRSB, MCZ, MNHB, MNHP). St. Jean du Maroni (4; MNHP); St. Laurent du Maroni (1; MNHP). TRINIDAD (1: BMNH).

Natural history. – One specimen in the St. Jean series bears a label "Fruit de l'Hymenaea courbaril" and the Trinidad specimen is labelled "Found in fruits of Hymenaea courbaril".

Geographic relationships. – *Rhinochenus x-rubra* is probably sympatric with several other species of the *stigma* group, and has been collected together with *R. pseudostigma* at St. Jean and St. Laurent in Cayenne. Distributional records are correlated neatly with the postulated Guyana Pleistocene forest refugium.

Phylogenetic relationships. – Except for the apotypic maculation, all characteristics, genital and external, are plesiotypic within the *stigma* group. I tentatively regard *R. x-rubra* as sister to the ancestor of all other members of the *stigma* group.

11. *Rhinochenus chorrensis* Whitehead, new species

Type-material. – Holotype: male labelled "N°. 830-18 Date 4-IV-57 Loc. Los Chorres Col. Dalton". Type-locality: Los Chorres, La Libertad, El Salvador. Type-depository: USNM, type # 73656. Allotype: female with same label data as holotype (USNM). Paratypes: 4 specimens from El Salvador (BMNH, MNHP, USNM).

Diagnostic combination. – This is the only species of the genus with pale tibial combs.

Description. – Length, pronotum + elytron, 12.6 - 13.4 mm. Vestiture squamose, scales below mostly pale tan, above varied from mostly dark orange except for pale tan along midline and base of pronotum, scutellum, base and suture of elytron, and rim of elytral macula, to mostly tan except for dark orange on elytral macula and pronotal disc. Head densely squamose from behind middle of rostrum laterally and from basal 0.25 of rostrum dorsally (Fig. 3). Rostrum with fine median carina in basal 0.50, nearly uniformly punctate and without conspicuous impunctate area along midline; microsculpture flattened; second funicular segment about 0.6 - 0.7 as wide as long and about as long as first funicular segment. Pronotum (Fig. 26) subconical, about as wide as long, slightly wider near middle than at base; LP/WP, 0.97 - 1.02; punctures coarse and dense, near middle of disc separated by average distances equal to about 0.50 diameter of each; scales broad and pale in wide ventropleural band, narrow or interrupted median vitta, and narrow or interrupted basal line, elsewhere orange and slightly narrower; microsculpture granulose. Elytron (Fig. 26) except for middle 0.33 of interval 9 densely squamose; lateral macula large, extended to or slightly inside of stria 2, nearly regular, semilunar, orange, rimmed with broad, pale scales; scales small and slender except for some marginal scales, rim of macula, and nearly circular scales of strial punctures; strial punctures not surrounded by glabrous spots, inconspicuous in apical 0.33; punctures fine, diameters near basal 0.33 of striae 5 and 6 less than width of interval 5; interval 10 in middle 0.33 narrow, flat, stria 10 shallow; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous, microsculpture flattened and isodiametric to strigose; middle 0.33 of metepisternum densely squamose; sides of metasternum densely squamose to margin. Abdomen (Fig. 7) with sternum 1 mesally concave and with scattered erect setae in male, convex and with slender suberect scales in female, scales elsewhere dense and broad; sterna 2 - 4 with scales slender and subrecumbent except laterally where broad and recumbent, sterna 3 - 4 each with transverse band of about 2 - 3 rows of punctures; sternum 5 convex apically in female and strongly biconvex in male, scales dense around margin, broad laterally and slender mesally. Legs with dorsal margins of tibiae orange in some specimens, ventral pads of tarsi orange, distal comb of tibia orange. Male genitalia with phallus (Fig. 51) broad, swollen subapically, apex (Fig. 56) narrowly rounded and lipped; endophallus with large field of long spicules. Female genitalia with spermatheca (Fig. 105), ramus and nodulus proximate; eighth sternite (Fig. 100) slender, stem with broad base, hyaline area vaguely acuminate basally, apical fringe of setae sparse.

Measurements, female from Los Chorres: length, LE, 9.9 mm + LP, 3.4 mm = 13.3 mm. WPmax, 3.5 mm; WPbase, 3.4 mm; WE, 5.6 mm; LR; 0.49 mm + 1.24 mm = 1.73 mm; WRmin, 0.71 mm; WRmax, 0.93 mm; WFmin, 0.89 mm; WFmax, 2.13 mm; LA, 1.11 mm + 1.24 mm + 0.53 mm = 2.88 mm.

Material examined. – I examined 6 specimens from two nearby localities in El Salvador (Fig. 139).

EL SALVADOR. La Libertad: Los Chorres (5; BMNH, MNHP, USNM); Santa Tecla (1; USNM).

Etymological note. – This species is named for the type-locality.

Natural history. – Nine specimens of *R. stigma* bear the same label data as do the 5 specimens of *R. chorrensis* from Los Chorres; I therefore conclude that the *R. chorrensis* specimens were reared or extracted from fruits of *Hymenaea courbaril,* the only known host species for the other Central American *Rhinochenus* species. In habits and behavior, *R. chorrensis* probably is a geographic counterpart of *R. transversalis* or *R. janzeni.*

Geographic relationships. – This species is known to be sympatric only with *R. stigma,* but *R. transversalis* may also occur in the area. The existence of this localized form in northern Central America may reflect a Pleistocene refugial area associated with the highlands of Guatemala.

Phylogenetic relationships. – I have no firm feelings about relationships of *R. chorrensis* since I discovered no clear synapotypic features shared with any other species, but suspect it is sister to the ancestor of *R. janzeni* and *R. thrombithorax.* Not only are geographic relationships more reasonable for this association than for any other, but male genital features are similar and the elytral maculae are similarly densely squamose in all three species.

12. *Rhinochenus janzeni* Whitehead, new species

Type-material. – Holotype: male labelled "CR. Puntarenas. Osa Penin. 12 Mar 72 D. Boucher" and "ex Hymenaea courbaril pods CR. Osa; D. Janzen 12 Mar 1972". Type-locality: Rincon, Osa Peninsula, Puntarenas, Costa Rica. Type-depository: USNM, type # 73657. Allotype: female, same label data as holotype (USNM). Paratypes: 18 specimens from various localities in Costa Rica and Panama (BMNH, FMNH, MNHP, MZSP, USNM).

Taxonomic note. – Champion (1905) treated this species as *R. stigma,* variety *a.*

Diagnostic combination. – This species is distinctive in habitus and coloration. Among Central American *Rhinochenus,* it is distinguished from *R. transversalis* by the glabrous metasternal sulcus, from *R. chorrensis* by the black tibial comb, and from *R. stigma* by the large semicircular, brick-red macula and generally orange elytral vestiture.

Description. – Length, pronotum + elytron, 12.8 -14.6 mm. Vestiture squamose; scales yellowbrown or orangebrown, dark orange on elytral macula and most of pronotal disc, light tan in median vitta on pronotum, scutellum, elytral base, and rim of macula. Head (Fig. 5) densely squamose from behind middle of rostrum laterally and from near base of rostrum dorsally. Rostrum with wide, flat, alutaceous median carina in basal 0.50, otherwise nearly uniformly punctate; microsculpture flattened; second funicular segment about 0.5 as wide as long and slightly shorter than first funicular segment. Pronotum (Fig. 25) subconical, transverse, slightly wider near middle than at base; LP/WP, 0.88 - 0.94; punctures coarse, near middle of disc separated by average distances about 0.50 diameter of each; broad scales in ventropleural band, complete or nearly complete median vitta, and broken basal line, otherwise slender; microsculpture granulose. Elytron (Fig. 25) with macula large, nearly regular, semilunar, extended to between striae 2 and 1, brick red, rimmed by pale yellowbrown, scales nearly as large as elsewhere on disc; scutellar area squamose; strial punctures each with broad scale, not surrounded by glabrous spot, inconspicuous in apical 0.33; punctures fine, at basal 0.33 punctures of striae 5 and 6 much narrower than interval 5; interval 10 in middle 0.33 narrow, feebly to distinctly carinate anteriorly; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous, microsculpture strigose; middle 0.33 of metepisternum with 1-2 irregular, sparse rows of scales, microsculpture strigose; sides of metasternum sparsely squamose, margin granulose. Abdomen (Fig. 8) with sternum 1 mesally concave and with erect setae in male and convex and with subrecumbent scales in female, no apical marginal scales, scales generally slender; sterna 2-4 with scales slender, subrecumbent except laterally where pale, broad, recumbent, sterna 3-4 each with median band of about 2-3 rows of punctures; sternum 5 convex apically in female, biconvex apically in male, scales sparse except apically, setiform except laterally. Legs with ventral pads of tarsi orangebrown, distal comb of tibia black. Male genitalia with phallus (Fig. 52) broad, swollen subapically, apex (Fig. 57) narrowly rounded and lipped; endophallus with large field of long spines. Female genitalia with spermatheca (Fig. 106); eighth sternite (Fig. 101) moderately broad, stem with base broad, hyaline area acuminate basally, apical fringe of setae sparse.

Measurements, holotype male: length, LE, 11.0 mm + LP, 3.5 mm = 14.5 mm; WPmax, 4.0 mm; WPbase, 3.8 mm; WE, 6.6 mm; LR, 0.44 mm + 1.42 mm = 1.86 mm; WRmin, 0.80 mm; WRmax, 1.09 mm; WFmin, 0.98 mm; WFmax, 2.22 mm; LA, 1.29 mm + 1.38 mm + 0.56 mm = 3.23 mm.

Material examined. – I examined 20 specimens from various localities in Costa Rica and western Panama (Fig. 139).

COSTA RICA (1; BMNH). Puntarenas: Rincon, Osa Peninsula (11; FMNH, MNHP, MZSP, USNM). San Jose; Pozo Azul de Pirris (3; BMNH); Escazu (1; BMNH). PANAMA. Chiriqui: 96.8 - 99 mi. E Canoas, Rio Tole (4; USNM).

Etymological note. – I name this attractive weevil for D. H. Janzen, with thanks.

Natural history. – Specimens have been extracted from pods of *Hymenaea courbaril* in January and March. According to Janzen (pers. comm.), one larva develops in each pod; the larva bores between 2 adjacent seeds, and is capable of coexisting with individuals of *R. stigma* in the same pod; and the adult can drill and escape through its own exit hole.

Geographic relationships. – This species is sympatric with *R. stigma* and *R. transversalis,* and at Rincon all three species were found in one fruit crop. If Pleistocene refugial areas are postulated to correspond to the South American refugia discussed by Vuilleumier (1971), then *R. janzeni* probably is associated with a refugium in the Chiriqui area and widely disjunct from its sister species, *R. thrombithorax,* associated with South Andean refugial areas. It may be that the Central American forms of at least *R. transversalis* and perhaps also *R. stigma* shared the same Chiriqui refuge. Curiously, the Osa Peninsula forms of both of the latter species are chromatically differentiated from those elsewhere, whereas the Osa sample of *R. janzeni* is indistinguishable from those elsewhere. The implication of this might be that the slightly differentiated Osa forms reflect a separate refugial area, one that harbored populations of *R. stigma* and *R. transversalis* but not *R. janzeni.* Another anomalous distributional datum is that the Biologia Centrali-Americana localities are in San Jose province, yet Janzen and associates have not found evidence of *R. janzeni* there despite intensive search; this hiatus may be an artifact, or may reflect ecological changes in the San Jose area wrought by human activity.

Phylogenetic relationships. – See discussion of *R. thrombithorax,* below.

13. *Rhinochenus thrombithorax* Whitehead, new species

Type-material. – Holotype: male labelled "16 IX 1965 Cachicoto HUANUCO, PERU 169 Coll. J. C. Hitchcock Jr.". Type-locality: Cachicoto, Huanuco, Peru. Type-depository: USNM, type #73658. Allotype: Female labelled "Rio Pachitea, Peru III.27, 1969 J. Schunke L." and "on fruit" (H&AH). Paratypes: 4 specimens with label "Tournavista Rio Pachitea 27 Mar 1969 J. Schunke L. " (H&AH, USNM).

Diagnostic combination. – Specimens of this species are distinguished from all other known *Rhinochenus* by the strongly gibbous, transverse pronotum, and by the erect setae of abdominal sterna 3-4.

Description. – Length, pronotum + elytron, 10.9 - 11.5 mm. Vestiture squamose, tan, dark orange in elytral macula, otherwise concolorous; scales of abdomen except margins setiform, erect (male) or sterna 1-2 with dense pad of scales in mesal 0.33 (female). Head densely squamose from behind middle of rostrum. Rostrum strongly arched above antennal insertion, with fine median carina in basal 0.50, densely punctate in basal 0.50 but otherwise nearly uniformly punctate and without conspicuous impunctate area along midline; microsculpture flattened; second funicular segment about 0.40 as wide as long and about as long as first funicular segment. Pronotum (Fig. 22) strongly gibbous, transverse, much wider near middle than at base; LP/WP, 0.84 - 0.90; punctures coarse and dense, near middle of disc separated by average distances equal to about 0.50 diameter of each; broad scales in wide ventropleural band and narrow basal line, elsewhere narrow; microsculpture granulose. Elytron (Fig. 22) with macula large, semilunar, extended to middle of interval 2, regular in outline, rimmed with large, pale scales, scales of macula nearly as large as elsewhere on disc but dark orange; strial punctures each with broad scale, not surrounded by glabrous spot, inconspicuous in apical 0.33; punctures at basal 0.33 fine, punctures of striae 5 and 6 narrower than interval 5; interval 10 in middle 0.33 narrow, flat, stria 10 shallow; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous, microsculpture granulose; middle 0.33 of metepisternum densely squamose except for granulose margin. Abdomen with sternum 1 mesally concave and with erect setae in male, mesally convex and with dense pad of recumbent scales in female, scales elsewhere broad and recumbent; sterna 2-4 with scales setiform and erect except laterally where broad and recumbent in male, sternum 2 with dense pad of recumbent scales in female, sterna 3-4 each with transverse band of about 2-3 rows of punctures; sternum 5 biconvex apically in male, convex apically in female, scales at base slender, sparse, erect, recumbent on margin, broad laterally. Legs with ventral pads of tarsi tan, distal comb of tibia black. Male genitalia with phallus (Fig. 53) broad, swollen subapically, apex (Fig. 68) narrowly rounded and lipped; endophallus with short field of short, broad spicules. Female genitalia with spermatheca (Fig. 107); eighth sternite (Fig. 102) moderately broad, stem with base broad, base of hyaline area acuminate, apical fringe of setae sparse.

Measurements, holotype male: length, LE, 8.4 mm + LP, 3.1 mm = 11.5 mm; WPmax, 3.7 mm; WPbase, 3.4 mm; WE, 5.2 mm; LR, 0.36 mm + 1.11 mm = 1.47 mm; WRmin, 0.71 mm; WRmax, 0.84 mm; WFmin, 0.76 mm; WFmax, 1.91 mm; LA, 1.02 + 1.22 mm + 0.53 mm = 2.77 mm.

Material examined. – I examined 6 specimens from Peru (Fig. 140).
PERU. Huanuco: Cachicoto (1; USNM); Rio Pachitea (5; H&AH, USNM).

Etymological note. – The epithet *thrombithorax* is derived from Greek, *thrombos* = humped + *thorax* = breast, in allusion to the gibbous form of the pronotum.

Natural history. – Specimens were collected "on fruit" in March (Rio Pachitea), and in September. The Rio Pachitea series was included in a series of *R. stigma* bearing identical label data, thus the "fruit" was presumably that of *Hymenaea courbaril.* The *R. thrombithorax* and *R. stigma* specimens are similar in size and maculation, thus possibly mimetic; but the pronotal form of *R. thrombithorax* is distinctive, thus mimicry is unlikely.

Geographic relationships. – This species is sympatric and syntopic with at least *R. stigma*, but apparently disjunctive with its sister species, *R. janzeni*. The known locality records correspond readily to the Peruvian refugia discussed by Vuilleumier (1971).

Phylogenetic relationships. – This species is regarded as sister to *R. janzeni,* the only other member of the *stigma* group having the transverse pronotum; this condition is presumed secondarily synapotypic. These two species are allopatric but may be considered as geographically proximal, and are very similar in elytral pattern; in both, the macula is densely clothed with comparatively large, dark scales rather than having reduced vestiture.[1]

14. *Rhinochenus caucensis* Whitehead, new species

Type-material. – Holotype: male labelled "Cauca Valley Venezuela" and "Museum Paris ex Coll. R. Oberthur". Type-locality: not clear from label data, but probably Valle del Cauca, Colombia (not Venezuela). Type-depository: MNHP. Allotype: female, same label data as holotype (MNHP). Paratypes: 5 specimens with same label data as holotype, 2 specimens from Colombia, and 1 specimen from Trinidad (IRSB, MNHP, USNM).

Diagnostic combination. – In vestiture pattern, with the elytral macula varied from absent to present as a narrow, irregular, transverse band, specimens of this species resemble only the northern South American forms of *R. transversalis,* but in addition to well marked genital characteristics differ by lacking erect scales in the median metasternal sulcus.

Description. – Length, pronotum + elytron, 15.0 - 16.1 mm. Vestiture squamose, scales pale yellow or tan, concolorous. Head densely squamose from behind middle of rostrum laterally and from near base of rostrum dorsally. Rostrum with conspicuous median carina in basal 0.50, nearly uniformly punctate and without conspicuous impunctate area along midline; microsculpture flattened; second funicular segment about 0.5 - 0.6 as wide as long and about as long as first funicular segment. Pronotum (Fig. 23-24) subconical, about as wide as long, slightly wider near middle than at base; LP/WP, 0.98 - 1.02; punctures fine and dense, near middle of disc separated by average distances equal to or less than diameters of each; broad scales in complete ventropleural band, short longitudinal paramedian rows basally, complete or interrupted transverse band at base, and along midline anteriorly, scales otherwise slender; microsculpture granulose.

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[1] I recently received from Mr. Will Stubblebine, University of California–Santa Cruz, a single male of an undescribed form closely related to *R. janzeni* and *R. thrombithorax.* It was collected from fruits of *Hymenaea intermedia* Ducke by J. H. Langenheim, from BRAZIL: Amazonas: Ducke Reserve, nr. Manaus, 17 May 1974, JHL no. 5803. This specimen keys to *R. janzeni* but is smaller and paler, and its phallus has the form of that of *R janzeni* but endophallic armature as in *R. thrombithorax.* Rather than describe it now I await additional material, as it and the 2 named forms may really be elements of a single, complexly varied species. The sample also included 3 larvae, plus 1 pod of *H. intermedia* with an exit hole and some damaged seeds. The fruit of *H. intermedia* is normally one-seeded, otherwise morphologically similar to that of *H. courbaril.* The bionomics of the weevil probably are similar to those of *R. janzeni,* in terms of the 1:1 ratio of fruit to larva, the 1 (or 2): 1 ratio of seed to larva, and the ability of the adult to escape from the fruit by drilling its own exit hole. However, 1 of the seeds had multiple larval holes, and I therefore suspect that the larvae included in this sample are not conspecific with the adult.

This record is of particular interest in that it is the first reliable report of *Rhinochenus* from a species of *Hymenaea* other than *H. courbaril.* This probably is because fruits of the other species are rarely collected. According to Langenheim (pers. comm.) the Amazon Basin is the center of diversity of *Hymenaea,* and *H. courbaril* is unusual in its tolerance for drier climates. The Hylaea species are forest emergents; their fruits are thus extemely difficult to collect from the trees, and the fallen fruits decompose so rapidly that they can rarely be found. Although Langenheim has found that chemical defenses are greatly varied in *Hymenaea,* I suspect that many or all of the Hylaea species are attacked by *Rhinochenus.* Detailed, long-term studies of these trees are underway, so that much useful, fresh information should accumulate in the near future; then, a useful reanalysis will become possible.

Elytron (Fig. 23-24) with macula variously represented by bare area at middle 0.33 of intervals 9-10 only, with additional small bare spot on interval 4, or by complete or broken irregular transverse band extended as far as stria 1, rim of macula not or feebly defined; scutellar area bare to near pronotal hind angles; strial punctures each with broad scale, not surrounded by glabrous spot, inconspicuous in apical 0.33; punctures fine, near basal 0.33 of striae 5 and 6 narrower than interval 5; interval 10 in middle 0.33 narrow, flat, stria 10 shallow to deep; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous, microsculpture finely granulose to substrigose; middle 0.33 of metepisternum densely squamose, microsculpture flattened and stretched; sides of metasternum densely squamose except for granulose margin. Abdomen with visible sternum 1 mesally concave and with scattered erect setae in males, convex and without erect setae in females, scales elsewhere moderately dense, slender mesally and broad laterally, with or without apical row of broad scales in middle 0.33; sterna 2-4 with scales slender and subrecumbent except laterally where broad and recumbent, sterna 3-4 each with transverse median band of about 2-4 rows of punctures; sternum 5 convex apically in female, biconvex apically in male, scales moderately dense, setiform apically, broad laterally. Legs with ventral pads of tarsi yellow, distal comb of tibia black. Male genitalia with phallus (Fig. 54) broad, apex (Fig. 62) narrowly rounded and lipped; endophallus with large field of long spines. Female genitalia with spermatheca (Fig. 108-109); eighth sternite (Fig. 103-104) moderately broad, stem with base broad, base of hyaline area not acuminate, apical fringe of setae sparse.

Measurements, holotype male: length, LE, 11.6 mm + LP, 4.2 mm = 15.8 mm; WPmax, 4.1 mm; WPbase, 4.0 mm; WE, 6.9 mm; LR, 0.44 mm + 1.60 mm = 2.04 mm; WRmin, 0.84 mm; WRmax, 1.16 mm; WFmin, 1.02 mm; WFmax, 2.36 mm; LA, 1.46 mm + 1.42 mm + 0.53 mm = 3.42 mm.

Variation. – The Trinidad specimen, a female, differs from the Colombian specimens by the proportionately shorter eighth sternite (Fig. 104) and by lacking discal elytral maculation except for the bare lateral area, but otherwise differs in no conspicuous way except for being less yellowish in color. This variation is probably geographic, but the elytral maculation is nearly as reduced in some of the Colombian specimens.

Material examined. – I examined 10 specimens from northern South America (Fig. 140).
COLOMBIA (2; IRSB). Valle del Cauca (7; MNHP, USNM). TRINIDAD (1; USNM).

Etymological note. – This species is named for the type-locality, the Cauca Valley which, presumably, is the Valle del Cauca of Colombia.

Geographic relationships. – Specimens of *R. caucensis* have not been collected in series with other *Rhinochenus*, but probably the species is sympatric with several others; other species known from Trinidad are *R. transversalis, R. x-rubra,* and *R. stigma.* The superficial appearance of these beetles is similar to that of *R. transversalis* in northern South America, suggesting that the two forms may form part of a mimetic or cryptic complex. Distributional data suggest affinity with one or more of the northwestern South American Pleistocene forest refugia.

Phylogenetic relationships. – I regard this species as sister to *R. cinereopunctatus,* distinguished principally by having fine rather than coarse strial punctures. The allopatric distributions, similarities in form and size, and similarities in genital characteristics such as broad phallus and large spicules in endophallus suggest that these two species may share a common ancestry with *R. chorrensis, R. janzeni,* and *R. thrombithorax.*

15. *Rhinochenus cinereopunctatus* Chevrolat

Rhinochenus cinereopunctatus Chevrolat 1871: 90; Fiedler 1951: 1110. Holotype: male (?) labelled “Bahia Coll. Jekel”, “Bahia Dupont”, “Rhinochenus cinereopunctatus Chvt type Bahia”, “Typus 1871”, “R. cinereopunctatus Chevt. typus!”. Type-locality: Bahia, Bahia, Brazil. Type-depository: Societa Entomologica Italiana, Genova.

Taxonomic notes. – The holotype was examined by C. W. O’Brien; the head and prothorax are missing, and the abdomen is hollowed out by dermestids. The elytral maculae are larger than normal, probably due to abrasion.

Diagnostic combination. – Specimens of this species are distinguished from other members of the *stigma* group by combination of coarsely punctate elytral striae, elytral macula not extended across elytra, and elytral vestiture dense, pale, macula either feebly defined or at least with strial punctures set in conspicuous patches of large scales. In most specimens the elytral macula is much less sharply defined than in specimens of other species except for specimens

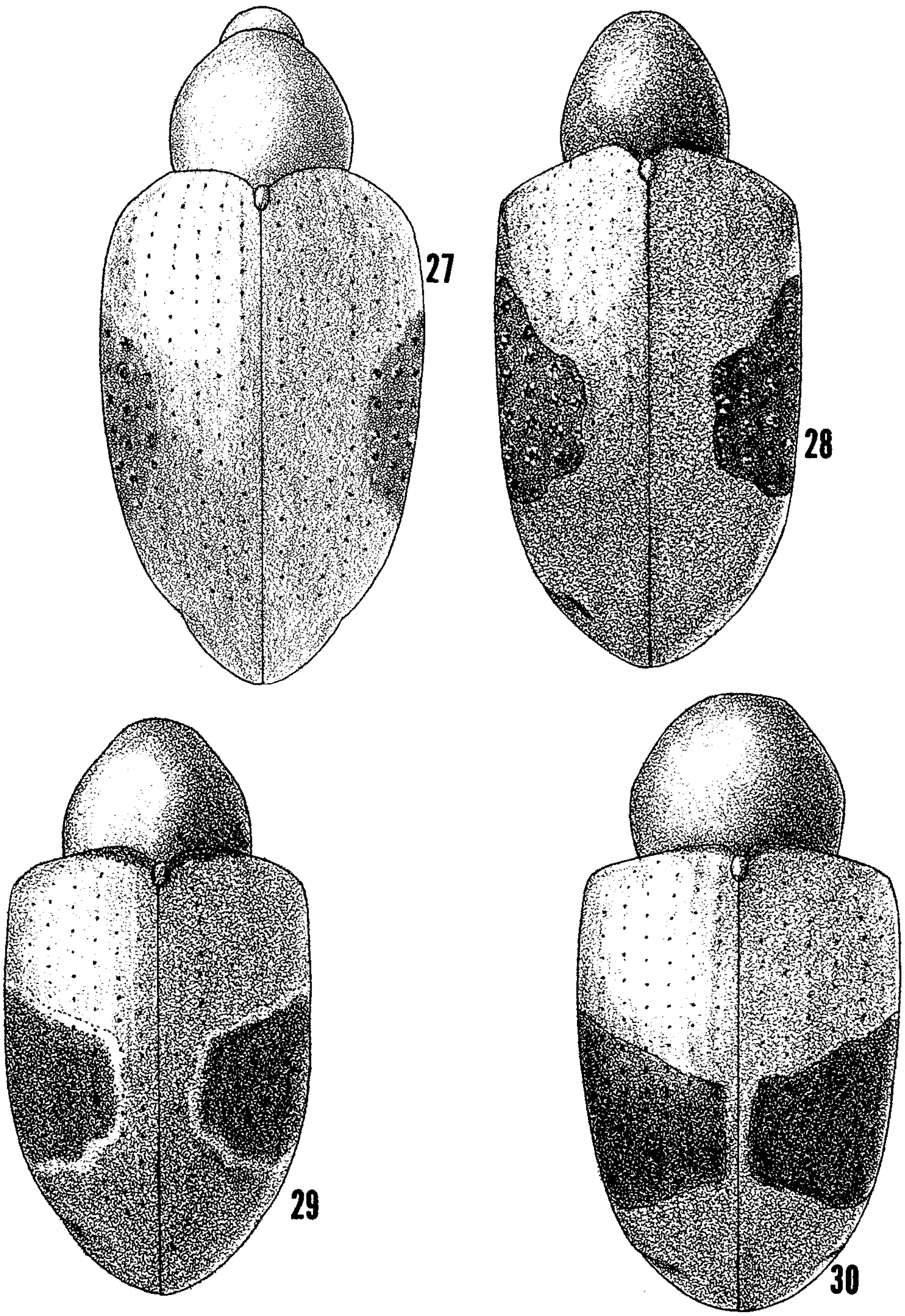

Fig. 27-30. *Rhinochenus* spp., habitus: 27-28, *R. cinereopunctatus,* Ilha do Bananal, Brazil, variation; 29, *R. brevicollis;* 30, *R. pseudostigma,* Santarem, Brazil, mimetic form.

of the Calabozo form of *R. brevicollis* which are much smaller and have finely punctate elytral striae.

Description. – Length, pronotum + elytron, 10.6 - 14.6 mm. Vestiture squamose, cinereous to pale yellow, concolorous except in some specimens darker on elytral macula. Head densely squamose from behind middle of rostrum laterally and from basal 0.25 of rostrum dorsally. Rostrum with conspicuous median carina in basal 0.50, nearly uniformly punctate and without conspicuous impunctate area along midline; microsculpture flattened; second funicular segment about 0.6 as wide as long and about as long as first funicular segment. Pronotum (Fig. 27-28) subconical, about as wide as long, slightly wider near middle than at base; LP/WP, 0.97 - 1.02; punctures fine and dense, near middle of disc separated by average distances equal to or less than diameter of each; broad scales in complete ventropleural band, generall also in complete basal band, elsewhere generally narrower but conspicuous; microsculpture granulose. Elytron (Fig. 27-28) with macula vague to distinct, semilunar to slightly oblique, generally somewhat irregular, with or without rim of broad pale scales, macula with scales variously barely narrower than elsewhere and concolorous to conspicuously narrowed and darkened, strial punctures of macula with conspicuous pale scales; scutellar area fully squamose; strial punctures each with broad scale, not surrounded by glabrous spot, inconspicuous in apical 0.33; punctures coarse, near basal 0.33 of striae 5 and 6 as wide or wider than interval 5; interval 10 in middle 0.33 *narrow, flat, not carinate, stria 10 shallow to deep; microsculpture granulose. Venter of thorax densely squamose; lateral processes* of mesosternum squamose, microsculpture granulose; middle 0.33 of metepisternum densely squamose, margins granulose. Abdomen with visible sternum 1 mesally concave and with scattered erect setae in male, convex and without erect setae in female, scales elsewhere dense and broad, without row of apical scales; sterna 2-4 with scales broad and recumbent laterally and narrower and suberect mesally, sterna 3-4 each with transverse median band of about 2 rows of punctures; sternum 5 convex apically in female, biconvex apically in male, scales dense, setiform apically, broad laterally. Legs with ventral pads of tarsi yellow, distal comb of tibia black. Male genitalia with phallus (Fig. 58-59) broad, swollen subapically, apex (Fig. 63-64) narrowly rounded and inconspicuously lipped; endophallus with large field of moderately large spicules. Female genitalia with spermatheca (Fig. 116-118); eighth sternite (Fig. 110-111) with base of stem broad, hyaline area feebly acuminate basally, apical setae sparse.

Measurements, male from Barra do Tapirape, Brazil: length, LE, 10.2 mm + LP, 3.8 mm = 14.0 mm; WPmax, 3.8 mm; WPbase, 3.7 mm; WE, 6.1 mm; LR, 0.40 mm + 1.42 mm = 1.82 mm; WRmin, 0.76 mm; WRmax, 1.00 mm; WFmin, 0.87 mm; WFmax, 2.18mm; LA, 1.36 mm + 1.38 mm + 0.53 mm = 2.37 mm.

Variation. – The elytral macula is vaguely defined in some specimens and sharply defined in others, apparently as intrapopulational variation. The specimens from Chiquitos, Bolivia are smaller than all Brazilian specimens except 1 from Bahia, but otherwise differ in no conspicuous way. One specimen in IRSB is tentatively considered this species ("Bresil", "Coll. Roelofs", "albiliquatus Dj Braz"), but has the elytra largely denuded in the front 0.66.

Material examined. – I examined 108 specimens from various localities in Bolivia and Brazil, from the Amazon River and southward (Fig. 140).

BOLIVIA. Santa Cruz: Chiquitos (5; MNHP). BRAZIL (5; BMNH, IRSB, MNHP, MZSP). Acre (1; MZSP). Bahia: Bahia (3; BMNH); Joazeiro (1; AMNH). Goias: Ilha do Bananal (3; USNM). Mato Grosso: Barra do Tapirape (70; FMNH, USNM); Chapada dos Guimarães (5; BMNH, CMPP); Campo Grande (3; AMNH); Rio Verde (2; UPCB); São Domingo (1; MZSP). Para (5; MNHB): Santarem (2; CMPP). Santa Catarina: Pinhal (1; AMNH).

Natural history. – Specimens from Barra do Tapirape and Ilha do Bananal were in association with fruits of "Jatoba" (*Hymenaea* sp., probably *H. courbaril*) and specimens from Bahia were in seeds of *Hymenaea courbaril.*

Geographic relationships. – This species is sympatric with all other *Rhinochenus* species known from south of the Amazon River, and has been taken in series with all of them. Its distribution is too great, and variation not known, to speculate about refugial relationships other than to suggest that it probably is associated with one or more of the refugia to the south of the Amazon River.

Phylogenetic relationships. – I regard this species and *R. caucensis* as sister species; see discussion of *R. caucensis.*

16. *Rhinochenus brevicollis* Chevrolat

Rhinochenus brevicollis Chevrolat 1871: 91; Fiedler 1951: 1110. Holotype: female (?) labelled "Para Coll. Jekel", "Typus 1871", "Rhinochenus brevicollis Jek Chev Para", "Para Amaz Slev", "Jek 11", "R. brevicollis Chevrol. typus!". Type-locality: Para, Brazil, here restricted to Santarem, Para, Brazil. Type-depository: Societa Entomologica Italiana, Genova.

Taxonomic notes. – The holotype was examined by C. W. O'Brien; the hind legs are missing,, and the metasternum, frons, and base of rostrum are concealed by mould.

Diagnostic combination. – Members of this species are smaller than those of any other *Rhinochenus* species, occasional dwarf individuals excepted. Additional diagnostic features are given in the key.

Description. – Length, pronotum + elytron, 7.2 - 9.7 mm. Vestiture squamose, scales cinereous to stramineous, in some specimens paler around rim of elytral macula, in some darker on pronotum and elytral macula, otherwise concolorous. Head densely squamose from behind middle of rostrum except along midline where bare nearly to base. Rostrum with distinct median carina in basal 0.50, nearly uniformly densely punctate, microsculpture flattened; second funicular segment 0.6 - 0.7 as long as wide and about 0.8 - 0.9 length of first funicular segment. Pronotum (Fig. 29) subconical, about as long as wide, wider near middle than at base; LP/WP, 0.98 - 1.02; punctures coarse and dense, near middle of disc separated by average distances much less than diameters of each; broad pale scales in complete or broken ventropleural band, in some specimens in small divided prescutellar spot, scales elsewhere slender and darker; microsculpture granulose. Elytron (Fig. 29) with large, transverse to nearly circular macula extended to between middle of interval 2 to middle of interval 1, macula tending to be regular in outline if wide but irregular if narrow, with or without rim of pale scales; scutellar area bare in most specimens; strial punctures each with broad, conspicuous scale, not surrounded by glabrous spot, inconspicuous in apical 0.33; punctures fine, at basal 0.33 of striae 5 and 6 narrower than interval 5; interval 10 in middle 0.33 narrow, well-defined in some specimens but not carinate; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous. microsculpture granulose; middle 0.33 of metepisternum with 1-2 irregular rows of scales, microsculpture flattened to granulose; sides of metasternum sparsely squamose, microsculpture flattened to granulose. Abdomen with visible sternum 1 flattened mesally, scales moderately dense and broad except in some specimens slender and subrecumbent mesally, without row of apical marginal scales; sterna 2-4 with scales subrecumbent and slender or setiform except laterally where broader and recumbent, sterna 3-4 each with transverse median band of about 2 rows of punctures; sternum 5 with scales slender and subrecumbent except along lateral margins where relatively broader, scales densest and narrowest apically, apex in male flattened and with scales in paramedian tufts, apex in female convex. Legs with ventral pads of tarsi yellow, distal comb of tibia black. Male genitalia with phallus (Fig. 60) slender, apex (Fig. 65) narrowly and evenly rounded; endophallus with short field of small spicules. Female genitalia with spermatheca (Fig. 120-122); eighth sternite (Fig. 112-113) narrow, stem with base broad, hyaline area acuminate basally, apical setae sparse.

Measurements, male from Itu, Brazil: length, LE, 6.1 mm + LP, 2.1 mm = 8.2 mm; WPmax, 2.2 mm; WE, 3.9 mm; LR, 0.31 mm + 0.80 mm = 1.11 mm; WRmin, 0.49 mm; WRmax, 0.62 mm; WFmin, 0.55 mm; WFmax, 1.33 mm; LA, 0.76 mm + 0.84 mm + 0.38 mm = 1.98 mm.

Variation. – Specimens from the Brazilian states of Bahia, Santa Catarina, and São Paulo tend to the wide, nearly circular elytral macula, whereas specimens from Goias, Minas Gerais, and Para tend to have the macula narrower, more transverse, and irregular in outline. There probably is some geographic variation in integumental coloration, but I lack sufficient material for interpretation. Scales of the pronotum and elytral macula vary in size and color; specimens from Calabozo, Venezuela are distinctive because the scales are relatively large and pale, the pronotum and macula therefore pollinose in appearance.

Material examined. – I examined 42 specimens from Venezuela to Paraguay and southern Brazil (Fig. 141).

VENEZUELA. Bolivar: Mantecal (5; UCV, USNM). Guarico: Calabozo (6; UCV, USNM). BRAZIL (3; MNHB, USNM). Bahia: Bahia (4; BMNH, MNHP, UPCB); Encruzilhada (1; CWOB); Joazeiro (2; AMNH). Goias: Goiania (1; FMNH). Mato Grosso: Chapada dos Guimarães (1; CMPP). Minas Gerais (1; MNHP): Belo Horizonte (2; BMNH). Para (1; BMNH): "Amazon" (2; BMNH); Monte Alegre (3; BMNH, USNM); Santarem (5; BMNH, CMPP). Santa Catarina: Brusque (1; UPCB). São Paulo: Itu (2; MZSP); Jundiai (1; USNM). PARAGUAY (1; BMNH).

Natural history. – Adults have been collected in February-April, July, and September-December. The Goiania specimen is labelled "at light", and is the only specimen of the genus with label data indicating either flight or nocturnal activity.

Unlike other *Rhinochenus* for which host records are available, *R. brevicollis* appears to feed exclusively on seeds of *Copaifera* rather than *Hymenaea*, but these 2 caesalpiniaceous genera probably are closely related. The "Brazil" specimen in USNM was intercepted at Washington, D. C. "with *Copaifera langsdorffii* seed", 1 of the Joazeiro specimens bears the label "*Copaifera*", and the Paraguay specimen was "found in seeds of *Copaifera langsdorffii*". I obtained the following additional data from examination of *Copaifera* herbarium material in the USNM: *Copaifera martii* Hayne (BRAZIL. Para: Monte Alegre, Igarape da Mulata, 26-IX-1953, R. L. Froes no. 30382), 2 of ca. 10 fruits with exit holes, 1 with fragments of *R. brevicollis*; and *C. trapezifolia* Hayne (BRAZIL. Santa Catarina: Brusque, Mata do Hoffman, 20-X-1949,

R. Klein, # 70), 1 fruit with exit hole – note that *R. brevicollis* is the only *Rhinochenus* reported from this locality. It is possible that *R. brevicollis* attacks *Hymenaea* as well as *Copaifera* since *R. stigma* and other *Hymenaea*-feeding species from Bahia, Chapada, Joazeiro, and Santarem bear similar label data, but these samples probably represent random rather than host-associated collections.

Copaifera and *Hymenaea* are closely but probably not immediately related. Fruits of *Copaifera* are small, single-seeded, thin-walled, at least partially dehiscent, and in at least some species produce defensive resins. Thus, they differ from those of *Hymenaea* morphologically but probably are similar biochemically. Because of the morphological differences, a different fauna is to be expected; I found a species of *Apion* in fruits of 2 samples of *Copaifera,* whereas no *Apion* is known from *Hymenaea.* So far as known, *R. brevicollis* has a 1 seed/1 weevil relationship, and exits through its own hole rather than awaiting pod dehiscence.

Geographic relationships. – This species apparently ranges through much of South America and thus is sympatric though probably not syntopic with most or all other South American *Rhinochenus.* The species is quite varied and populations perhaps are associated with various of the Pleistocene refugia, but no such associations can be specified at this time. Except for size, specimens of this species closely resemble specimens of some other species, notably some forms of *R. pseudostigma,* and though apparently not associated with the same host plants may still be involved in a mimetic or cryptic complex with them. Curiously, integumental color of the host seed, at least in herbarium material, is much darker than is integumental color in most samples of the weevil.

Phylogenetic relationships. – I regard *R. brevicollis* as sister to *R. pseudostigma,* because of external and genital morphological resemblance; they are, however, sympatric and independently varied. These 2 species are in turn related to *R. stigma,* as indicated by the narrow phallus and the small spicules of the endophallus. Since *R. stigma* adults are incapable of emerging through the thick pod wall of *Hymenaea,* the same may be true for *R. pseudostigma* and *R. brevicollis*; thus, *R. brevicollis* may be preadapted to feed on the thin-walled fruit of *Copaifera.*

17. *Rhinochenus pseudostigma* Whitehead, new species

Type-material. – Holotype: male labelled "Faz. Taperinha prox. Santarem, PA 29 XII. 1967-9.I.1968 Exp. Perm. Amaz.". Type-locality: Fazenda Taperinha, Santarem, Para, Brazil. Type-depository: MZSP. Allotype: female labelled "MUSEUM PARIS GUYANNE FRANCAISE St-Jean du Maroni R. BENOIST 1914" and "Fruit de l'Hymenaea courbaril" (MNHP). Paratypes: 8 specimens from various localities in Brazil, Cayenne, and Guyana (CMPP, MNHP, UPCB, USNM).

Diagnostic combination. – Adults of *R. pseudostigma* are best distinguished by characteristics given in the key. In Cayenne and northern Brazil, specimens of *R. stigma* normally have the mesosternal lobes squamose in addition to having much coarser strial punctures. The only known specimen of *R. mangabeirensis,* in addition to its very different female eighth sternite, differs by having a broad, impunctate, alutaceous area near the middle of the rostrum and by having a fringe of posterior marginal scales on visible sternum 1. Specimens of *R. brevicollis* differ by being much smaller on average and by differences in form of male phallus, and specimens from Cayenne andnorthern Brazil differ also by generally having the elytral macula narrower, more transverse, and more irregular in outline.

Description. – Length, pronotum + elytron, 10.4 - 11.4 mm. Vestiture squamose, scales pale orange, darker scales on pronotum and elytral macula, otherwise concolorous. Head densely squamose from behind middle of rostrum. Rostrum with fine median carina in basal 0.5, nearly uniformly punctate and without conspicuous impunctate area along midline, microsculpture subgranulose; second funicular segment about 0.7 as wide as long and about as long as first funicular segment. Pronotum (Fig. 30) subconical, about as wide as long, slightly wider near middle than at base; LP/WP, 0.98 - 1.02; punctures coarse and dense, near middle of disc separated by average distances equal to or less than diameter of each; broad scales in complete ventropleural band, some specimens with few broad prescutellar scales, scales otherwise slender; microsculpture granulose. Elytron (Fig. 30) with large, nearly circular to transversely oval macula extended to middle of interval 2 or middle of interval 1, macula with or without rim of broad pale scales, outline of macula regular; strial punctures each with conspicuous broad scale, not surrounded by glabrous area, inconspicuous in apical 0.33; punctures fine, at basal 0.33 of striae 5 and 6 narrower than interval 5; interval 10 in middle 0.33 narrow, flat, well defined in most specimens; microsculpture granulose. Venter of thorax densely squamose; lateral processes of mesosternum glabrous, with granulose microsculpture; middle 0.33 of metepisternum with about 1-2 irregular rows of scales, granulose; sides of metasternum densely squamose except for granulose margin. Abdomen with visible sternum 1 concave mesally, without apical marginal scales, scales setiform and suberect mesally, elsewhere scales slender, sparse, recumbent; sterna 2-4 with scales slender and subrecumbent except on lateral margins where broad and recumbent, sterna 3-4 each with transverse median band of about 1-2 rows of punctures; sternum 5 with scales slender and subrecumbent except along lateral margins where broad and recumbent, dense apically, male with apex flattened and scales most dense in paramedian tufts, female with apex more convex and scales most dense mesally. Legs with ventral pads of tarsi yellow, distal comb of tibia black. Male genitalia with phallus (Fig. 61) slender; apex (Fig. 66-67) narrowly rounded, lipped; endophallus with short field of small spicules. Female genitalia with spermatheca (Fig. 119); eighth sternite (Fig. 114-115) narrow, stem with base broad, hyaline area acuminate basally, apical setae sparse.

Measurements, holotype male: length, LE, 7.6 mm +LP, 2.8 mm = 10.4 mm; WPmax, 2.8 mm; WE, 4.5 mm; LR, 0.30 mm + 1.09 mm = 1.39 mm; WRmin, 0.62 mm; WRmax, 0.76 mm; WFmin, 0.67 mm; WFmax, 1.60 mm; LA, 1.04 mm + 1.11 mm + 0.44 mm = 2.59 mm.

Variation. – Specimens from Santarem have the elytral macula more transverse, extended to middle of interval 1, and with sharper color contrast. Specimens from Cayenne and Guyana have the macula more circular, extended to about middle of interval 2, and with color darker.

Material examined. – I examined 10 specimens from Cayenne, Guyana, and northern Brazil (Fig. 141).

No locality (1; MNHP). BRAZIL. Para: Jacareacanga (1; UPCB); Santarem (2; CMPP, MZSP). CAYENNE (1; MNHP): St. Jean du Maroni (1; MNHP); St. Laurent du Maroni (3; MNHP, USNM). GUYANA (1; CMPP).

Etymological note. – The epithet *pseudostigma* is given in reference to the superficial similarity of this species to sympatric forms of *R. stigma.*

Natural history. – The allotype bears a label indicating that the host plant is *Hymenaea courbaril.* Specimens of *R. amapensis* and *R. x-rubra* from the Cayenne localities bear similar label data and may have been associated with the same fruit crops. At Santarem, *R. pseudostigma* is probably syntopic with *R. klagesi, R. maculipes, R. cinereopunctatus,* and *R. stigma.* The Santarem form of *R. pseudostigma* is superficially extremely like specimens of *R. klagesi,* suggesting that they form part of a mimetic complex.

Geographic relationships. – This species is sympatric and probably syntopic with all of the above mentioned species and probably with several others in northern South America, and is sympatric but probably not syntopic with *R. brevicollis.* The distribution of *R. pseudostigma* corresponds to the Pleistocene refugium in the Guiana highlands.

Phylogenetic relationships. – This species is probably most closely related to *R. brevicollis,* but is sympatric with that species, specimens are larger and are distinct in form of phallus, and apparently not associated with the same host plant.

18. *Rhinochenus stigma* (Linnaeus)

Circulio stigma Linnaeus 1758: 382; Linnaeus 1764: 48; Linnaeus 1767: 612; Fabricius 1775: 137; Fabricius 1781: 174; Fabricius 1787: 105; Olivier 1790: 504; Fabricius 1792: 426. *Rhynchaenus stigma,* Fabricius 1801: 463; Illiger 1806: 242; Olivier 1807: 83. *Cryptorhynchus stigma,* Schönherr 1837: 63; Schönherr 1844: 305. *Rhinochenus stigma,* Chevrolat 1871: 89; Champion 1905: 537; Fiedler 1951: 1111. Type-material: not seen by me. Type-locality: Cayenne, here restricted to Cayenne, Cayenne. Type-depository: Zoological Institute, Uppsala, Sweden.

Curculio piger Fabricius 1798: 169; Fabricius 1801: 463 (placed in synonymy). *Rhynchaenus piger,* Illiger 1806: 243. *Cryptorhynchus piger,* Schönherr 1837: 63 (returned to synonymy). *Rhinochenus piger,* Chevrolat 1871: 90; Champion 1905: 537 (returned to synonymy). Lectotype: here designated, female from Fabricius' collection labelled "Typus . . . piger F. 14.8.53 Kuschel". Type-locality: Trinidad. Type-depository: Zoologisk Museum, Copenhagen.

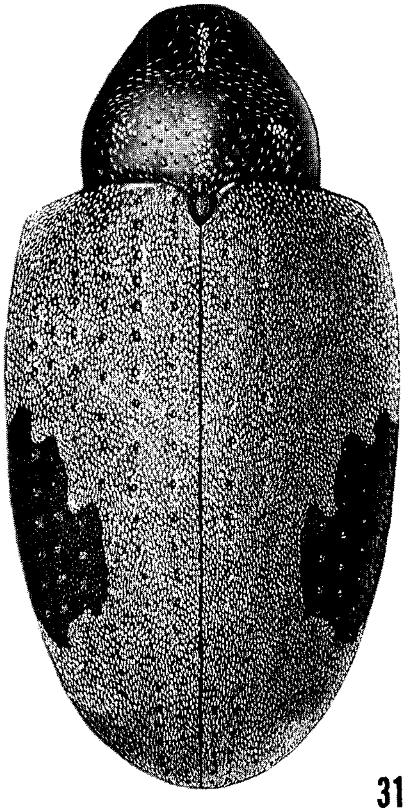

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Fig. 31. *Rhinochenus stigma*, habitus.

Rhynchaenus nota Illiger 1806: 243. *Cryptorhynchus nota,* Schönherr 1837: 63 (placed in synonymy). Type-material: none seen by me. Type-locality: not known. Type-depository: not known.

Rhinochenus sticticus Lucas 1857: 71; Chevrolat 1871: 93; Fiedler 1951: 1109. Lectotype: here designated, male labelled with disc (green above and with "7 47" below), "Cryptorhynchus sticticus, sp. n.", "Chenorhinus (g.n.) sticticus, s. n.", "MUSEUM PARIS BRESIL MINAS-GERAES DE CASTELNAU 1847", etc. Type-locality: Minas Gerais, Brazil. Type-depository: MNHP. Paralectotypes: 3 with Minas Gerais label as above, and 4 with disc reading "6 47" and "MUSEUM PARIS GOYAZ a CUYABA DE CASTELNAU 6-47" (MNHP). NEW SYNONYMY.

Rhinochenus striatus Chevrolat 1871: 88; Fiedler 1951: 1113 (placed in synonymy). Lectotype: here designated, male (?) labelled "ex mus Lacord." (green), "6 Striatus Chvr Bras . . ." (partly illegible), "var. 2 Champ", etc. Type-locality: Brasilia". Type-depository: RMSS.

Rhinochenus fimbriatus Chevrolat 1871: 88; Fiedler 1951: 1113 (placed in synonymy). Lectotype: here designated, female labelled "Brasilia" (green), "TYPUS", "Rhinochenus fimbriatus Chev.", etc. Type-locality: "Brasilia". Type-depository: RMSS.

Rhinochenus trilineatus Chevrolat 1871: 89; Fiedler 1951: 1108. Holotype: male (?) labelled "Amazzoni Coll. Jekel", "Typus 1871", "Rhinochenus trilineatus Chv. Amazoni", "R. trilineatus Chevt. typus!". Type-locality: "Amazona". Type-depository: Societa Entomologica Italiana, Genova. NEW SYNONYMY.

Rhinochenus stenaspis Chevrolat 1871: 90; Champion 1905: 537 (placed in synonymy). Lectotype: here designated, male labelled "Nova Grenada" (green), "TYPUS", "p 90. Nov Gren", "Rhinochenus stenaspis Chevr.", etc. Type-locality: "Nova-Granata". Type-depository: RMSS.

Rhinochenus rougieri Chevrolat 1871: 93; Fiedler 1951: 1109. Lectotype: here designated, male labelled "TYPUS", "Rougieri Chv. p. 92 Bahia", "Rhinochenus rougieri Chev.", etc. Type-locality: Bahia, Bahia, Brazil. Type-depository: RMSS. NEW SYNONYMY.

Rhinochenus scutellaris Chevrolat 1880: cxiii; Fiedler 1951: 1113 (placed in synonymy). Lectotype: here designated, male labelled "TYPUS", "Col . . . SF. Mollin" (partly illegible), "Rhinochenus scutellaris Chev. ", etc. Type-locality: "Brasilia". Type-depository: RMSS.

Rhinochenus triangulifer Chevrolat 1880: cxiv; Fiedler 1951: 1112 (placed in synonymy). Lectotype: here designated, female labelled "de Gaulle", "TYPUS", "Rhinochenus triangulifer Chev.", etc. Type-locality: "Brasilia". Type-depository: RMSS.

Taxonomic notes: – Champion (1905) did not distinguish the Central American species of *Rhinochenus,* and only his last 2 varieties (δ and σ) belong to *R. stigma*. These 2 varieties are light and dark color phases that in Costa Rica occur in various proportions at different localities; they do not merit formal recognition.

This species is extremely varied, as evidenced by the long synonymic list. Following are notes on type-specimens of all described forms except *R. nota,* which I have not seen; these are ascribed to geographic forms as discussed in the section on variation.

R. stigma: characteristic of specimens from area 3, Cayenne form. Type-material examined by D. H. Janzen.

R. piger: characteristic of specimens from area 4, a transitional area. This form was described from "Insula Trinidad Dom. Ryan. Mus. Dom. Lund.". I examined 3 specimens from the Zoologisk Museum, Copenhagen, including 1 from the S. & T. Lund collection and 2 from Fabricius' Kiel collection. Zimsen (1964) specified the Lund specimen as type but noted that Kuschel had seen the Kiel specimens. The Lund specimen bears the labels "TYPE" and "Essiquibo. Smidt. Mus. S. & T. L. Piger. Fabr. Stigma Fabr.". Although from the Lund collection as specified in the original description, this specimen apparently cannot be an original specimen: the locality label is not an original label, and both locality (Essequibo, Guyana) and collector

(Smidt) are incorrect; moreover, the specimen is characteristic of specimens from area 1, the São Paulo form—not of specimens from Trinidad. Neither of the Kiel specimens bears locality data, but both are characteristic of the form in Trinidad. Thus, despite the presence of these specimens in the Kiel collection rather than the Lund collection, I regard them as original type-material and select the lectotype accordingly.

R. sticticus: characteristic of specimens from area 6, Mato Grosso form.

R. striatus: characteristic of specimens from area 1, São Paulo form. Of the 2 specimens labelled "*striatus*" in the Riksmuseum, one is a male labelled "TYPUS" (red), "Rhinochenus striatus Chev.", etc. This specimen does not match the original description of either the nominotypical form or of "Var. A", and hence I think it is incorrectly labelled; it is an abraded specimen, possibly conspecific with *R. x-rubra* rather than *R. stigma* based on comparison of male genitalia. The specimen selected herein as lectotype agrees with the description of the nominotypical form, and is from the Lacordaire collection to which Chevrolat had access at the time of his monograph.

R. fimbriatus: characteristic of specimens from area 2, Bahia form.

R. trilineatus: characteristic of specimens from area 3, Cayenne form. The holotype was examined by C. W. O'Brien; the head and prothorax are missing.

R. stenaspis: characteristic of specimens from area 3, Cayenne form, or perhaps transitional to area 4.

R. rougieri: characteristic of specimens from area 6, Mato Grosso form. The lectotype is badly rubbed. The type-locality is unquestionably incorrect. This form does occur in western parts of the state of Bahia but not in the coastal areas. See also comments regarding the type-locality of *R. bahiensis*, described in the same publication.

R. scutellaris: characteristic of specimens from area, 2, Bahia form.

R. triangulifer: characteristic of specimens from area 1, São Paulo form.

Diagnostic combination. – This is a notably varied species, best distinguished by a process of elimination as in the key to species. Some geographic forms are distinguished from other members of the *stigma* group by dark, mottled coloration, and others by having the strial punctures of the posterior 0.33 of the elytra conspicuous and surrounded by glabrous spots. Specimens from other areas are distinguished from most other members of the *mangabeirensis* and *stigma* groups by having relatively coarse strial punctures, from specimens of *R. cinereopunctatus* by having the elytral macula sharply defined and lacking either pollinose appearance or clusters of white scales in the strial punctures of the macula, and from specimens of *R. x-rubra* by different elytral maculation.

Description. – Length, pronotum + elytron, 7.5 - 13.3 mm, normally over 10 mm. Dorsum rufocastaneous to rufopiceous, elytron in some specimens piceous in apical 0.33 and along suture; venter rufous to rufopiceous. Vestiture squamose, pale cinereous to flavous. Head (Fig. 4) densely squamose from behind middle of rostrum laterally and from basal 0.25 of rostrum dorsally. Rostrum with fine or indistinct median carina in basal 0.50, most specimens with broad, flat, alutaceous area near middle, punctation dense and more or less confused basally, microsculpture granulose or slightly flattened; second funicular segment about 0.50 as wide as long and about as long as first funicular segment. Pronotum (Fig. 31-39) subconical in most specimens but conical in some from southern Brazil, about as wide as long; LP/WP, 0.94 - 1.02; punctures coarse and dense, near middle of disc separated by average distances equal to or less than diameter of each; broad scales variously present in fine and interrupted basal border, caudolateral longitudinal lines, small anterolateral spot on each side, and broad ventropleural border; microsculpture granulose, opaque in most specimens. Elytron (Fig. 31-39) with greatly varied vestiture pattern, middle 0.33 of intervals 9-10 sparsely squamose to nearly bare; lateral macula of varied size and shape, regular or irregular in outline, rufous or brick red to piceous, with or without pale rim; disc elsewhere either with dense pale vestiture or dark and mottled; scales small and slender, broader in rim and strial punctures in some forms, notably slender and sparse in macula in some forms; strial punctures coarse, at basal 0.33 of striae 5 and 6 wider than interval 5, in apical 0.33 inconspicuous to conspicuous and surrounded by glabrous areas or not; microsculpture granulose. Venter of thorax (Fig. 9) densely squamose; lateral processes of mesosternum glabrous to squamose, microsculpture flattened to granulose; middle 0.33 of metepisternum with about 1-3 irregular rows of scales; sides of metasternum densely squamose except for granulose margin. Abdomen (Fig. 9) with sternum 1 with slender, subrecumbent or suberect scales near middle, elsewhere with moderately dense broad scales, no posterior marginal scales; sternum 1 slightly more convex mesally in female than in male; sterna 2-4 with scales subsquamose to hairlike,

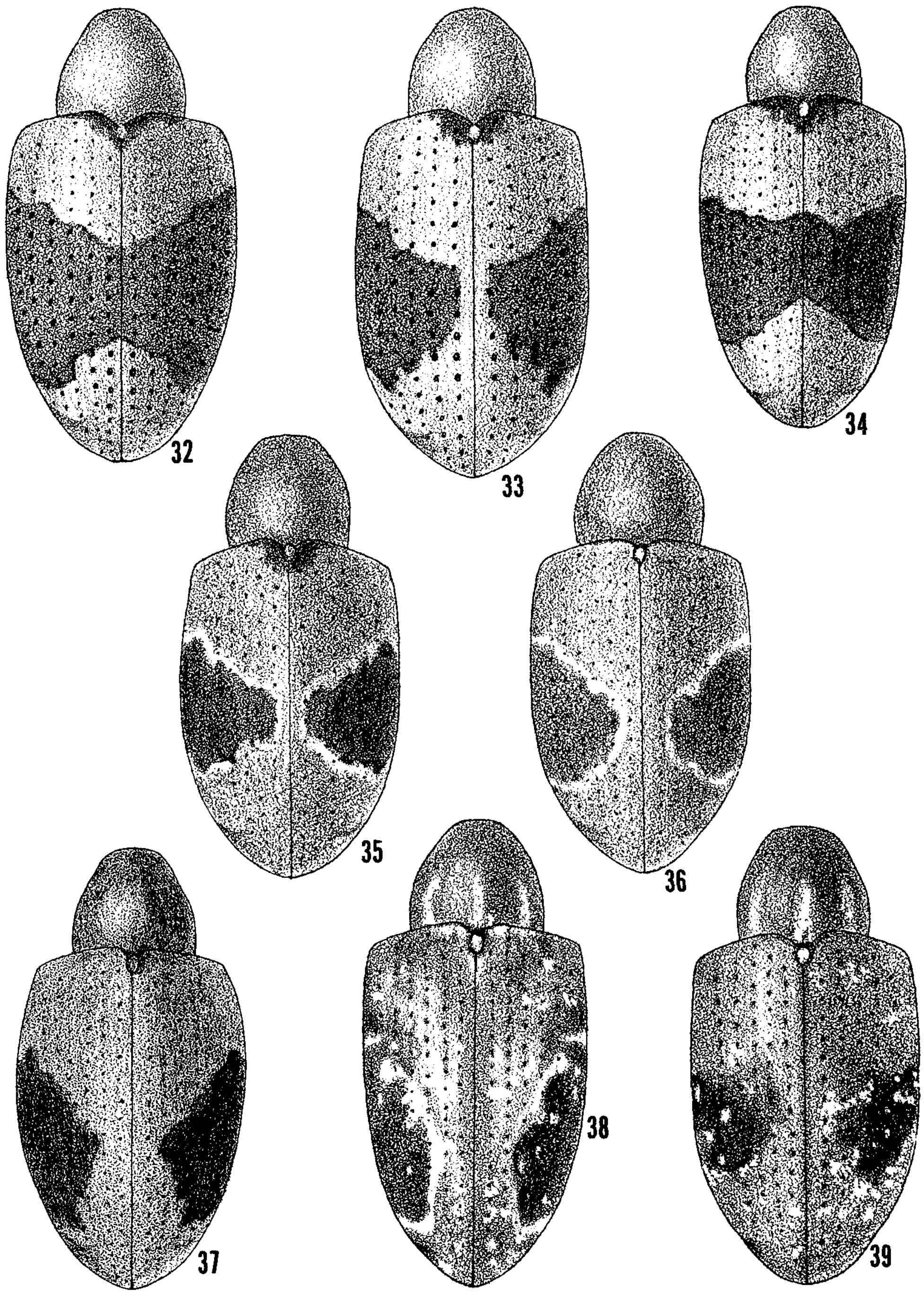


Fig. 32-39. *Rhinochenus stigma,* chromatic variation: 32, Leopoldo de Bulhoes, Brazil, area 1 or São Paulo form; 33, Sitio Bananal, Brazil, area 1 or São Paulo form; 34, Paranapiacaba, Brazil, area 2 or Bahia form; 35, Bahia, Brazil, area 2 or Bahia form; 36, Santarem, Brazil, area 3 or Santarem form; 37, Kalacoon, Guyana, area 4 or transitional form; 38, Villa Colon, Costa Rica, area 5 or Central American form; 39, Chapada dos Guimarães, Brazil, area 6 or Mato Grosso form.

suberect, sterna 3-4 each with transverse median band of about 2-3 irregular rows of punctures; sternum 5 in male biconvex with dense fine scales on convexities, in female with dense apical fine scales. Legs with ventral pads of tarsi pale to dark tan, distal comb of tibia black or dark brown. Male genitalia with phallus (Fig. 69-73) normally slender; apex (Fig. 74-79) normally broadly rounded and inconspicuously lipped, but variable; endophallus with short field of inconspicuous or small spicules. Female genitalia with spermatheca (Fig. 123-125); eighth sternite (Fig. 126-136) narrow, stem with base normally narrow except in some specimens from southern Brazil, hyaline area normally not acuminate basally, apical setae sparse.

Measurements, male of Central American form from Villa Colon, Costa Rica: length, LE, 8.5 mm + LP, 2.9 mm = 11.4 mm; WPmax, 2.9 mm; WE, 5.0 mm; LR, 0.47 mm + 1.21 mm = 1.68 mm; WRmin, 0.60 mm; WRmax, 0.87 mm; WFmin, 0.73 mm; WFmax, 1.84 mm; LA, 1.11 mm + 1.20 mm + 0.51 mm = 2.82 mm.

Measurements, male of Mato Grosso form from Ilha do Bananal, Brazil: length, LE, 7.8 mm + LP, 2.8 mm = 10.6 mm; WPmax, 3.0 mm; WE, 5.4 mm; LR, 0.44 mm + 1.18 mm = 1.62 mm; WRmin, 0.62 mm; WRmax, 0.82 mm; WFmin, 0.73 mm; WFmax, 1.87 mm; LA, 1.02 mm + 1.16 mm + 0.44 mm = 2.52 mm.

Measurements, male of Cayenne form from Santarem, Brazil: length, LE, 7.8 mm + LP, 2.6 mm = 10.4 mm; WPmax, 2.8 mm; WPbase, 2.7 mm; WE, 4.9 mm; LR, 0.45 mm + 1.07 mm = 1.52 mm; WRmin, 0.58 mm; WRmax, 0.76 mm; WFmin, 0.69 mm; WFmax, 1.66 mm; LA, 0.92 mm + 1.07 mm + 0.44 mm = 2.43 mm.

Measurements, male of Cayenne form from Caqueta, Colombia, genital variant (Fig. 72): length, LE, 7.9 mm + LP, 2.8 mm = 10.7 mm; WPmax, 2.9 mm; WPbase, 2.8 mm; WE, 4.9 mm; LR, 0.46 mm + 1.04 mm = 1.50 mm; WRmin, 0.60 mm; WRmax, 0.81 mm; WFmin, 0.67 mm; WFmax, 1.67 mm; LA, 0.93 mm + 1.09 mm + 0.47 mm = 2.49 mm.

Measurements, female of São Paulo form from Franca, Brazil: length, LE, 8.8 mm + LP, 3.0 mm = 11.8 mm; WPmax = WPbase, 3.0 mm; WE, 5.4 mm; LR, 0.53 mm + 1.10 mm = 1.63 mm; WRmin, 0.58 mm; WRmax, 0.84 mm; WFmin, 0.78 mm; WFmax, 1.81 mm; LA, 0.98 mm + 1.13 mm + 0.44 mm = 2.55 mm.

Measurements, male of São Paulo form from Chiquitos, Bolivia, genital variant (Fig. 73): length, LE, 9.5 mm + LP, 3.2 mm = 12.7 mm; WPmax = WPbase, 3.3 mm; WE, 5.6 mm; LR, 0.49 mm + 1.33 mm = 1.82 mm; WRmin, 0.67 mm; WRmax, 0.93 mm; WFmin, 0.84 mm; WFmax, 1.91 mm; LA, 0.98 mm + 1.11 mm + 0.53 mm = 2.62 mm.

Variation. – Distribution patterns of major chromatic forms are mapped (Fig. 142), and selected individuals of these forms are illustrated in semidiagrammatic form (Fig. 32-39). In specimens from area 1 (São Paulo form), the elytron has sparse vestiture in the scutellar area, a complete or narrowly interrupted transverse median band, and glabrous spots surrounding strial punctures in the apical 0.33. Specimens from the southern part of area 2 (Bahia form) have the bare scutellar area, most have the transverse band complete, and all lack glabrous spots; specimens from the northern part of area 2 are varied and approach the more uniform samples from area 3. All specimens from area 3 (Cayenne form) have the scutellar area squamose and the transverse band interrupted, broadly so in most specimens. Specimens from area 4 are varied, intermediate between specimens from areas 3 and 5; darker than specimens from area 3, tending to have an irregular pattern. Specimens from areas 5 (Central American form) and 6 (Mato Grosso form) are dark, with elytral pattern irregular and frequently mottled with small white patches, and with pronotum tending to be basally trivittate; they are not strongly differentiated from one another.

Some populations within areas 5 and 6 are differentiated in color. Thus, specimens from peripheral localities in area 6, such as Rurrenabaque and Gorotire, are much paler than most specimens from elsewhere in area 6, and most specimens from the Osa Peninsula in Costa Rica are paler and less variegated than specimens from most other localities in Central America and northwestern South America. The pale forms of area 6 are from northern and western peripheral localities and thus proximal to and probably intergrade with forms in area 3. Samples from Rincon, Osa Peninsula and the nearby (ca. 25 miles) Boruca locality are conspicuously differentiated from one another. Differentiation of the Osa populations of *R. stigma* and *R. transversalis* reflects a repetitive pattern of genetic isolation and geographic limitation in the Osa and Chiriqui areas which has been discussed elsewhere (Kingsolver and Whitehead 1976). I here suggest that this phenomenon reflects differentiation in Pleistocene refugial areas, with distinct refugia on the Osa Peninsula and in the Chiriqui area.

The mesosternal lobe is glabrous in all or nearly all specimens from area 1 and the southern part of area 2, in most from the northern part of area 2, in a few from area 3, and in none or nearly none from areas 4 and 5. It is squamose in about 50% of specimens from most samples from area 6, but among the pale, peripheral forms it is squamose in most specimens (e.g., in all 6 specimens from Gorotire and in 20 of 25 specimens from Rurrenabaque).

There is also some variation in both male and female genitalia. I examined the apex of the phallus of more than 100 males and the entire phallus of more than 35, and the eighth sternite of more than 35 females. In 1 exceptional specimen from Joazeiro, Bahia, Brazil the phallus is atypically broad, with apex subacute and spicules of endophallus enlarged (Fig. 71, 79); in external features the specimen is indistinguishable from other specimens from Joazeiro, thus implying that it is conspecific with them (if not, then mimetic!). In most other males, the phallus is slender, parallel-sided, broadly rounded apically, and with spicules of endophallus fine (Fig. 69-70); some individuals lack the preapical constriction, and 1 specimen was constricted on 1 side only. Geographic exceptions are the following: specimens from the far western part of area 3 are indistinguishable from other specimens from area 3 externally (except that the female from "Ecuador" resembles specimens from the southern part of area 2), but males (Borba, Caqueta, Rio Beni, and Rio Pachitea) have the phallus narrowly rounded and more or less strongly lipped apically (Fig. 72); and the only male of the São Paulo form known from within the range of the Mato Grosso form (Chiquitos) also has the phallus narrowly rounded and lipped (Fig. 73). Variations in the female eighth sternite (Fig. 126-136) include some specimens from southeastern Brazil (area 1 and southern part of area 2) with the base broad (e.g., Fig. 131, but intermediate conditions are also represented in series from that area), and in 1 specimen from an unknown locality the base of the hyaline area is acuminate rather than rounded.

In the area where forms 1 and 6 overlap, in the northern part of the Plata drainage basin, only 2 or 3 specimens of the São Paulo form are represented (the location of "Organ Mt., M. G." is not known). Character displacement is suggested, as not only is the São Paulo form here divergent in phallic structure but the specimens are at the extreme upper limit in body size for *R. stigma* unlike the much smaller Mato Grosso form, and the elytral macula is larger than usual for the São Paulo form in added contrast to the Mato Grosso form.

Material examined. – I examined more than 725 specimens from southern Mexico to Panama and more than 828 specimens of several chromatic forms from various localities in South America (Fig. 142). In the following list, localities from which specimens are labelled as extracted or reared from fruits of *Hymenaea courbaril* are indicated by an asterisk. Some South American specimens so marked may be from other species of *Hymenaea*: e.g., Rurrenabaque specimens are from "Paco bean" (*Hymenaea* sp.), Ilha do Bananal specimens from "jatoba" (= *H. courbaril* or *H. stigmocarpa*), and Santo Amaro specimens from "jatahy" (variant spelling of "jatoba").

MEXICO. Chiapas: Pacific slope of Cordillera. GUATEMALA. Sacatepequez: Capetillo. EL SALVADOR. La Libertad: Los Chorres. NICARAGUA. Chontales. COSTA RICA. Alajuela: Atenas*; 3.5 mi. W Rio Prendas*; Guanacaste: Bagaces*; 7 km. N Cañas*. Puntarenas: Boruca*; 9 mi. E. Esparta*; Monteverde Road (10 mi. N 24th Noviembre)*; Osa Peninsula (Rincon)*; Surubres. San Jose: Ciruelas*; Pozo Azul: Sabanilla; San Jose*; Villa Colon*. PANAMA. Santa Cruz. Canal Zone: Ancon*; Barro Colorado Island. Chiriqui: Chiriqui; Tole*. Panama: Panama. COLOMBIA. Caqueta: Morelia. VENEZUELA. Aragua: El Limon. Bolivar: Suapure. Carabobo: Macapo*. TRINIDAD*. Morne Bleu. GUYANA. Georgetown; Kalacoon. CAYENNE. Cayenne; Gourdonville; Roches de Kourou. BRAZIL. Amapa: Serra do Navio. Amazonas: Borba; Hyutanahan; Manaus. Bahia: Bahia*; Barra; Juazeiro; Salobro. Espiritu Santo: Corrego do Ita; Espiritu Santo; Linhares. Goias: Ilha do Bananal*; Jatai; Leopoldo de Bulhoes. Maranhao: Igarape Gurupa (50 km. E Caninde). Mato Grosso: Barra do Tapirape*; Chapada dos Guimarães;Guaicurus; Rio dos Mortes; São Domingos. Minas Gerais: Pedra Azul; Sabara; Vicosa. Para: Aldeia Coraci (11 km. W Caninde); Gorotire; Obidos; Santarem. Rio de Janeiro: Anellas. São Paulo: Corumbatai; Franca; Ipiranga; Mogi Guassu; Paranapiacaba; Santo Amaro*; São Paulo; Sertaozinho; Sitio Bananal (Guarulhos); Vera Cruz. Locality not known: Diamantes; Organ Mt., M.G.; Tijuca. BOLIVIA. Beni: Rio Machupo; Rurrenabaque*. Santa Cruz: Chiquitos. PERU. Huanuco: Rio Pachitea. ECUADOR.

Natural history. – So far as presently known, larvae of *R. stigma* develop exclusively in fruits of *Hymenaea courbaril,* but in South America they may attack other *Hymenaea* species. A published record from *Copaifera langsdorffii* most probably is based on the superficially similar but smaller *R. brevicollis.* According to D. H. Janzen (pers. comm.), each seed may be used by several larvae. Janzen names this species the "non-holedriller", since the adult is incapable of producing its own exit hole and accordingly depends on external agents such as rodents or deer to open the pods. Consequently, adults may be long-lived within the fruits;

Janzen found a year-old fruit fall at Rincon to still contain living weevils.

Most specimens from south of the equator were collected from September to December, but as early as July and as late as February. Most specimens from north of the equator were collected between February and May, but specimens were extracted from seeds as early as 8 January at Tole and as late as 17 July at Ancon, and specimens from Atenas were collected in October. Specimens are rarely collected except in association with *Hymenaea* fruits. Janzen observes that adults are capable of flight but do not normally do so, and that they are not collected at lights. My own field observations in Costa Rica indicate that when the pod is cracked open, the weevils first play dead, and some time later run off.

Forms from areas 1-4 resemble in pattern other species in several groups, but I have observed no precise match with sympatric forms of other species; thus I cannot predict whether mimicry occurs or not, as this general color pattern (cf. Fig. 32-37) is considered cryptic and plesiotypic. Forms from areas 5 and 6 are dark and mottled, unlike any other *Rhinochenus,* apparently cryptic to match the discoloration of the fruit pulp caused by the habits of these weevils.

Geographic relationships. – The known range of *R. stigma* encompasses those of all other *Rhinochenus* except, perhaps, in extreme southern Brazil; *R. stigma* is known to be sympatric with most other species and probably is with all of them. It probably is syntopic with all of the other species except *R. brevicollis,* which is known to attack *Copaifera* and may not attack *Hymenaea.*

The pattern of variation may represent a slightly complicated circle of races, with overlap occurring between the São Paulo and Mato Grosso forms (Fig. 142); but if a circle, then areas 5 and 6 must be continuous, yet the available evidence is that the intervening area is occupied by the Cayenne form (with male genitalia modified), only. The geographic pattern indicates the following genetic (gene flow) relationships: southern part of area 2 through northern part of area 2 to area 3, continuous; area 3 through narrow hybrid zone of area 4 to area 5, continuous; northeastern part of area 3 to extreme western part of area 3, probably continuous but in need of additional study; area 3 to area 6, probably continuous, but intermediate areas need to be sampled; area 5 to area 6, possibly continuous but no evidence available (if so, then Cayenne form is sympatric in extreme west); area 1 to area 2, apparently parapatric in south but probably with limited gene flow at least in north (evidence: broadened range of variation in female eighth sternite in area 1 and southern part of area 2; approximation in elytral maculation in same areas; mesosternal processes bare in both areas; etc.); and area 1 to area 6, probably reproductively isolated (evidence: sympatric in Plata drainage, with character displacement in male phallus, body size, elytral maculation).

Sympatry and character displacement: where this is known to occur, in the Plata drainage between the São Paulo and Mato Grosso forms, and where it is suspected, along the eastern front of the Andes between the Cayenne and Central American-Mato Grosso forms, reproductive isolation must have taken place; yet the overall picture suggests that there is reproductive continuity over the range of *R. stigma* as a whole. The evidence for sympatry and character displacement for the Cayenne and Central American-Mato Grosso forms is two-fold: the apotypic coloration of the Central American and Mato Grosso forms, and the atypical male phallus of the Cayenne form; the hypothesis needs verification.

Speciation: it is possible that full reproductive isolation has in fact been attained, and that the São Paulo form is in fact a distinct species. Even though specimens from areas 1 and 2 are constantly distinguishable, however, concordance between samples from area 1 and the southern part of area 2 is unlikely to be coincidence, and I therefore regard them as conspecific. In the northern part of the Plata drainage, the São Paulo and Mato Grosso forms are sympatric and divergent, and obviously reproductively isolated. Here, curious events have occurred: not only has character displacement occurred (on part of the São Paulo form), but the São Paulo form is much scarcer than elsewhere in its range; presumably there has been niche specialization, and I suspect also that the São Paulo form has been largely displaced from this area.

Incomplete though the pattern is, and despite its complexity, it is neatly understood in terms of the system of postulated Pleistocene forest refugia summarized by Vuilleumier (1971). Thus, area 1 corresponds to the Mato Grosso de Goias refugium; area 2 may be either an extension of area 3, or may represent the Belem refugium; area 3 represents the Guyana refugium, or perhaps a combination of this and one or more of the western refugia (not resolvable on available material); area 4 is a hybrid zone; area 5 encompasses the Choco, Nechi, Catabumbo, and Cordillera de la Costa refugia, which may have been a continuum; and area 6 corresponds nicely with the Madeira-Tapajoz refugium, though perhaps continuous with the eastern Peru refugia. If the refugial areas were small enough and of long enough duration, then the isolations brought about during the latest glacial phase of the Pleistocene are probably sufficient to account for all observed variation. Area 2 populations, whether a separate refugial form (Bahia form) or a spur of the Cayenne form (area 3), spread along coastal drainages of Brazil; they presumably are continuous with area 3 populations, and probably with those populations of area 1 that have spread into the coastal drainages (e.g., the Sabara, Minas Gerais locality). The area 3 populations spread outward from the Guyana refugium along the northeastern coast of South America and inland far up the Amazon basin, establishing contact and hybridizing with the Central American form in Guyana and eastern Venezuela; probably hybridizing with the Mato Grosso form along southern tributaries of the Amazon; and probably establishing secondary contact with the Central American-Mato Grosso forms on the Upper Amazon and there undergoing character displacement. Area 5 populations probably originated from a series of refugia in Central America and northwestern South America, spreading eastward to Trinidad and northward to Mexico, hybridizing with area 3 populations in eastern Venezuela and Guyana, perhaps linking with area 6 populations southward along the Andes, and perhaps in secondary contact with westernmost area 3 populations. The refugial area for area 6 may have been drained by southern tributaries of the Amazon or by upper parts of the Plata, or both; regardless, the Mato Grosso form has expanded its range in all directions to include as well the Upper Amazon and coastal drainages of northeastern Brazil (e.g., Barra), and secondary contact has been established with areas 1, 2, 3, and perhaps 5. Hybridization is suspected for the Mato Grosso form with the Bahia form and eastern Cayenne form, sympatry is known with the São Paulo form and suspected with the western Cayenne form, and hybridization is postulated with the Central American form. The São Paulo form (area 1) is parapatric with the Bahia form at least in the south and is sympatric with the Mato Grosso form in the west: its postulated history is refuge in the Mato Grosso de Goias (i.e., Plata) refugium, with subsequent expansion; parapatry with the Bahia form in the south, maintained by mountain barriers, but probable hybridization in the north where the São Paulo form expanded to a coastal drainage basin; and physical, ecological, and morphological displacement in the west following penetration of its range by the Mato Grosso form.

Phylogenetic relationships. – The elytral maculation (of the plesiotypic Cayenne and Bahia forms), slender phallus, and fine endophallus spicules indicate relationships with *R. brevicollis* and *R. pseudostigma.* Similarity of the other 2 species with one another, coupled with the coarsely punctate elytral striae of *R. stigma,* suggest that *R. stigma* is sister to the ancestor of *R. brevicollis* and *R. pseudostigma.*

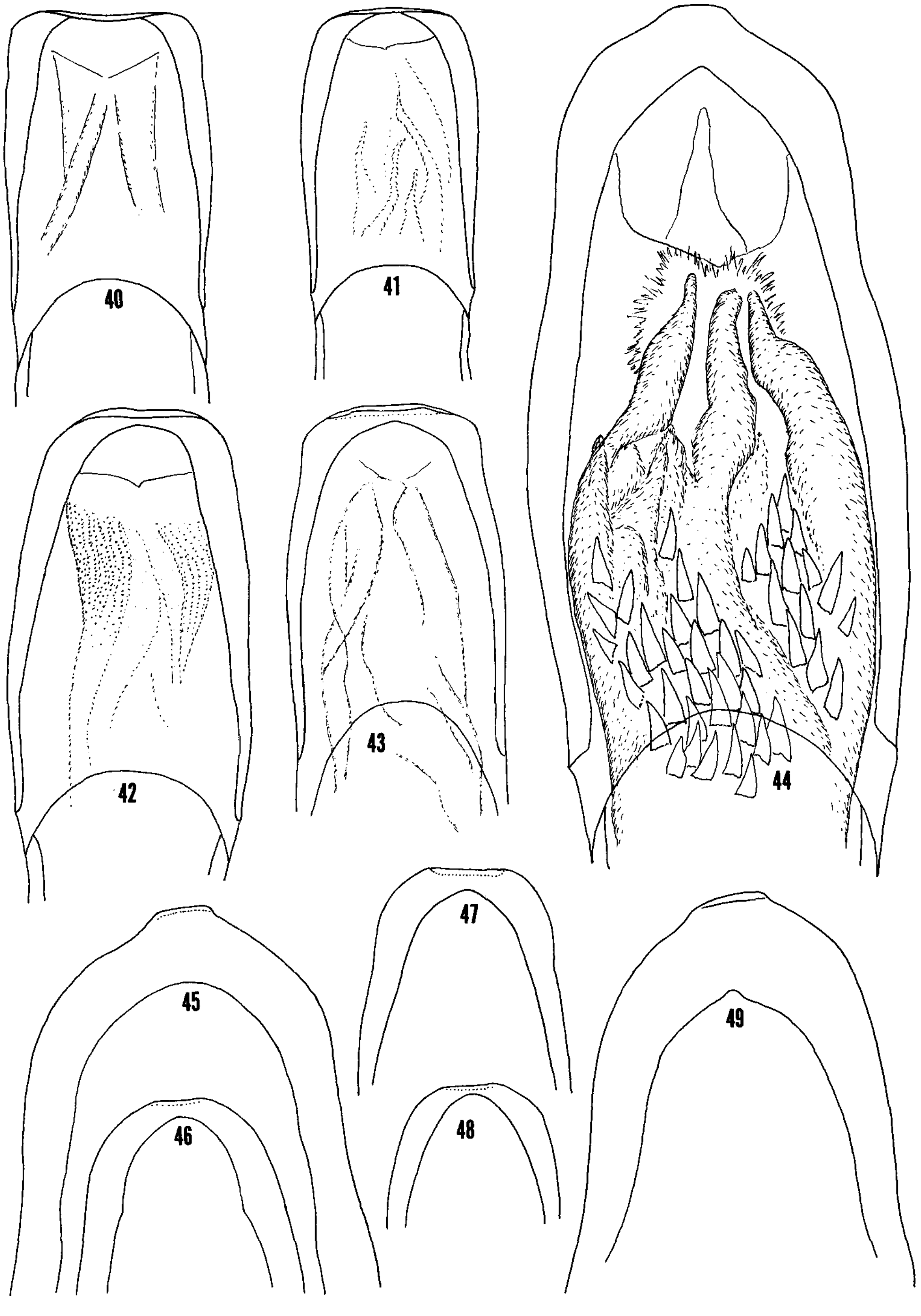
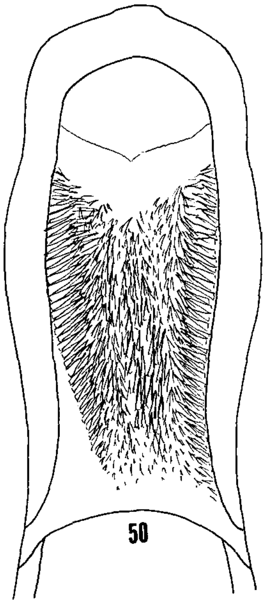


Fig. 40-44. *Rhinochenus* spp., phallus ventral aspect: 40, *R. fiedleri*; 41, *R. klagesi*; 42, *R. maculipes*; 43, *R. transversalis*; 44, *R. chevrolati*. Fig. 45-49. *Rhinochenus* spp., phallus apex, dorsal aspect: 45, *R. reichei*; 46, *R. maculipes*; 47, *R. transversalis*; 48, *R. klagesi*; 49, *R. chevrolati*.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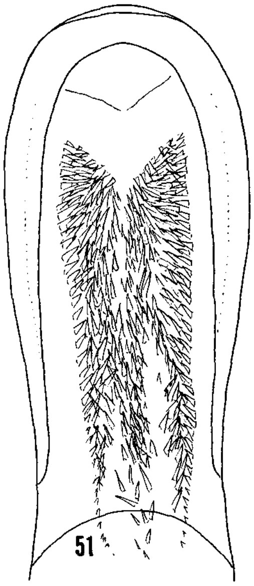
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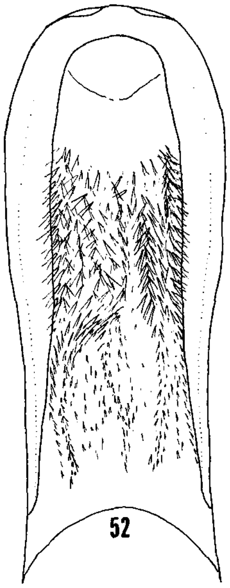
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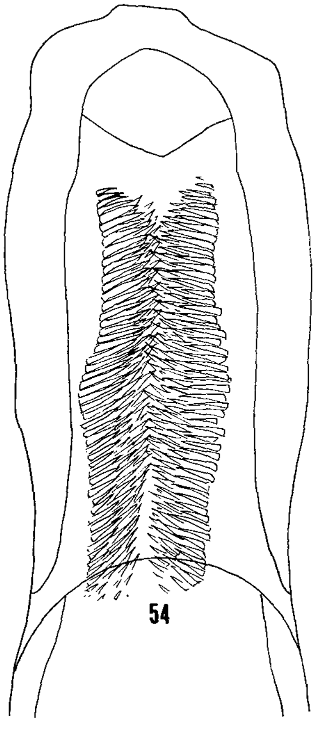
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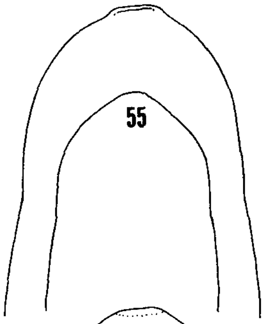
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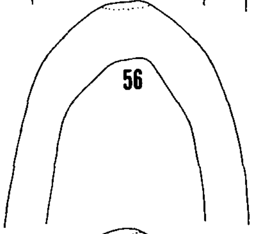
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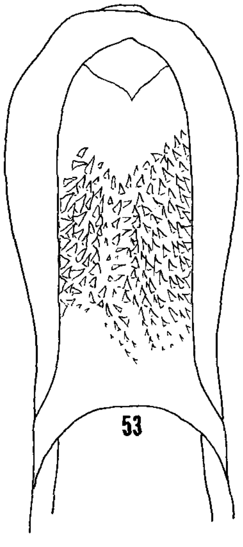
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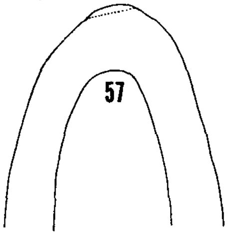
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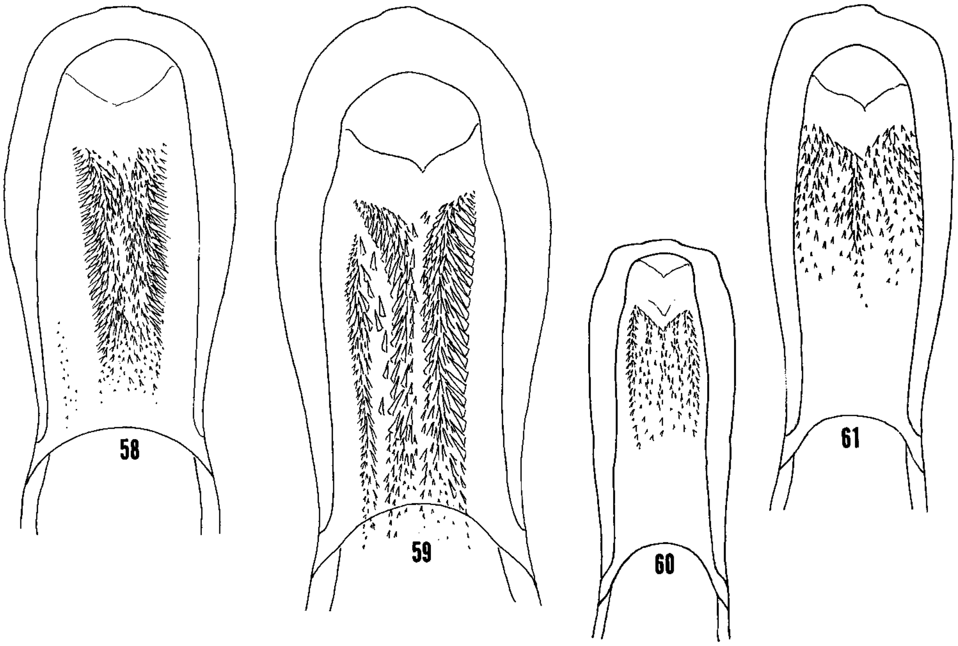
Fig. 50-54. *Rhinochenus* spp., phallus, ventral aspect: 50, *R. x-rubra*; 51, *R. chorrensis;* 52, *R. janzeni;* 53, *R. thrombithorax;* 54, *R. caucensis.* Fig. 55-57, *Rhinochenus* spp., phallus apex, dorsal aspect: 55, *R. x-rubra*; 56, *R. chorrensis;* 57, *R. janzeni.*



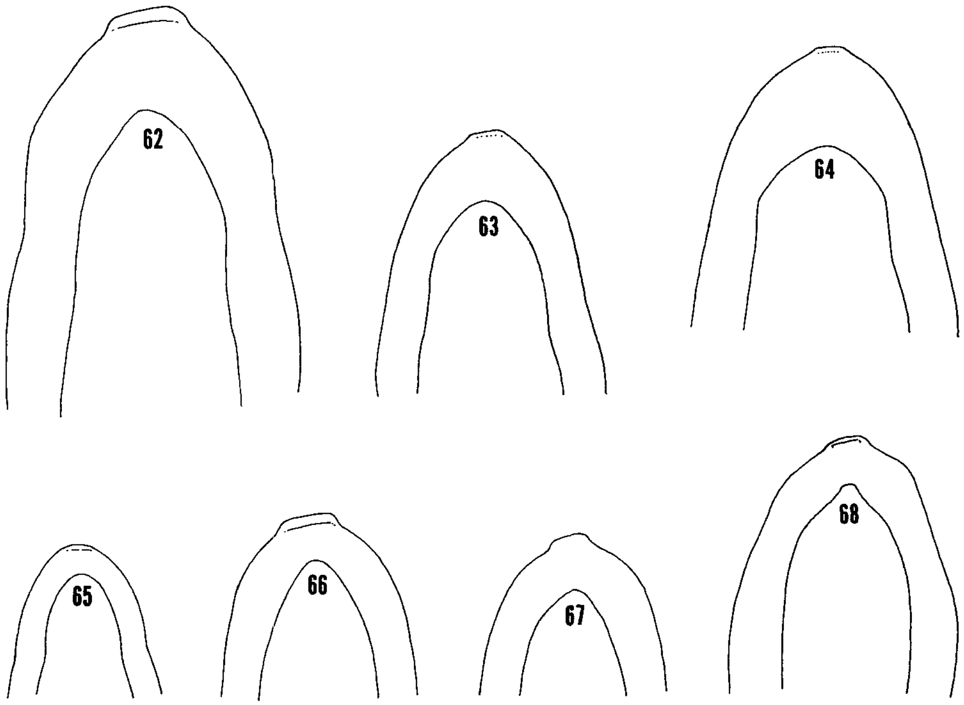
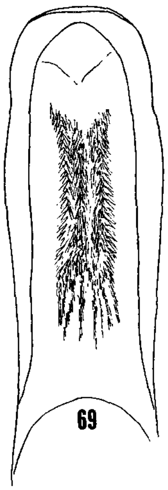
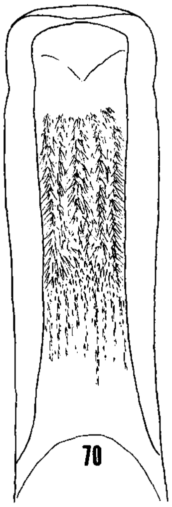
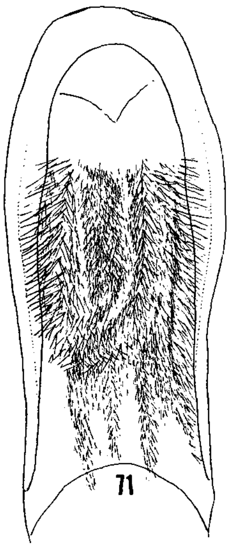
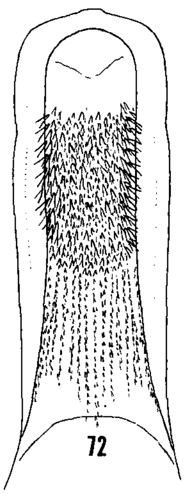


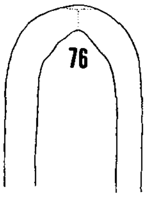
Fig. 58-61. *Rhinochenus* spp., phallus, ventral aspect: 58, *R. cinereopunctatus*, Chiquitos, Bolivia; 59, same, Campo Grande, Brazil; 60, *R. brevicollis*, Mantecal, Venezuela; 61, *R. pseudostigma*, St. Laurent, Cayenne. Fig. 62-68, *Rhinochenus* spp., phallus apex, dorsal aspect: 62, *R. caucensis*; 63, *R. cinereopunctatus*, Chiquitos, Bolivia; 64, same, Campo Grande, Brazil; 65, *R. brevicollis*, Mantecal, Venezuela; 66, *R. pseudostigma*, Santarem, Brazil; 67, same, St. Laurent, Cayenne; 68, *R. thrombithorax*.

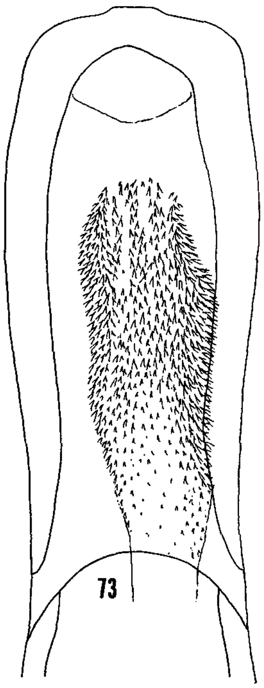


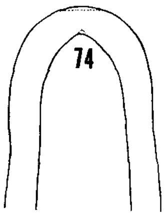


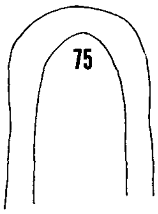


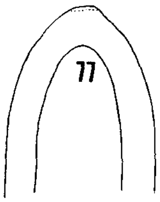


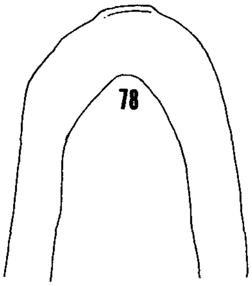












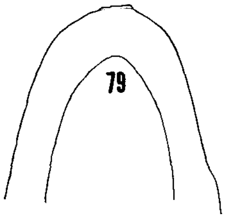


Fig. 69-73. *Rhinochenus stigma,* phallus, ventral aspect: 69, Santarem, Brazil; 70, Bahia, Brazil; 71, Joazeiro, Brazil (aberration); 72, Caqueta, Colombia; 73, Chiquitos, Bolivia. Fig. 74-79. *Rhinochenus stigma,* phallus apex, dorsal aspect: 74, Santarem, Brazil; 75, Bahia, Brazil; 76, Ilha do Bananal, Brazil; 77, Caqueta, Colombia; 78, Chiquitos, Bolivia; 79, Joazeiro, Brazil (aberration).

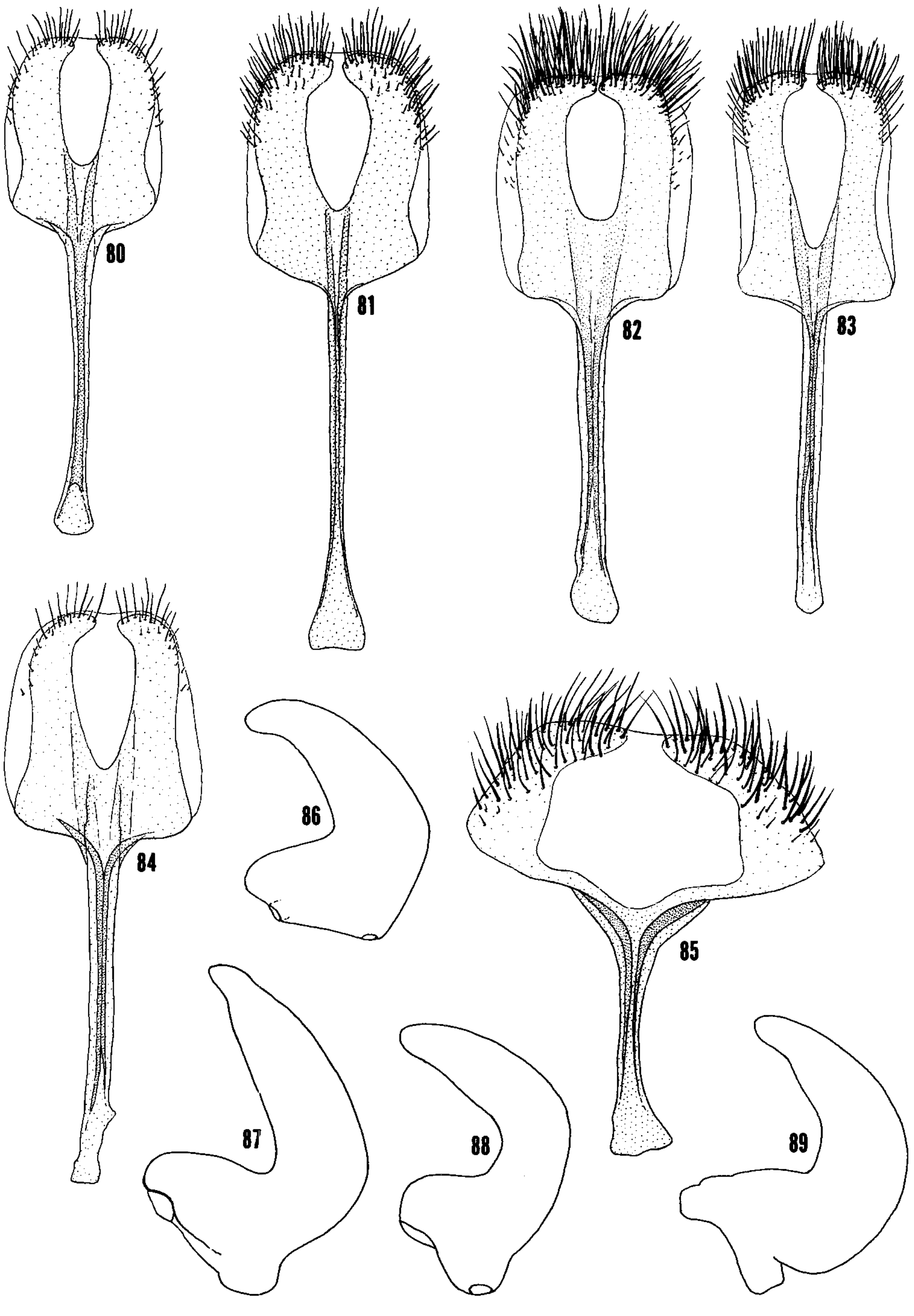


Fig. 80-85. *Rhinochenus* spp., female eighth sternite: 80, *R. klagesi*; 81, *R. maculipes*; 82, *R. transversalis*, Villa Colon, Costa Rica; 83, same, Kourou, Cayenne; 84, same, Esparta, Costa Rica (aberration); 85, *R. mangabeirensis*. Fig. 86-89. *Rhinochenus* spp., spermatheca: 86, *R. klagesi*; 87, *R. maculipes*; 88, *R. transversalis*; 89, *R. mangabeirensis*.

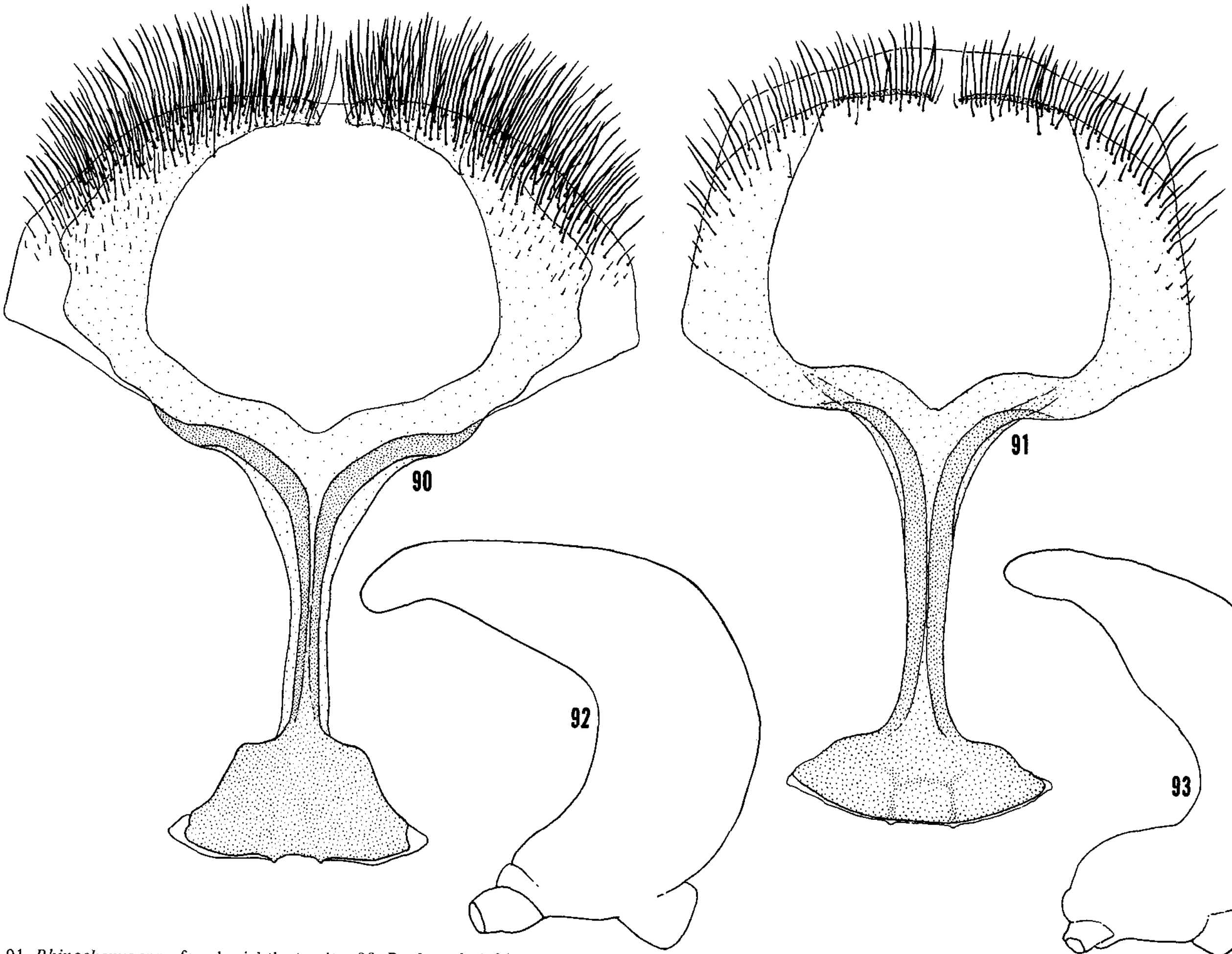


Fig. 90-91. *Rhinochenus* spp., female eighth sternite: 90, *R. chevrolati*; 91, *R. reichei*. Fig. 92-93. *Rhinochenus* spp., spermatheca: 92, *R. chevrolati*; 93, *R. reichei*.

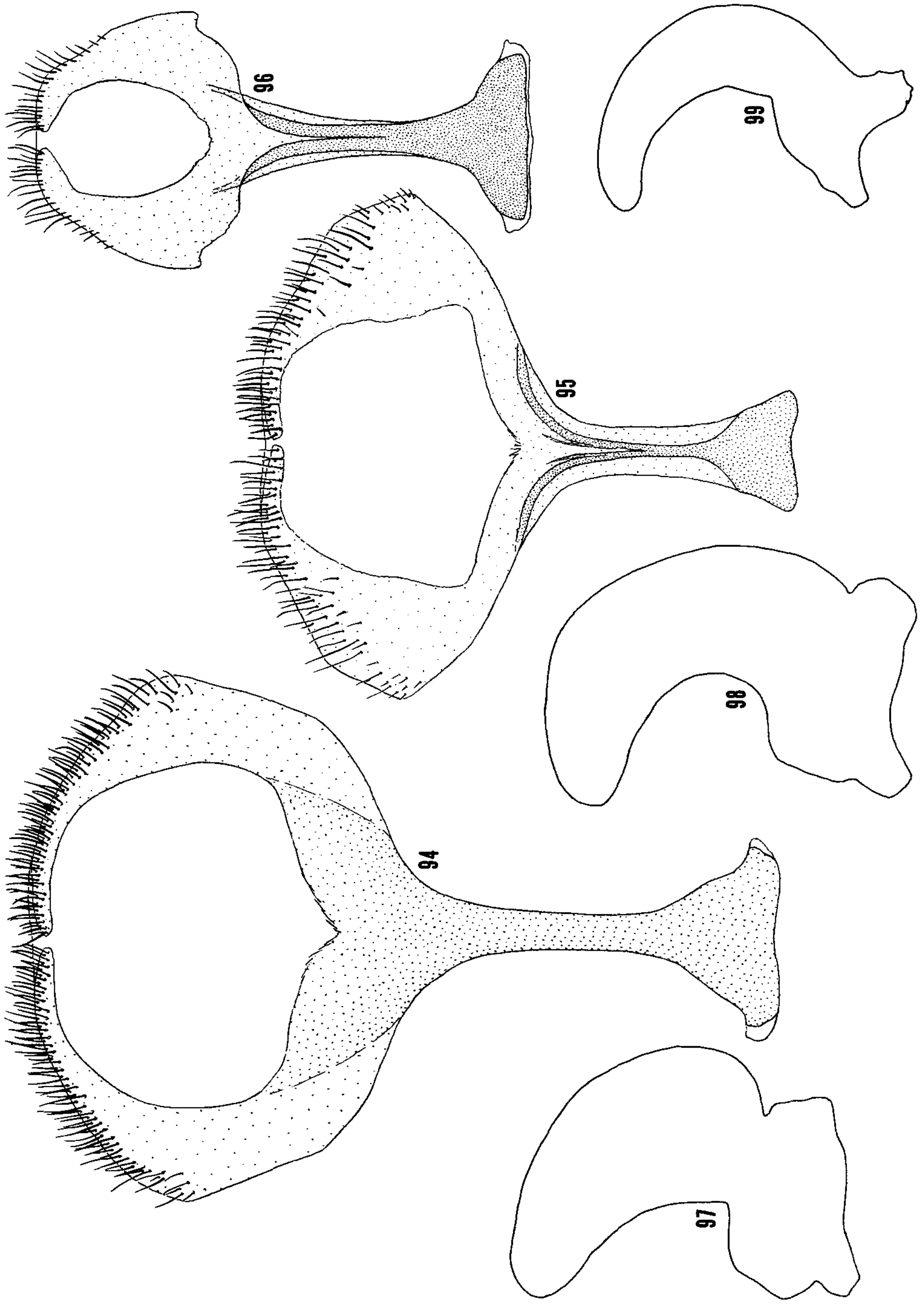


Fig. 94-96. *Rhinochenus* spp., female eighth sternite: 94, *R. hercules*; 95, *R. amapensis*; 96, *R. x-rubra*. Fig. 97-99. *Rhinochenus* spp., spermatheca: 97, *R. hercules*; 98, *R. amapensis*; 99, *R. x-rubra*.

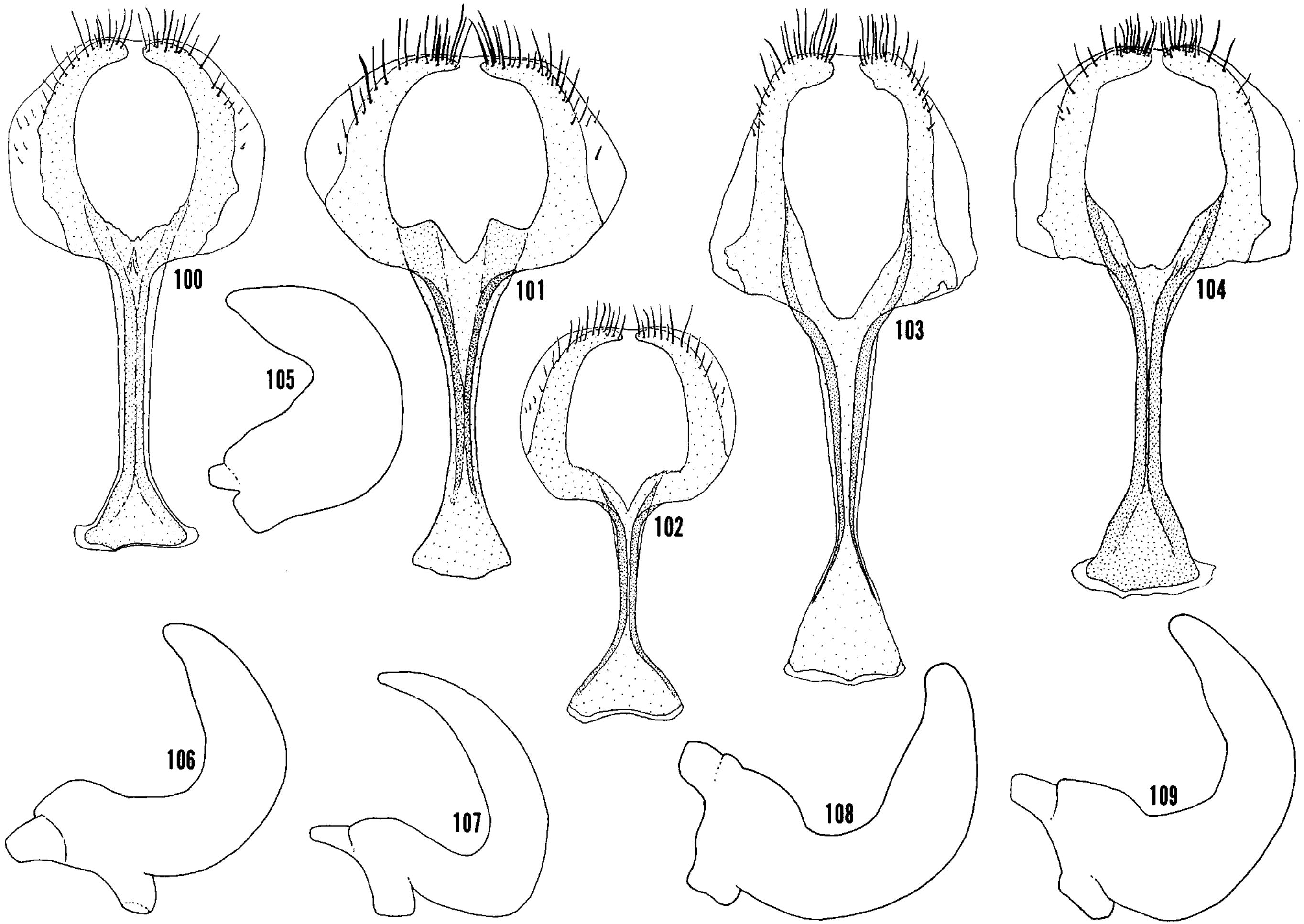


Fig. 100-104. *Rhinochenus* spp., female eighth sternite: 100, *R. chorrensis*; 101, *R. janzeni*; 102, *R. thrombithorax*; 103, *R. caucensis*, Valle del Cauca, Colombia; 104, same, Trinidad.
Fig. 105-109. *Rhinochenus* spp., spermatheca: 105, *R. chorrensis*; 106, *R. janzeni*; 107, *R. thrombithorax*; 108, *R. caucensis*, Trinidad; 109, same, Valle del Cauca, Colombia.

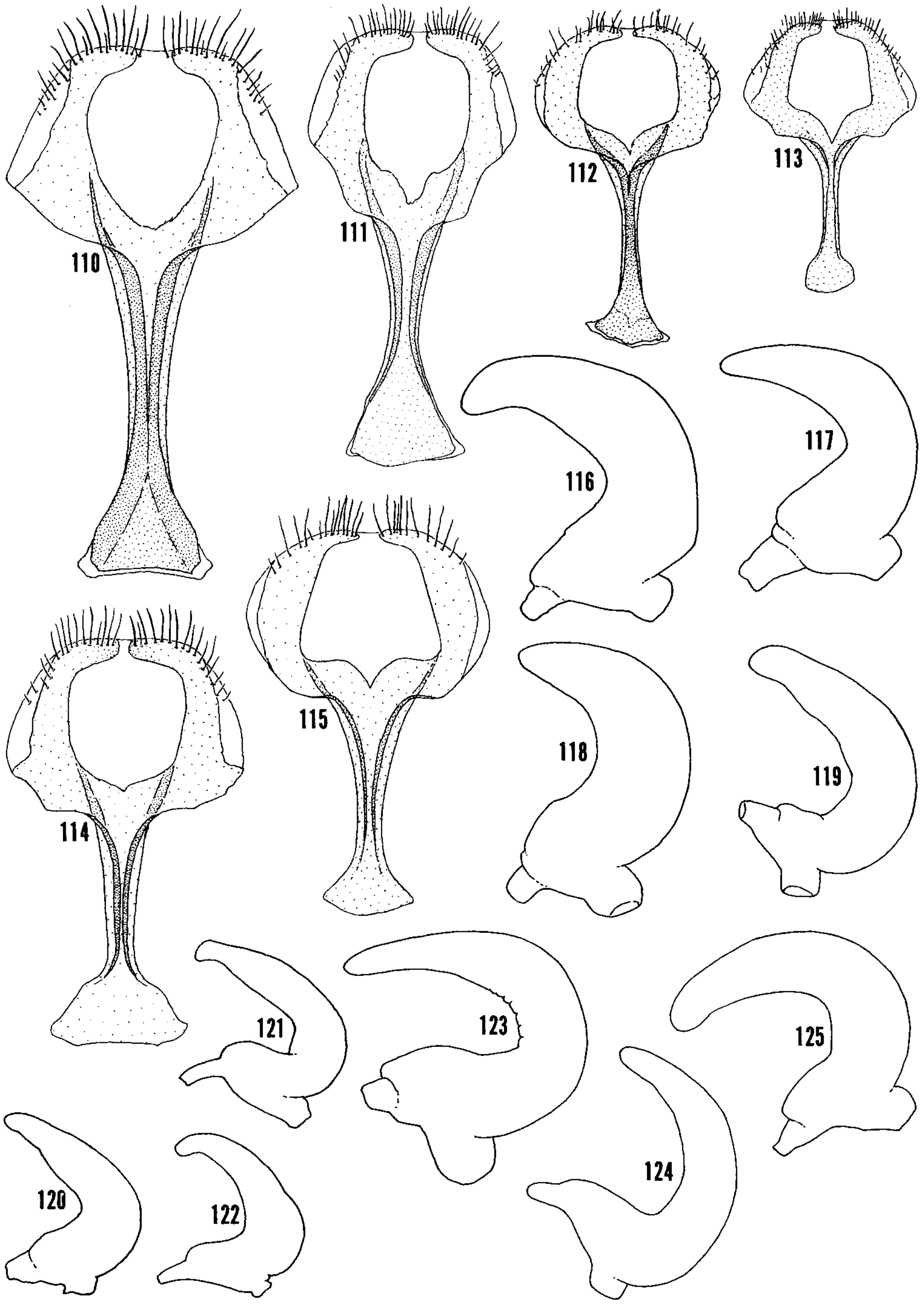


Fig. 110-115, *Rhinochenus* spp., female eighth sternite: 110, *R. cinereopunctatus*, Campo Grande, Brazil, 111, same, Chiquitos, Bolivia; 112, *R. brevicollis*, Mantecal, Venezuela; 113, same, Jundiai, Brazil; 114, *R. pseudostigma*, St. Laurent, Cayenne; 115, same, Santarem, Brazil. Fig. 116-125. *Rhinochenus* spp., spermatheca: 116, *R. cinereopunctatus*, Acre, Brazil; 117, same, Campo Grande, Brazil; 118, same, Chiquitos, Bolivia; 119, *R. pseudostigma*; 120, *R. brevicollis*, Mantecal, Venezuela; 121, same, Calabozo, Venezuela; 122, same, Jundiai, Brazil; 123, *R. stigma*, Chiquitos, Bolivia; 124, same, Boruca, Costa Rica; 125, same, Organ Mountain, Brazil.

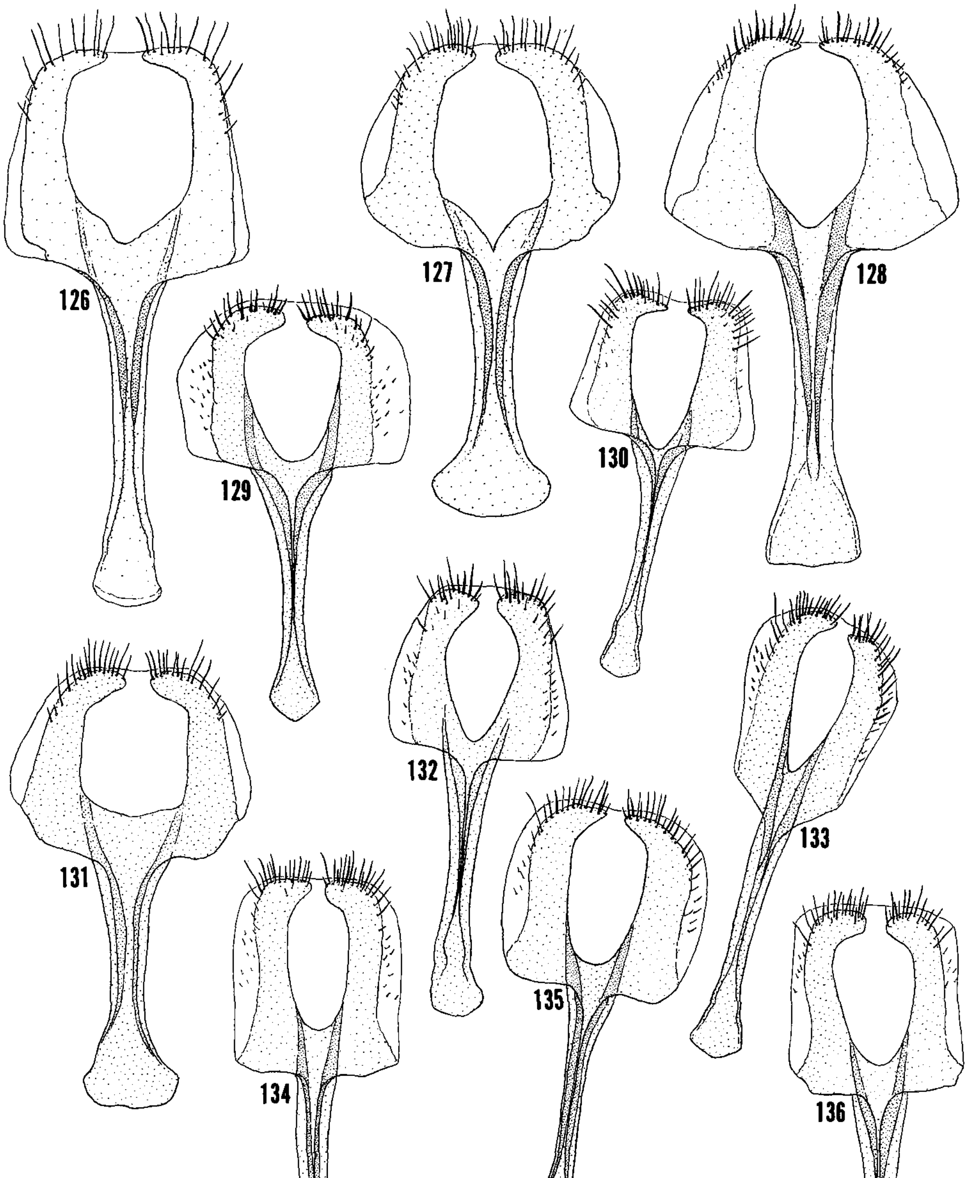


Fig. 126-136. *Rhinochenus stigma,* variation in female eighth sternite: 126, Chiquitos, Bolivia, area 1 or São Paulo form, western variant; 127, locality unknown, variant of São Paulo form; 128, Organ Mountain, Brazil, São Paulo form, western variant; 129, São Paulo, Brazil, São Paulo form; 130, Bahia, Brazil, area 2 or Bahia form; 131, Joazeiro, Brazil, Bahia form, variant; 132, same, normal; 133, Santarem,Brazil, area 3 or Santarem form; 134, Georgetown, Guyana, area 4 or transitional form; 135, Villa Colon, Costa Rica, area 5 or Central American form; 136, Ilha do Bananal, Brazil, area 6 or Mato Grosso form.

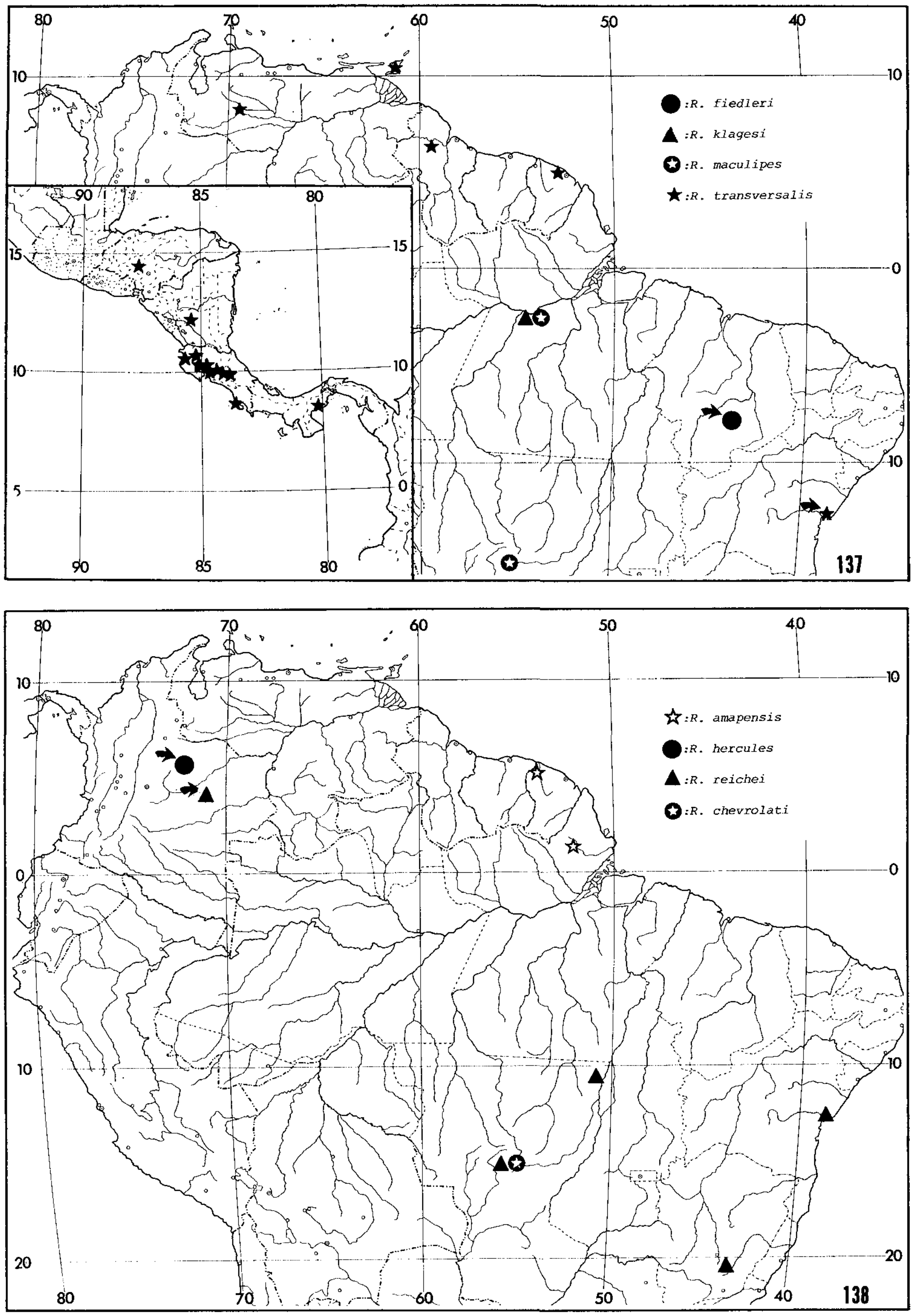
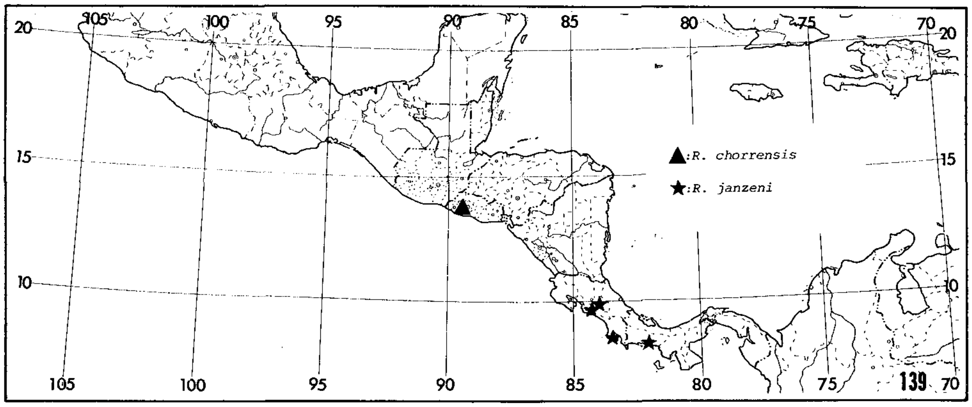


Fig. 137-138. *Rhinochenus* spp., distribution records, arrows indicate imprecise or dubious records: 137, *transversalis* group (inset has Central American records of *R. transversalis*); 138, *hercules* and *reichei* groups.



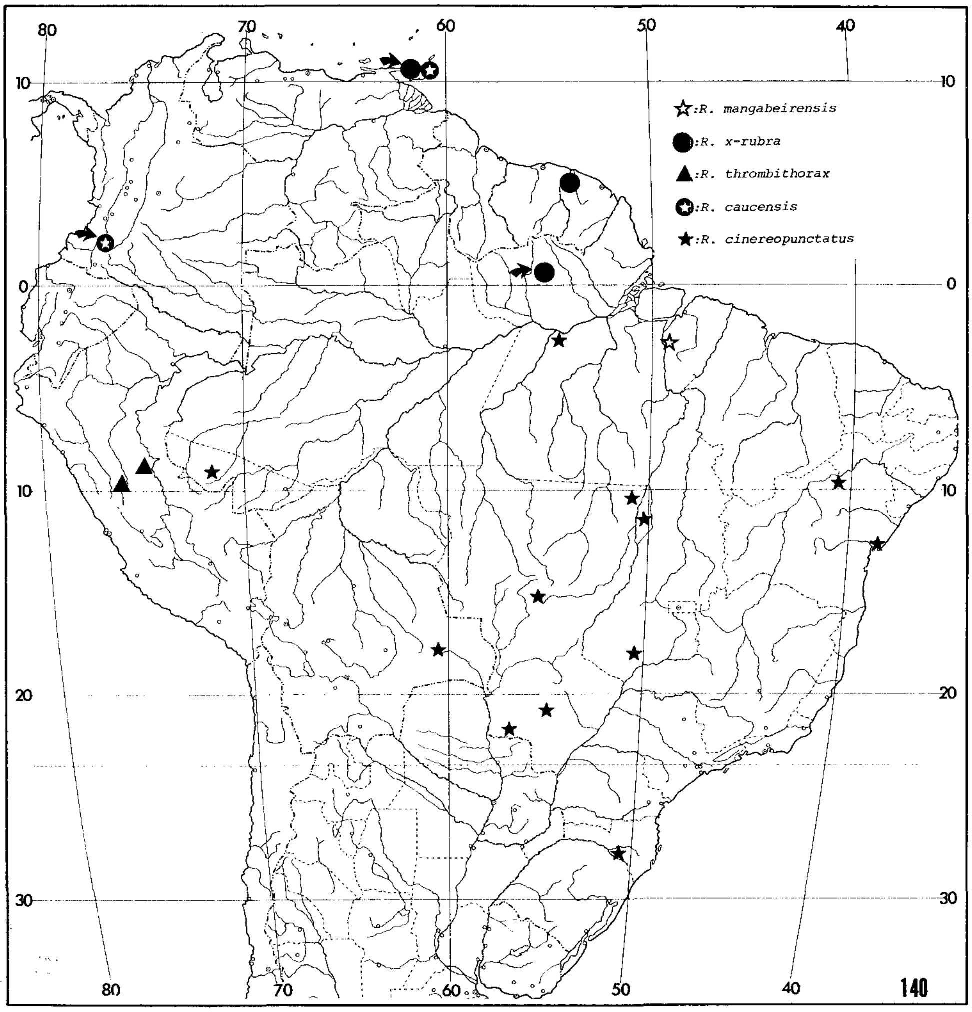


Fig. 139-140. *Rhinochenus* spp., distribution records, arrows indicate imprecise or dubious records: 139, *R. chorrensis* and *R. janzeni*; 140, *R. mangabeirensis, R. x-rubra, R. thrombithorax, R. caucensis,* and *R. cinereopunctatus.*

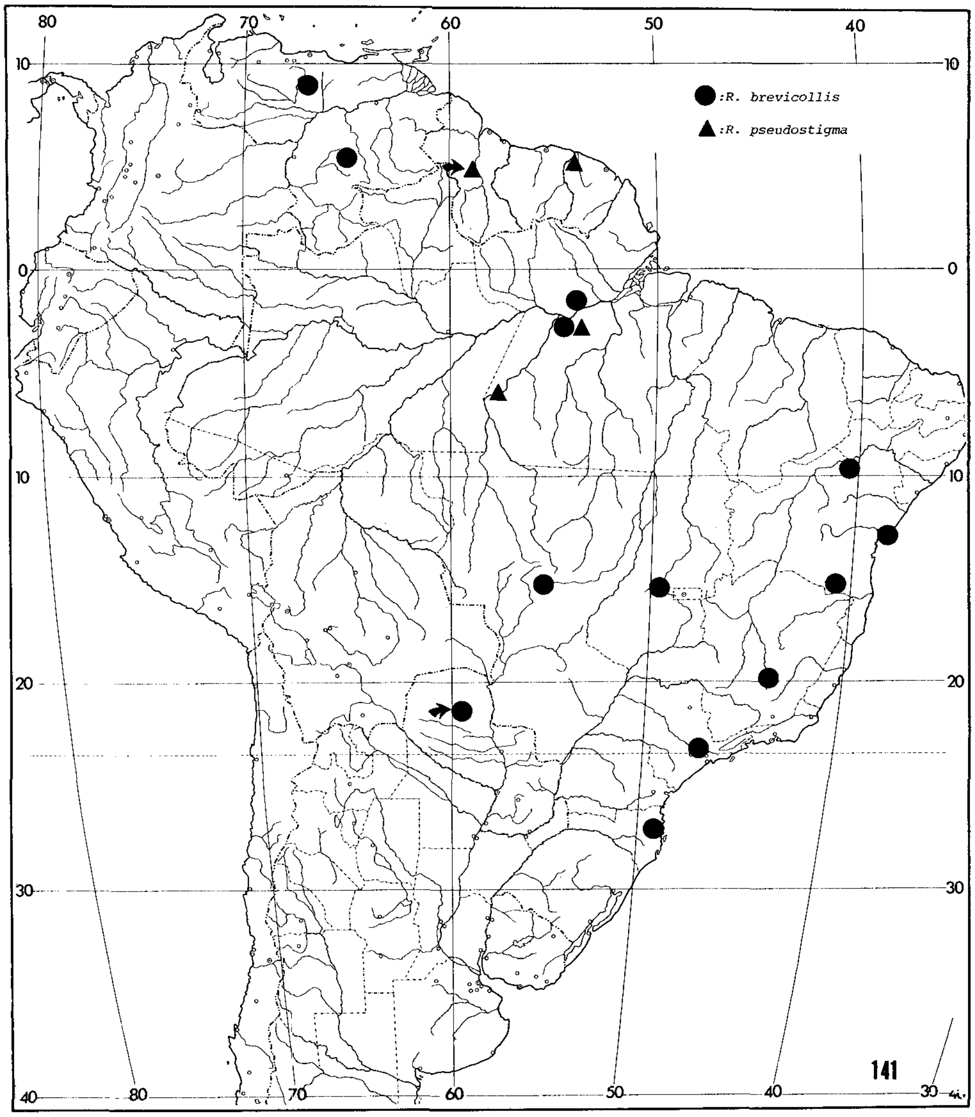


Fig. 141. *Rhinochenus brevicollis* and *R. pseudostigma*, distribution records.

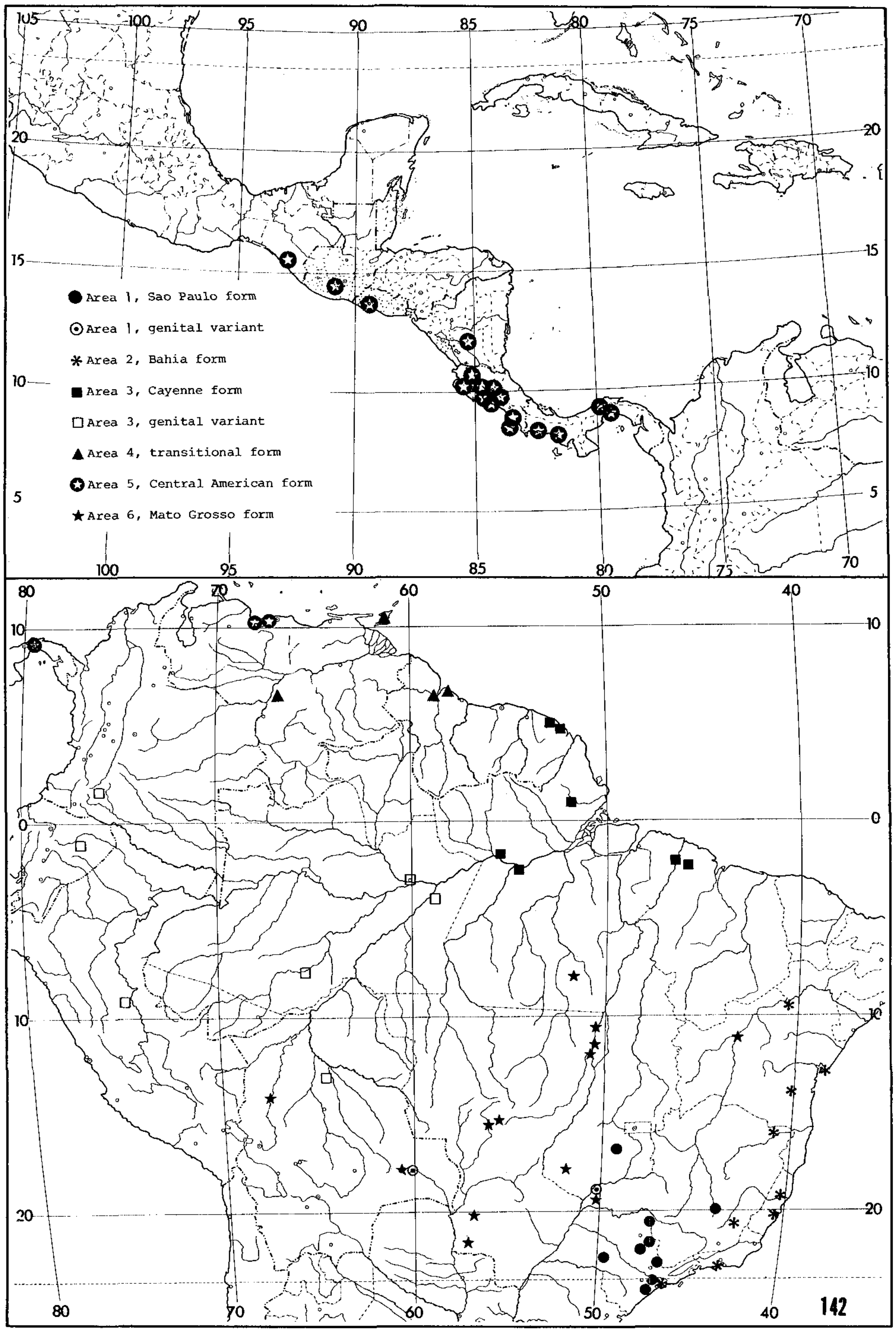


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Fig. 142. *Rhinochenus stigma*, distribution records in Central America (above) and South America (below; see text for discussion of genital and chromatic variation.

EVOLUTIONARY CONSIDERATIONS

In a previous study (Whitehead 1972) I explained at some length my philosophical and procedural approaches concerning the "why" and "how" of evolutionary analyses. For additional discussion of theory and application, see Ball (1975). In this section I attempt to reconstruct evolutionary pathways of *Rhinochenus*, briefly, and to develop a preliminary, general synthesis of Middle American zoogeography with particular relation to cyclic Pleistocene climatic events, at length.

The reconstructed phylogeny

To classify character states of the carabid genus *Phloeoxena* for phylogenetic analysis, Ball (1975) used "ex-group", "in-group", and "group trend" comparisons. To use all 3 sets of comparisons it is necessary to have intimate knowledge of related and peripheral taxa. As a recent convert to weevil systematics, I lack such in-depth knowledge and therefore cannot sucessfully make "ex-group" comparisons. Consequently my notations about apotypy and plesiotypy for the basal dichotomy of the reconstructed phylogeny (Fig. 143) are based exclusively on "in-group" and "group trend" comparisons.

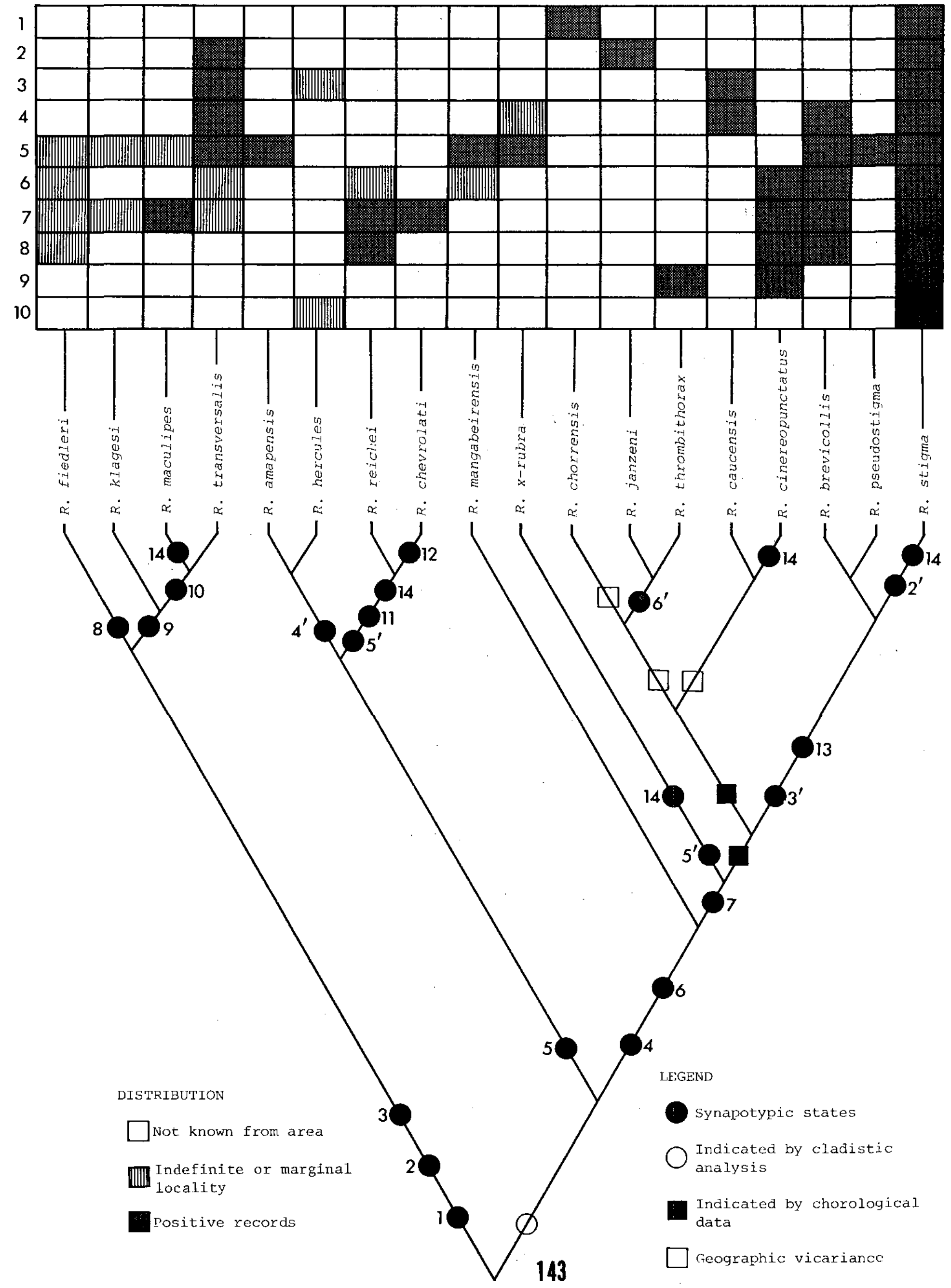
Phylogenetic analysis of *Rhinochenus* is difficult because the species are similar and, I believe, to a large extent relatively recently differentiated. The only major morphological differences, in male genitalia and in external features, are those of the basal dichotomy. Added to the pattern of overall morphological similarity are, on the one hand, extensive variation, and on the other hand, cryptic or mimetic convergences. Thus, in the widespread and greatly varied *R. stigma,* structural variation of the male genitalia greatly decreases reliability of this organ for phylogenetic analysis, and in some geographic areas cryptic resemblance to other species indicates convergences that becloud the classification of character states. Moreover, some species are known from one sex only, and in particular no males are known for the *hercules* and *mangabeirensis* groups. As a result, I have not been able to detect synapotypic states for all stem species, and have therefore resorted to chorological data to suggest likely relationships in some parts of the reconstruction.

Weevil/host-plant associations also provide no useful phylogenetic clues. One species from 1 lineage of the *stigma* group (*R. brevicollis*) has apparently shifted from *Hymenaea* to *Copaifera,* but its phylogenetic interest is limited to the potential for a future *Copaifera/Rhinochenus* radiation similar in complexity to the existing *Hymenaea/Rhinochenus* radiation; see discussions of natural history and phylogenetic relationships of *R. brevicollis.*

The reconstructed phylogeny is illustrated in Fig. 143, with character states classified in table 1 and refugial areas mapped in Fig. 150. An interpretive summary follows, below.

The *transversalis* group: this group is defined by metasternal and male genital characteristics, arbitrarily treated as synapotypic. Its sister group lacks definition by stated synapotypy, but is structurally homogeneous and exhibits "group trends" in various character states which themselves suggest common ancestry. Within the *transversalis* group, *R. fiedleri* is unique among *Rhinochenus* in having scattered punctations on sterna 3-4, and the other 3 species are synapotypic in having the rostrum impunctate medially basad to the frontal fovea. I suspect that radiation of this group occurred during the Pleistocene.

The *hercules* and *reichei* groups: large body size and bare elytral base are synapotypic for these groups ("in-group" comparisions), and the position of the antennal insertion defines their sister lineage as monophyletic; also the pronotum of the sister lineage is proportionately narrow, secondarily wide in some members of the *stigma* group. The *reichei* group is defined by synapotypic reduction of elytral vestiture, coarse strial punctures, and alternately raised elytral intervals. The *hercules* group is defined by the basal placement of the antennal insertion; the male



	R. fiedleri	R. klagesi	R. maculipes	R. transversalis	R. amapensis	R. hercules	R. reichei	R. chevrolati	R. mangabeirensis	R. x-rubra	R. chorrensis	R. janzeni	R. thrombithorax	R. caucensis	R. cinereopunctatus	R. brevicollis	R. pseudostigma	R. stigma
1	□	□	□	□	□	□	□	□	□	□	■	□	□	□	□	□	□	■
2	□	□	□	■	□	□	□	□	□	□	□	■	□	□	□	□	□	■
3	□	□	□	■	□	▥	□	□	□	□	□	□	□	■	□	□	□	■
4	□	□	□	■	□	□	□	□	□	▥	□	□	□	■	□	■	□	■
5	▥	▥	▥	■	■	□	□	□	■	■	□	□	□	□	□	■	■	■
6	▥	□	□	▥	□	□	▥	□	▥	□	□	□	□	□	■	■	□	■
7	▥	▥	■	▥	□	□	■	■	□	□	□	□	□	□	■	■	□	■
8	▥	□	□	□	□	□	■	□	□	□	□	□	□	□	■	■	□	■
9	□	□	□	□	□	□	□	□	□	□	□	□	■	□	■	□	□	■
10	□	□	□	□	□	▥	□	□	□	□	□	□	□	□	□	□	□	■

DISTRIBUTION

□ Not known from area

▥ Indefinite or marginal locality

■ Positive records

LEGEND

● Synapotypic states

○ Indicated by cladistic analysis

■ Indicated by chorological data

□ Geographic vicariance

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Fig. 143. Reconstructed phylogeny of species of *Rhinochenus*, and occurrence in major refugial areas; see text and tables 1-2.

Table 1. Characters and character states used for reconstructed phylogeny of *Rhinochenus* (Fig. 143). States are classified as apotypic by "in-group" (*), "group-trend" (+), or arbitrary (o) comparisons.

Character, plesiotypic state	Apotypic state
Metasternum, median sulcus: glabrous	1, with erect setae basally (o)
Phallus, apex: acute, lipped	2, truncate (o); 2′, arcuate, not lipped (*)
Endophallus, spicules: large	3, absent (o); 3′, fine (*)
Antennal insertion: behind basal 0.33 of rostrum	4, in front of basal 0.33 (+); 4′, far behind basal 0.33 (*)
Elytral vestiture: dense basally	5, bare basally (+); 5′, reduced in basal 0.66 (+); 5″, x-cruciate (*)
Pronotum, proportions: transverse	6, about as long as wide (*); 6′, transverse (*)
Female eighth sternite, apical setae: dense	7, sparse (*)
Abdominal sterna 3-4, punctures: in transverse bands	8, scattered (*)
Rostrum, vestiture in front of frontal fovea: dense	9, bare (*)
Pronotum, form: subconical	10, conical (*)
Elytral intervals: regular	11, alternately costate (*)
Head, vestiture: dense	12, bare (*)
Phallus, form: broad	13, narrow (*)
Strial punctures: fine	14, coarse (*)

genitalia are unknown. These 2 groups are distinguished only for convenience; they obviously are closely related and probably evolved into their vicarious component species during the Pleistocene.

The *mangabeirensis* group: the only known specimen, a female, is not herein defined by synapotypy; its sister group is defined as monophyletic by modification of the female eighth sternite. The presence in northeastern Brazil of this species, of representatives of all other major lineages, and of various divergent components of the *stigma* group suggests that this area may have been an important proving ground for *Rhinochenus* radiation.

The *stigma* group: this group is defined as monophyletic by characteristics of the female eighth sternite, notably by reduction of the apical setae to a single row fringe. Within the group, analysis is exceedingly difficult, because of lack of morphological definition. The position of *R. x-rubra*, notably, is dubious: this species is highly apotypic in pattern, plesiotypic in other respects, and could alternatively be placed as another allopatric component of the *chorrensis-janzeni-thrombithorax-caucensis-cinereopunctatus* complex—(1), as sister to this complex; (2), as sister to *caucensis-cinereopunctatus*; or (3), as sister to *R. cinereopunctatus*. These alternatives are not tempting: there is no morphological basis for (1) or (2); and for (3) the only morphological basis is relatively coarse strial punctures, a less convincing basis for relationship than the overall similarity of *R. caucensis* and *R. cinereopunctatus*. If, alternatively, *R. x-rubra* is considered related to *brevicollis-pseudostigma-stigma*, then all 4 species are sympatric and an explanation of geographic differentiation is made improbably complicated.

Suggested relationships of other components of the *stigma* group are the following: *brevi-*

collis-pseudostigma-stigma share similarities in appearance, narrow male phallus, and fine spicules in the endophallus; the other species have the plesiotypic broad phallus and coarser spicules, and appear to be vicarious elements of a single lineage. In this latter lineage, *janzeni-thrombithorax* are unequivocal sisters by virtue of secondarily broadened pronotum, and *caucensis-cinereopunctatus* are probable sisters as judged by their common trend to uniformly pale elytra. For additional considerations, see discussions of phylogenetic relationships for each species.

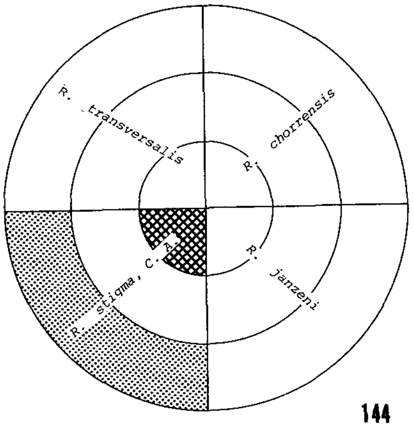
Cryptic and mimetic patterns

In 1 exchange of letters with D. H. Janzen, I noted that there seemed to exist instances of mimicry among distantly related species of *Rhinochenus* at some localities. In response, Janzen pointed out that the coloration of *Rhinochenus* is probably cryptic, with the bare pronotum and elytral maculae resembling the seed coat and the vestiture resembling interstitial pulp of *Hymenaea* fruits. In the discussions of some of the species I have remarked briefly on these matters. Here, I attempt to integrate these observations in a geographic context (Fig. 144-149). In this summary, the term "standard color pattern" refers to the normal pattern of "bare" (sparsely squamose, or with dark scales) pronotum and large, "bare" elytral macula contrasted against a dense field of pale elytral vestiture. The generalized "standard" color pattern is widespread among adult *Rhinochenus,* a roughly similar pattern recurring in all major phyletic lineages and probably plesiotypic. Other color patterns are termed "non-standard": (1) dark, mottled; (2) pale, macula reduced to at most a narrow fascia; (3) elytra x-fasciate; or (4) elytra glabrous in basal 0.66.

For background, some aspects of natural history require discussion. Adults of some "hole-driller" species are capable of emerging from the *Hymenaea* fruits through their own exit holes—*R. transversalis* and *R. janzeni* are known to do so—and perhaps most species have this ability. Adults of other species—including at least the Central American and Cayenne forms of *R. stigma*—are "non-holedrillers", dependent on external agents such as agoutis, peccaries, or deer to chew or break an opening in the pod wall.

At least 2 factors are critical for interpretation of cryptic patterns. First, for cryptic resemblance to seed and pulp to exist, the beetles must be subject to exposure against them as background. Such exposure obviously occurs with the non-holedrillers, but what of the holedrillers? Field observations provide the answer: though the holedrillers are, as species, capable of making their own exit holes, a conspicuous proportion of individuals do not use them. When the pods are cracked open, the beetles initially tend to be thanatose (i.e., "play dead") in an adaptive response to avoid predation. Second, members of some species cause the fruit pulp to discolor, and some do not. In Central America, fruits attacked by the non-holedrillers have discolored (darkened and mottled) pulp, whereas the pulp of fruits attacked by the hole-driller species *R. janzeni* and *R. transversalis* is not as discolored. The coloration and maculation of adults of these 3 weevil species match these observations.

For the standard Batesian or Muellerian forms of mimicry to occur, distasteful or otherwise noxious models must be known or postulated. The adult *Rhinochenus* is neither of these (Janzen has subjected them to predator acceptability tests), nor is there any known model. Yet, for 2 classes of reasons, I believe mimicry exists. First, certain "non-standard" color patterns are shared by distantly related species in certain areas but are not known in any species from other areas. Specifically, in northwestern South America (Fig. 145), *R. caucensis* and *R. transversalis* adults agree in varying from an elytral maculation consisting of a complete, narrow, irregular transverse band through a band broken into small spots to completely immaculate; these species are sympatric, and probably syntopic. Also, in southern South America (Chapada, Brazil, Fig. 148), *R. maculipes* and the Mato Grosso form of *R. stigma* are conver-



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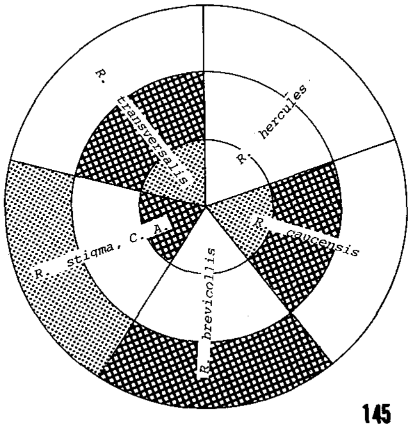

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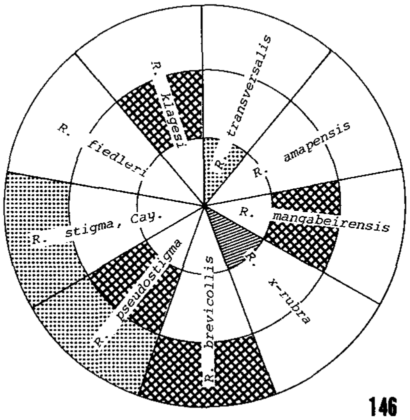

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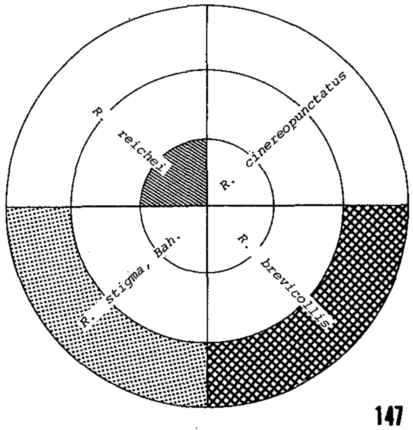

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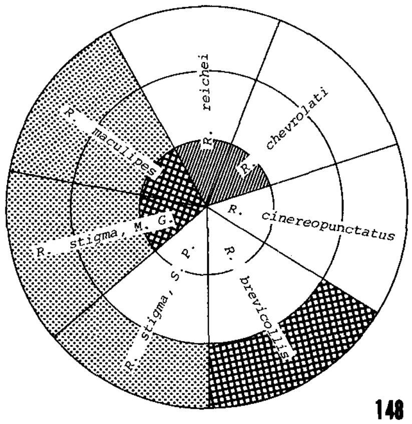

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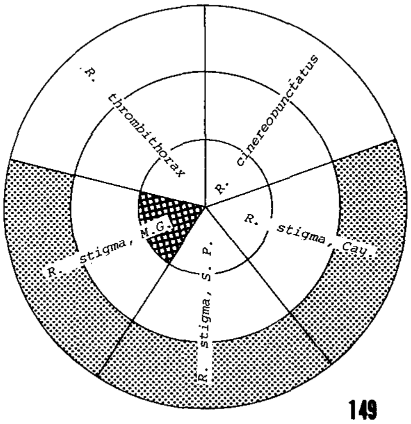

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Fig. 144-149. *Rhinochenus* spp., correlation of color pattern, possible mimicry, and behavior with geographic distribution: 144, Central America; 145, northwestern South America; 146, northeastern South America; 147, southeastern South America; 148, southern South America; 149, western South America. Color pattern, inner ring: blank, "standard" pattern; stipple, reduced maculae; line, reduced vestiture; hatch, mottled. Mimicry, middle ring: blank, no; hatch, yes. Behavior, outer ring: blank, holedriller; stipple, non-holedriller; hatch, *Copaifera*-eating.

gent in dark, mottled appearance and may also be mimetic, though in this pair the geographic correlation is weak (i.e., the Central American form of *R. stigma* also is dark and mottled; and at Santarem, Brazil, *R. maculipes* is sympatric with the Cayenne form of *R. stigma* which is wholly different in appearance). Second, where the "standard" pattern is represented it tends to be represented by several species, and, more important, at certain localities 2 or more distantly related species may be virtually precisely matched superficially. The most notable exexample is at Santarem (cf. Fig. 146), where (1) the "standard"pattern is represented by at least *R. klagesi, R. brevicollis, R. pseudostigma, R. stigma,* and *R. cinereopunctatus,* and (2) *R. klagesi* and *R. pseudostigma* form a precise match in size, form, color, and pattern. This seems to be no evolutionary accident, because (1), *R. pseudostigma* is geographically varied, and at other localities is not a precise match for the Santarem forms of *R. klagesi* or *R. pseudostigma* (nothing is known of variation in *R. klagesi*); (2), at Santarem, despite limited material, it is clear that there is little varation in either species; (3), these 2 species are quite distantly related, in fact are members of distantly related species groups; and (4), a member of still another species group, *R. mangabeirensis* is also nearly a precise match—it is from a geographically proximal locality, and I suspect that all 3 species are sympatric. I do not think the essentially precise match is plesiotypic, and cannot believe that it is coincidence. That is, whereas the generalized, "standard" pattern probably is symplesiotypic or ancestral, its perfection into a precise match among biologically distinct populations at any given locality indicates a special, local adaptation herein regarded as mimetic.

As a footnote to this general background, one which because of extremely limited data I cannot investigate in depth at this time, I add the observation that there are other, unidentified cryptorhynch weevils which closely resemble some *Rhinochenus* in form, size, and color pattern. One might expect such convergence, considering the marked diversity of tropical American Cryptorhynchinae. But, this convergence does not appear to be mere coincidence: these convergent forms are sympatric with the particular *Rhinochenus* that they most resemble, such as the Bahia and São Paulo forms of *R. stigma* with the complete elytral fascia. Why? Is this a further indication that mimetic complexes exist? Are these convergent weevils distasteful and thus the models for such mimetic complexes? Or are they, alternatively, another component of the *Hymenaea* fauna? I have no answers to these important questions.

With this background, I turn now to a more detailed analysis and synthesis. I do this in a geographic context (Fig. 144-149) to emphasize the correlation of sympatry with the various cryptic and mimetic patterns. I also attempt to suggest biological implications that may be worthy of investigation. Specifically, the ability to emerge through exit holes is phylogenetically primitive, and dependence on external agents is clearly a specialization. The Central American form of *R. stigma* is a non-holedriller; it also is dark and mottled, in cryptic adaptation to discoloration of fruit pulp. For purposes of this analysis, I suggest that these characteristics are coordinate. Consequently, I consider *R. maculipes* and the Central American and Mato Grosso forms of *R. stigma* as non-holedrillers. I suspect also that *R. pseudostigma* as well as the other forms of *R. stigma* are non-holedrillers that have not had sufficient evolutionary time to evolve the appropriate cryptic response; the rationale for this premise stems from the phylogenetic position of *R. brevicollis,* presumed to have evolved from a non-holedriller ancestor. These matters need field investigation.

Central America, southern Mexico to Panama (Fig. 144). – This area, particularly Costa Rica, is relatively well sampled. Four species are known to occur in Central America, 2 extending with various geographic forms into South America. Two, *R. chorrensis* and *R. stigma,* are sympatric in the north, and 3, *R. transversalis, R. janzeni,* and *R. stigma,* are sympatric in the south. All 4 are distinctive, thus no mimetic patterns exist. Three, *R. chorrensis, R. janzeni,* and *R. transversalis,* have the "standard" color pattern; probably all 3 are holedrillers, causing little or no pulp discoloration. The Central American form of *R. stigma* has a dark, mottled pattern, similar to that of the Mato Grosso form of *R. stigma*; this is a non-holedriller, with cryptic coloration to match fruit pulp discoloration.

Northwestern South America, northern Colombia to Venezuela and Trinidad (Fig. 145). – This area is poorly sampled, but does contain some obvious patterns. Species known are: *R. transversalis,* transitional from the "standard" Central American form to the nearly immaculate Cayenne form; *R. caucensis,* convergent with the sympatric form of *R. transversalis*; *R. hercules* and *R. brevicollis,* "standard" pattern; and *R. stigma,* mottled Central American form. One apparent mimetic system involves the sympatric and presumably syntopic *R. caucensis* and *R. transversalis* (cf. Fig. 19-20, 23-24). Probably, the only non-holedriller is *R. stigma,* and this probably is the only species causing pulp discoloration. Trinidad, eastern Venezuela, and Guyana form a transitional area, represented also by forms characteristic of northeastern South America and by transitional forms.

Northeastern South America, Guianas and northeastern Brazil to Amazon River (Fig. 146). – This area has been reasonably well sampled in general, but much more detailed investigation is needed. Species known are: *R. fiedleri* ("Brazil"), *R. klagesi, R. amapensis, R. mangabeirensis, R. brevicollis, R. pseudostigma,* and Cayenne form of *R. stigma,* "standard" pattern; *R. x-rubra,* elytra x-fasciate; and *R. transversalis,* elytra immaculate or nearly so. Along the Amazon River occur also some forms here treated as parts of more southern faunas (*R. maculipes* and *R. cinereopunctatus*); these are discussed under appropriate sections. None of the northeastern forms are dark, and none, therefore, are cryptic for discolored fruit pulp. At least 5 are sympatric along the Amazon River, have the "standard" pattern, and are quite similar in superficial appearance (except that *R. brevicollis* specimens are small). They may represent, or form part of, a mimetic complex. Nowhere else are so many similar forms congregated in the same area. In particular, *R. klagesi, R. mangabeirensis,* and *R. pseudostigma* (cf Fig. 12, 30)–members of separate species groups–nearly precisely match one another in form, size, and color pattern; I believe their resemblance must be mimetic.

Southeastern South America, Amazon River and coastal rivers to southern Brazil (Fig. 147). – This region is reasonably well sampled. Species known are: *R. cinereopunctatus, R. brevicollis,* and Bahia form of *R. stigma,* "standard" pattern; and *R. reichei,* elytra glabrous basally. These are non-mimetic. Probably all except *R. stigma* are holedrillers. The reduced vestiture pattern of *R. reichei* (and also of *R. chevrolati* from the next geographic area) suggests either that the interstitial pulp is darkened or that a larger proportion of the pulp is cleared away from the seed coat.

Southern South America, southern tributaries of Amazon River and northern tributaries of Plata River (Fig. 148). – This region is reasonably well sampled. Species known are: *R. maculipes* and Mato Grosso form of *R. stigma,* dark, mottled; the sister species *R. chevrolati* and *R. reichei,* see previous paragraph; and *R. cinereopunctatus, R. brevicollis,* and São Paulo form of *R. stigma,* "standard" pattern. Possibly, *R. maculipes* and the Mato Grosso form of *R. stigma* are mimetic; perhaps both are non-holedrillers causing pulp discoloration. Also, the only *Rhinochenus* with conspicuous glabrous spots around the posterior strial punctures occur in this area, all probably sympatric and syntopic: *R. reichei* (and to a lesser degree *R. chevrolati*), *R. maculipes,* and the São Paulo form of *R. stigma.*

Western South America, southern Colombia to Bolivia (Fig. 149). – This fauna is extremely poorly known, and unquestionably is much more extensive than discussed here. The only unquestioned components of this fauna are 2 forms with the "standard" pattern, *R. thrombithorax* and the "Cayenne" form of *R. stigma* with pointed phallus. These are non-mimetic. In Bolivia are 3 additional forms (*R. cinereopunctatus* and the Mato Grosso and São Paulo forms of *R. stigma*), and these may be part of the overall fauna. In fact, I hypothesize that the Mato

Grosso and/or Central American forms of *R. stigma* do (or did) occur throughout this area to account for apparent character displacement in the male genitalia of western populations of the Cayenne form; similar character displacement is evident in western populations of the São Paulo form (Chiquitos, Bolivia) where sympatric with the Mato Grosso form.

Historical zoogeography of *Rhinochenus*

Vuilleumier (1971), in citing recent studies of birds and lizards stated that " . . . many areas of disjunction, hybridization, secondary sympatry, and introgression exist in the Amazon Basin. Since these areas of secondary contact do not correspond to any modern, observable, physical or ecological barriers, they must, therefore, be the result of historical causes". She agreed with the authors of those studies that Pleistocene events were responsible; specifically, that the Amazon forest was repeatedly fragmented during dry periods, and that these forest remnants served both as refugia and as foci for increased differentiation. Locations of the principal postulated refugia are indicated in Fig. 150.

My observations on *Rhinochenus* agree will with this general scenario. On the one hand are the observations that (1), the beetles apparently are not highly vagile and do not outcross extensively, hence tend either to have relatively small geographic ranges or to be complexly varied geographically; (2), morphological differentiation, especially within species groups, is slight; and (3), biotic differentiation, in the sense that nearly all species are seed predators of *Hymenaea courbaril,* is also slight. These observations all imply that radiation of *Rhinochenus* potentially, at least, was rapid and recent. On the other hand is the correspondence of geographic data with the postulated refugia: this correspondence, both for geographically limited species and for broadly distributed but varied species, is imperative, and appropriate data are available for most of them. Among the 16 South American species, 2 (*R. hercules* and *R. fiedleri*) lack specific locality data, and 2 others (*R. brevicollis* and *R. cinereopunctatus*) are widely distributed but too poorly represented for analysis of geographic variation. Otherwise, refugial relationships are generally either obvious, or readily inferred from phylogenetic relationships; only for *R. klagesi,* known only from 1 site along the Amazon River—a suture zone between northern and southern refugia—are refugial relationships difficult to interpret. These refugial relationships are treated in the discussions of each species and summarized in table 2.

Three questions are immediately raised. First, is this observed correspondence a reflection of real distributions, or is it an artifact of circular reasoning? I submit that the pattern is real, subject to refinement and extension but not to radical change. Second, if the postulated refugia apply to rain-forest animals, how do they apply to *Rhinochenus* which are more characteristic of drier forests? The refugium hypothesis is that the forests were broken by open savannah; I conclude that the dry forest refugia were peripheral to the wet forests, and areally limited. Third, if cyclic Pleistocene weather conditions caused the pattern of cyclic forest refugia in the Amazon Basin, then why not elsewhere? I assume that they did so; specifically, in Central America I propose that there were 2 major refugial areas for tropical forests, 1 in the north associated with the Guatemala highlands (particularly the high volcanos Tacaná and Tajumulco) and another in the south associated with the Costa Rica-Panama highlands (particularly the Volcan de Chiriqui).

If the main refugial areas are those for wet forests, there is of course no reason why there may not have been additional, secondary refugia for dry forests. I think there were. I recognize no refugia for coastal Brazil, because no such action is compelled by my distributional data; yet, 1 or more such refugia would be useful, particularly in explaining variation in *R. stigma.* Among the postulated circum-Amazon refugia, the Guyana refugium stands out as anomalous; I suspect that the dry forest components of this refugium were divided into northern and southern sections, because (1) some *Rhinochenus* such as *R. x-rubra* and the Cayenne form of

R. transversalis are known definitely only from areas north of this refugium, and more particularly because (2) *R. pseudostigma* has geographically differentiated northern and southern components derivative from this refugium. In Central America, I suspect that there was a dry forest refugium on the Osa Peninsula which was at least partially isolated from the main Chiriqui refugium, because existing populations of 2 species (*R. stigma* and *R. transversalis*) are visibly differentiated from nearby mainland populations.

How often were refugial systems in effect? Probably at least 4 times, correlated with each of the major periods of Pleistocene glaciation. There may have been other refugial periods, correlated with minor glacial advances. Meggers (1975) believes that more recent, minor cycles have played an important role in human cultural evolution in South America. Moreover, the severity of dry phases probably varied greatly, and hence the refugia during some dry phases may have been much more or much less developed than during others, and thus their effects on evolution may have varied greatly. I will assume, for simplicity, that the postulated refugia existed during 4 successive periods, at equivalent intensities. These periods are hereafter termed "dry phases 1-4:", and the intervals between them "interphases 1-3".

With this general background I turn now to a consideration of historical zoogeography of *Rhinochenus.* If species differentiation occurred during each successive refugial period, then according to the reconstructed phylogeny (Fig. 143) we may suggest that the only material diversification in *Rhinochenus* up to 1,000,000 years B. P. was the origin of the ancestors of the *transversalis, hercules* + *reichei, mangabeirensis*, and *stigma* groups, with perhaps a preliminary diversification of the latter into ancestral *R. x-rubra* and the progenitor of the rest of the *stigma* group. If pre-Pleistocene environmental conditions were reasonably stable, this early diversification may arbitrarily be assumed to have occurred much more gradually, to correspond to the 3,000,000 year interval between dichotomies as suggested by Whitehead (1972) for continental forms of speciation (Pleistocene radiation in *Rhinochenus* reflects an islandic form of speciation related to forest fragmentation). Using this scheme, I suggest that evolution of *Rhinochenus* may have occurred wholly within the last 15,000,000 years, or since late Miocene. It is obvious that the Amazon Basin of South America was the cradle of evolution of the genus. However, since all major (pre-Pleistocene) lineages are sympatric, it is not possible to suggest any single particularly meaningful evolutionary zoogeography for them.

It is possible to discuss each major established lineage in terms of its subsequent zoogeogarphy, however, since probable vicariance and dispersal patterns are evident. The *mangabeirensis* and *x-rubra* lineages are monobasic, with no known or suspected Pleistocene diversification: that they are essentially sympatric with one another and with components of the other lineages not only makes any discussion of ancestral geographic relationships impractical but also suggests that current known distributions do not adequately reflect the past. Here, I regard the refugial relationships (Guyana refugium) as relictual rather than as evolutionary. But, it would be reasonable to predict that related species will eventually be discovered, and that these will clarify phylogenetic and zoogeographic relationships.

Of the 3 pluribasic lineages (*transversalis, hercules* + *reichei,* and *stigma*), the *transversalis* lineage is the least readily interpreted in a geographic context because no useful geographic data are available for *R. fiedleri* and because refugial relationships of *R. klagesi* are unclear. Apparent mimetic associations of *R. klagesi* with some distantly related Guyana refugial elements suggest that modern *R. klagesi* is derived from the latest Guyana refugium. Phylogenetic relationships, however, indicate that its origin is in a penultimate refugium, probably the Madeira-Tapajoz. The species *R. maculipes* and *R. transversalis* are sisters and geographically vicarious, probably having diverged during dry phase 4. Their ancestor was probably northern (Guyana), as judged from the extensive distribution of *R. transversalis*: I suspect this ancestor was the northern vicar of ancestral *R. klagesi.* I suspect that this ancestor became widespread during interphase 3, then in dry phase 4 had its distribution fragmented into several refugia in

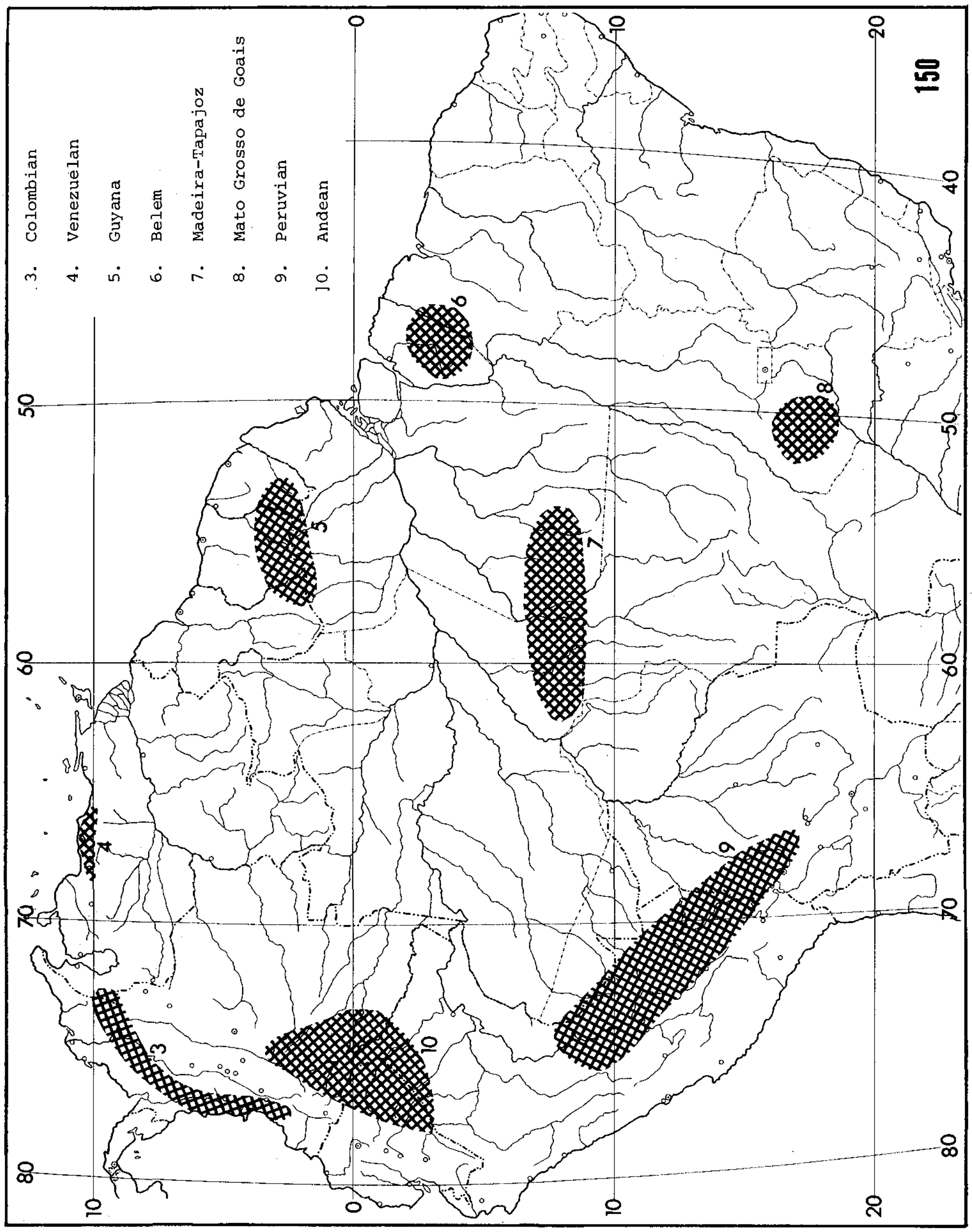

Fig. 150, principal Pleistocene refugia in tropical South America, adapted from Vuilleumier (1971). Central American refugia are (1) nuclear and (2) southern Central America; see text and table 2.

Table 2. Refugial relationships of species and geographic forms of *Rhinochenus*: compare with Fig. 150 for locations of South American refugia. Key: * , principal refuge; + , additional distribution, or transitional; ?, uncertain localities, or peripheral; o, absent.

Taxon	Refugium									
	–Central America–		–South America–							
	nuclear	southern	3	4	5	6	7	8	9	10
R. fiedleri	o	o	o	o	?	?	?	?	o	o
R. klagesi	o	o	o	o	*?	o	*?	o	o	o
R. maculipes	o	o	o	o	+	o	*	o	o	o
R. transversalis:										
Central American	o	*	o	o	o	o	o	o	o	o
transitional	o	o	+	*	o	o	o	o	o	o
Cayenne	o	o	o	o	*	?	?	o	o	o
R. amapensis	o	o	o	o	*	o	o	o	o	o
R. hercules	o	o	?	o	o	o	o	o	o	?
R. reichei	o	o	o	o	o	o	+	*	o	o
R. chevrolati	o	o	o	o	o	o	*	o	o	o
R. mangabeirensis	o	o	o	o	*	?	o	o	o	o
R. x-rubra	o	o	o	+	*	o	o	o	o	o
R. chorrensis	*	o	o	o	o	o	o	o	o	o
R. janzeni	o	*	o	o	o	o	o	o	o	o
R. thrombithorax	o	o	o	o	o	o	o	o	*	o
R. caucensis	o	o	*	+	o	o	o	o	o	o
R. cinereopunctatus	o	o	o	o	o	+	+	+	+	o
R. brevicollis	o	o	o	+	+	+	+	+	o	o
R. pseudostigma	o	o	o	o	*	o	o	o	o	o
R. stigma:										
São Paulo	o	o	o	o	o	o	+	*	+	o
Bahia	o	o	o	o	o	*	o	?	o	o
Cayenne	o	o	o	o	*	+	o	o	+	+
transitional	o	o	o	+	+	o	o	o	o	o
Central American	*	*	*	*	o	o	o	o	o	o
Mato Grosso	o	o	o	o	o	o	*	+	+	?

Central America and northern South America (*R. transversalis*) and in southern South America (*R. maculipes*).

The *hercules* + *reichei* lineage includes 4 essentially allopatric elements, and as indicated in the phylogeny only 2 successive refugial periods are needed to account for their evolution. I suspect the 2 species groups are older than thus indicated, because of the degree of differentiation, but lack of geographic complexity may be a contraindication. Regardless, the evolutionary zoogeography is simple and obvious: an originally widespread common ancestor differentiated during a penultimate dry phase into northern (*hercules-amapensis*) and southern (*chevrolati-reichei*) ancestors, and these in turn differentiated into the extant taxa during dry phase 4.

The evolutionary history of the *stigma* group, reflecting the much greater diversity of this group is more complex. During dry phase 1 was a probable split into northern (*stigma*) and southern (*cinereopunctatus*) lineages. Geographic relationships at this stage are speculative because no vicarious patterns are apparent. However, the Guyana and Madiera-Tapajoz refugia probably have been notably important in *Rhinochenus* speciation generally; thus, it seems significant that the *cinereopunctatus* lineage appears to have no extant Guyana elements.

The 5 members of the *cinereopunctatus* lineage are allopatric, and vicarious relationships—though admittedly not well documented—seem obvious. During interphase 1 ancestral *cinereopunctatus* became widespread in southern and western South America. The first vicariance arose during dry phase 2, with ancestral *chorrensis-janzeni-thrombithorax* having crossed the Andes and ancestral *caucensis-cinereopunctatus* remaining in the Amazon Basin. During interphase 2, the former entered Central America, and during dry phase 3 differentiated into Central American (*R. chorrensis*) and South American components; during interphase 3 the South American ancestor expanded again into Central America and also back into the Amazon Basin, to differentiate during dry phase 4 into *R. janzeni* and *R. thrombithorax*, respectively. Meanwhile, during either dry phase 3 or 4, ancestral *caucensis-cinereopunctatus* separated into Orinoco (*R. caucensis*) and Amazon (*R. cinereopunctatus*) components.

In contrast, the 3 members of the *stigma* lineage are sympatric, and their evolutionary history is therefore much less simply envisioned. Morphologically, *R. brevicollis* and *R. pseudostigma* are very similar, yet their sister-relationship probably is not recent: both are geographically variable as well as sympatric, and *R. brevicollis* is widespread and, so far as known, restricted to a different host plant. Elsewhere, I have discussed variations in both *R. pseudostigma* and *R. stigma* as reflections of isolation patterns during dry phase 4; thus, species differentiation probably occurred no later than dry phase 3—indicating that the first dichotomies in the *cinereopunctatus* and *stigma* lineages were contemporary. During interphase 1, ancestral *stigma* expanded throughout much of the Amazon Basin, becoming sympatric with its sister (ancestral *cinereopunctatus*). During dry phase 2, *R. stigma* differentiated from ancestral *brevicollis-pseudostigma*; the geographic vicariance probably involved the Guyana and Madeira-Tapajoz refugia. During interphase 2, both *R. stigma* and ancestral *brevicollis-pseudostigma* redispersed. During dry phase 3, the ranges of both ancestors fragmented, with no consequent development of reproductive isolation in *R. stigma* but with *R. pseudostigma* in the Guyana refugium differentiating from *R. brevicollis* in the Madeira-Tapajoz. During interphase 3, the already variable *R. stigma* redispersed over much of South America, and during dry phase 4 emerged the beginnings of the complex pattern of variation, partial reproductive isolation, and character displacement that is found at present.

This discussion may be oversimplified[2], in that no detailed reference to host-plant associations is yet possible. According to Langenheim *et al.* (1973) there are some 13 Neotropical species of *Hymenaea,* yet only *H. courbaril* and *H. intermedia*[3] are known definitely to be attacked by *Rhinochenus.* Moreover, Langenheim *et al.* note some distributional anomalies, and no doubt the distributional oscillations during the Pleistocene both modified and reinforced distribution and differentiation in *Rhinochenus.*

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[2] See footnote 1. The new form mentioned there is a mere hint of wonders yet awaiting discovery, particularly in upper Amazon areas. If it is treated as a distinct species, then the logical, ordered, dichotomous system used here to describe diversification of the "*cinereopunctatus* lineage" requires an extra cycle of isolation and dispersal. If other undescribed forms are discovered, they too will complicate the pattern described here; but the hypothesis will not suffer extreme damage unless the reconstructed phylogeny itself is incorrect. Moreover, as implied in the discussion of isolation of geographic forms of *R. stigma,* I do not regard the dichotomous approach as vital to understanding geographic isolation (indeed, the new form, *R. janzeni,* and *R. thrombithorax* may be geographic forms of 1 species). By logical extension, even if dichotomous species diversification is assumed, there is no absolute reason to assume that there cannot be more than 1 dichotomy in a period of isolation. I do so here, both for simplicity and as a probability statement. I wish only to emphasize the point that the overall pattern of cyclic periods of isolation, differentiation, and redispersal is highly plausible and also is consistent with the refugial hypothesis.

[3] See footnote 1 for the only authentic record of a species of *Hymenaea* other than *H. courbaril* as host for *Rhinochenus.* Probably all records cited by Silva *et al.* (1968) pertain to *H. courbaril.*

TOWARD A SYNTHESIS OF QUATERNARY ZOOGEOGRAPHY FOR MIDDLE AMERICA

One reason why Godman and Salvin undertook their massive *Biologia Centrali-Americana* project was to derive generalizations about the flora and fauna of this complex region. I here undertake to make some generalizations about distributions; my examination of evolutionary zoogeography of *Rhinochenus* introduced me to recent literature on Pleistocene refugia in the Amazon Basin, providing insights for understanding Quaternary Middle American zoogeography. Early and Late Tertiary geologic histories of Central America, as currently understood, have been summarized by Rosen (1975) and Ball (1975), respectively. Here, I shall be concerned mainly with developing an initial synthesis of Quaternary zoogeography, to show how cyclic Pleistocene events have affected various ecological components of the fauna. I will gradually lead into this discussion, first by considering certain peripheral questions, and second by comparing the results of certain systematic studies.

Patterns of species differentiation: continental and islandic

By these terms, I mean only to contrast species differentiation among widespread, highly vagile species vs. areally limited (endemic) organisms. There is, naturally, a gradient between the 2 general types of patterns, but as generalized patterns they clearly do exist. Obviously, cyclic refugial systems have superimposed islandic differentiation patterns on the evolution of continental biotas. Where, and how, can continental and islandic patterns be distinguished? This is an important biogeographic question because on its answer depends the interpretation of evolutionary rates and hence of the correlation of cladistic and historical events.

Obvious island-type situations are found where populations are disjunctive and differentiated: on oceanic islands, in cave systems, on mountaintops, in desert springs. But extrinsic disjunctions may be intrinsically overcome by high vagility. Thus, I suggested that the riparian carabid genus *Schizogenius* enjoys a continental pattern (Whitehead 1972): there are no repetitive patterns of endemism on any occupied drainage systems, and there also is no reason to think there were cyclic alterations in these drainage patterns except in the extreme north. I suggested, as an analytical tool rather than as a statement of fact, that one might use a regular 3,000,000 year interval as the rate of speciation, i.e., the interval between dichotomies on the most developed lineage. In contrast is the cloud forest carabid genus *Cyrtolaus* (see Whitehead and Ball 1975); in this genus the pattern is clearly both islandic and cyclic, and speciation rates obviously were greatly increased by cyclic events. Often, islandic and continental patterns may be intermixed; the carabid genus *Evarthrus* (cf. Freitag 1969) may be an example, in view of the relatively high degree of endemism—high, that is, compared to that in *Schizogenius* or *Brachinus* (cf. Erwin 1970) but low compared to that of *Cyrtolaus*.

T. L. Erwin (pers. comm.) has begun a detailed comparison of the carabid faunas of 2 long-term biological study areas: a temperate deciduous site in Maryland (Plummers Island) and a tropical humid site in Panama (Barro Colorado Island). Both were intensively sampled in early decades of this century during early phases of their status as preserves, and again in the last several years. The faunas have altered as the sites have matured, in ways not yet fully documented, but some points relevant to cyclic phenomena and islandic patterns can be made. The total lists of carabid species known from these sites number about 200 and 250, respectively. The faunas of the 2 sites are radically different in composition, in that the percentage of arboreal forms is very low at Plummers Island but very high at Barro Colorado. But the terrestrial faunas at each site are similar in diversity, each represented by a low species/genus ratio; in contrast, the species/genus ratio of the arboreal component of the Barro Colorado fauna is high. What predictions can be made from these observations? I predict that when the systematics of tropical lowland terrestrial carabids are examined critically, most will be found to have continental patterns; in contrast, I predict that the arboreal faunas will be found to exhibit islandic patterns.

Are there reasons to support these predictions? I believe there are. The terrestrial forms occupy diverse habitats but are, mostly, generalist predators. Those forms that are associated with wetland habitats, e.g. streams and marshes (*Schizogenius* would be an example), probably did not suffer radical Pleistocene disturbances. Many of those forms that are associated with forest litter in tropical lowland forests differ in 1 respect from their temperate counterparts: they are adapted to locate fermenting fruit and flower falls and thereby to locate *Drosophila* larvae and other prey, and consequently have constantly changing, spotty local distributions. Nevertheless, any forest stand large enough to insure a continuing food supply through the active season is large enough to maintain populations of these species. Thus, these vagile species tend to be widespread and hence probably suffered little from Pleistocene weather cycles: populations probably were less strongly isolated during dry periods and hence less subject to differentiation than were arboreal forms, and their periods of isolation more transient. In contrast, much of the arboreal component of tropical carabid faunas is composed of higher "Truncatipennes", in which specialized, ectoparasitoid habits are known for some (Erwin, pers. comm.) and probably involve most. With these, it is obvious that population levels and geographic distributions are likely to be limited in general, that with their very particular ecological requirements these species must be highly susceptible to environmental change, and that, therefore, Pleistocene cycles must have led to islandic patterns of species differentiation.

To return to the question of how to distinguish continental from islandic patterns, it is obvious that each problem must be decided on its own merits. The matter is relatively simple at higher elevations, where dispersal barriers are obvious. At lower elevations, a suggested rule of thumb would be that the more specialized or habitat-restricted the organism, the more likely it is to be responsive or subject to cyclic changes, and therefore, the more likely that islandic patterns of species differentiation have played their part. It is easy to think of exceptions; I refer to a generalized pattern, only.

Vulcanism vs. Pleistocene cycles

Kingsolver and Whitehead (1976) discussed a particularly sharp faunal transition in the boundary region between Costa Rica and Panama as resulting from Pleistocene vulcanism in the Chiriqui area. This discussion was based mainly on systematic treatments of various insect groups done by me (Whitehead 1972, 1974) or jointly by J. M. Kingsolver and me (Kingsolver and Whitehead 1974a, 1974b, 1976; Whitehead and Kingsolver 1975). Duellman (1970) found a similarly sharp transition for hylid frogs in Pacific coastal lowlands, but in Atlantic coastal lowlands found that the transition zone is more sharply developed in Nicaragua. Here, I suggest that both vulcanism and Pleistocene refugia played important roles in the Chiriqui area during the last 1,000,000 years.

Distributional limits of genera, subgenera, species groups, and perhaps species must have been influenced by vulcanism, at least in the Pacific lowlands. Operational premises are that the Panamanian seaway was closed ca. 3-5,000,000 years ago in the Darien area, that long-term vulcanism occurred ca. 1,000,000 years ago in the Chiriqui area, and that faunal limits correspond to the latter but not to the former. Regardless of refugial cycles, the only explanation for the extremely sharp demarcation of faunal limits seems to be the postulated vulcanism effect, i.e., a highly effective long-term dispersal barrier.

Some, or most, species limits may equally well, or better, be ascribed to refugial cycles, though a detailed reanalysis is beyond the scope of my present intentions. But it is obvious that to have interpreted variation patterns as related to vulcanism was superficial. The coreid genus *Hypselonotus* is a classic fit to refugial systems, and therefore worthy of a much more careful and thorough analysis than I was able to provide (Whitehead 1974). My point here is that the Chiriqui forms—which I previously interpreted as just intermediates between trans-Chiriqui elements— reflect clearly a Chiriqui Pleistocene refuge. The 2 strange, endemic forms of the bruchid *Caryedes brasiliensis* of the Osa Peninsula and the Chiriqui area (Kingsolver and and Whitehead 1974b) may be derived from Osa and Chiriqui refugia, respectively, the strongholds of each only recently overrun by the widespread, standard form of *C. brasiliensis.* We described a probable sequence of evolutionary events to account for the existence and distribution of these forms; Pleistocene refugial cycles provide a mechanism. Thus, also, extant forms of Central American *Rhinochenus* are herein interpreted as refugial derivatives: *R. chorrensis,* Tacaná-Tajumulco; *R. stigma,* Tacaná-Tajumulco and Chiriqui, since rejoined, plus Osa, still distinctive; *R. janzeni,* Chiriqui and/or Osa; and *R. transversalis,* Chiriqui and Osa, still distinctive.

Some literature on tropical American refugia

Lindroth (1969), in an admirable discussion of boreal Pleistocene refugia, stated that their biological importance was in preserving sensitive portions of the biota rather than in forming centers of speciation. In contrast, hypothesized tropical Pleistocene refugia are thought to have been dynamic centers of differentiation, a contrast to be expected because of the contrast in environmental energetics. At this point, it seems desirable to note that there is a considerable and expanding body of recent botanical and zoological literature on cyclic Pleistocene events in South America, and even some for Central America. I will not here attempt to discuss the biological significance of Pleistocene events in the South American highlands; see Simpson (1975) for a cogent summary of Pleistocene colonization and differentiation in the high tropical Andes.

Vuilleumier (1971) and Vanzolini (1973) summarized certain signal contributions on birds (Haffer 1969) and anoles (Vanzolini and Williams 1970). The latter is especially rich, showing that a tremendous amount of biogeographically significant data can be generated from careful analysis of geographic variation of single species. Vanzolini and Williams made the point that the major patterns of refugia postulated by them roughly approximate those proposed by Haffer. Details differ, as could well be expected in these early phases of investigation. Prance (1973), in a study of plant distribution patterns, and Meggers (1975) in a study of human cultural distrubutions, again found basically storng support for the general outline of Pleistocene refugia in the Amazon Basin but differences in detail. Additional references are given in the literature cited by these authors.

B. B. Simpson allowed me to examine a copy of a manuscript by J. Haffer (1973) on "Pleistocene changes in the avifauna of the Amazon Basin" . In this summary, based on studies of several hundred bird species, Haffer designated 15 forest refugia for tropical America. Three of these refugia are in Central America: 1 on the Atlantic slopes of the Chiapas-Guatemala highlands, 1 on the Atlantic slopes of the Costa Rica-Panama highlands, and 1 on the Pacific slopes in the Osa Peninsula area. These 3 refugia correspond well with those proposed by me: Tacaná-Tajumulco, Chiriqui, and Osa, respectively.

Duellman (1970) found that the humid lowlands of the Golfo Dulce (Osa) region form a southern barrier to dispersal of hylids from subhumid areas to the north. The Osa and Chiriqui biotas are now continuous or nearly so, yet as indicated by distinctive forms of *Rhinochenus* weevils must once have been disjunctive. A tentative explanation of these observations is formulated by extrapolation from Simpson's (1975) discussion of climatic changes of coastal Peru: during glacial periods, Pacific coastal lowlands were drier than now, whereas uplands were wetter than now. The Golfo Dulce area was then, as now, moderated by the Chiriqui uplands: hence, drier than now but less so than elsewhere, and effectively isolated from the

Chiriqui area by more arid areas.

Is there any other type of support for Central American refugia? Van der Hammen (1974) summarized the evidence for climatic pulsations in northwestern South America, and by inference one must suppose that similar pulsations occurred in Central America. To date, palynological evidence is lacking. B. Simpson (pers. comm.) indicates that there have been palynological studies done in Costa Rica and Panama but that they do not corroborate suspected Pleistocene forest fluctuations. Obviously, it is imperative to continue the search. The richly varied topography of Central America compared to that of the Amazon Basin leads to the expectation of a much higher level of overall complexity emerging when refugial systems are worked out in detail.

Central American Coleoptera: some comparisons

Ball (1975) observed that the pattern of pre-Pleistocene dispersal of beetles from South America to "nuclear Middle America", and secondary radiation there, is extraordinarily common. For examples among carabid beetles, see Ball (1975, *Phloeoxena*); Goulet (1974, *Pelmatellus*); Noonan (1973, *Notiobia*, etc.); Whitehead (1972, *Schizogenius*); among bruchid beetles, see Kingsolver and Whitehead (1976, *Meibomeus*) and Whitehead and Kingsolver (1975, *Gibbobruchus*). Two other major patterns are common: origin in North and/or nuclear Middle America (Ekis 1976, clerid genus *Perilypus*; Erwin 1970, carabid genus *Brachinus*; Whitehead and Ball 1975, carabid genus *Cyrtolaus*); and recent dispersal from South America, with little or no radiation in Middle America (Kingsolver and Whitehead 1974a and 1974b, bruchid genera *Ctenocolum* and *Caryedes*; and this paper, *Rhinochenus*).

Can these analyses be compared in a way that will shed light on general zoogeographic patterns, and can such comparisons be used to generate a useful set of hypotheses and predictions? To explore these questions, I choose to define nuclear Middle America as the area lying between the Isthmus of Tehuantepec and southern Nicaragua (including the Tacaná-Tajumulco refugium) and southern Middle America as including Costa Rica and Panama (including the Chiriqui and Osa refugia). Distributions are examined, in the context of reconstructed phylogenies if possible, primarily to note patterns of endemism and secondarily to note distributional limits corresponding approximately to the boundary between these 2 areas. I examine first those patterns that are relatively simple: those that can be classified readily as either low or high altitude patterns. Then, I examine the more complex patterns, with an attempt to integrate them with the simpler patterns.

The low altitude groups include the bruchids, weevils, and carabid genera *Brachinus, Notiobia,* and *Schizogenius*; the data are incomplete, as for all except *Rhinochenus* the systematic accounts apply particularly or exclusively to North and Central American species and as the Central American species of the subgenus *Notiobia* were not investigated. These data are summarized in Table 3, for Middle American taxa only. Part 1 lists 29 species of South American affinity: 12 South American species that extend to North America, 3 more to nuclear Middle America, and 9 more to southern Middle America, plus 5 that are not known from South America but have sisters there. Part 2 lists 14 species endemic to Middle America but with South American affinity: *Ctenocolum janzeni* is treated here because its sister is a Middle American endemic; of the other 13, 3 are endemic to nuclear Middle America and 9 to southern Middle America; sister relationships suggest that *Schizogenius sculptilis* is not a true endemic, and that some of the southern forms extend into South America. Part 3 lists 28 species of North American affinity: 3 that extend to South America, 11 more to southern Middle America, and 14 more to nuclear Middle America. Part 4 lists 4 species endemic to Middle America but with North American affinity: 2 occur in nuclear Middle America only, and 2 extend to southern Middle America. The North American lineages thus express a simple subtraction pattern, north to south,

Table 3. Low altitude beetles in Central America. Key: A-D, distribution of taxon in North America, nuclear Middle America, southern Middle America, and South America, respectively; E-H, distribution of sister group, same breakdown.
Part 1. South American lineages, widespread species.

Family	Genus	Species	A	B	C	D	E	F	G	H
Bruchidae	*Caryedes*	7 species	+	+	+	+	(southern)			
Bruchidae	*Caryedes*	2 species	+	+	+	-	(southern)			
Bruchidae	*Caryedes*	1 species	-	+	+	+	(southern)			
Bruchidae	*Caryedes*	6 species	-	-	+	+	(southern)			
Bruchidae	*Ctenocolum*	3 species	+	+	+	+	(southern)			
Bruchidae	*Ctenocolum*	2 species	+	+	+	-	(southern)			
Bruchidae	*Gibbobruchus*	1 species	-	-	+	+	(southern)			
Bruchidae	*Meibomeus*	1 species	+	+	+	+	(southern)			
Bruchidae	*Meibomeus*	1 species	-	+	+	+	(southern)			
Carabidae	*Schizogenius*	1 species	+	+	+	+	(southern)			
Carabidae	*Schizogenius*	1 species	+	+	+	-	(southern)			
Carabidae	*Schizogenius*	1 species	-	-	+	+	-	+	+	-
Curculionidae	*Rhinochenus*	1 species	-	+	+	+	(southern)			
Curculionidae	*Rhinochenus*	1 species	-	-	+	+	(southern)			

Table 3. (continued). Part 2. South American lineages, endemic species.

Family	Genus	Species	A	B	C	D	E	F	G	H
Bruchidae	*Caryedes*	*brasiliensis* II	-	-	+	-	-	-	+	-
Bruchidae	*Caryedes*	*brasiliensis* III	-	-	+	-	-	-	+	-
Bruchidae	*Caryedes*	*nevermanni*	-	-	+	-	-	-	?	+
Bruchidae	*Caryedes*	*limonensis*	-	-	+	-	-	-	-	+
Bruchidae	*Caryedes*	*godmani*	-	-	+	-	-	-	-	+
Bruchidae	*Ctenocolum*	*janzeni*	+	+	+	-	-	+	-	-
Bruchidae	*Ctenocolum*	*salvini*	-	+	-	-	+	+	+	-
Bruchidae	*Ctenocolum*	*biolleyi*	-	-	+	-	+	+	+	+
Bruchidae	*Meibomeus*	*panamensis*	-	-	+	-	-	-	-	+
Carabidae	*Schizogenius*	*sculptilis*	-	+	-	-	-	-	-	+
Carabidae	*Schizogenius*	*optimus*	-	+	+	-	-	-	+	+
Carabidae	*Schizogenius*	*darlingtoni*	-	-	+	-	-	-	-	+
Curculionidae	*Rhinochenus*	*chorrensis*	-	+	-	-	-	-	+	+
Curculionidae	*Rhinochenus*	*janzeni*	-	-	+	-	-	-	-	+

Table 3. (continued). Part 3. North American lineages, widespread species.

Family	Genus	Species	A	B	C	D	E	F	G	H
Bruchidae	*Gibbobruchus*	1 species	+	+	+	+	(northern)			
Bruchidae	*Gibbobruchus*	1 species	+	+	+	-	(northern)			
Bruchidae	*Gibbobruchus*	2 species	+	+	-	-	(northern)			
Bruchidae	*Meibomeus*	4 species	+	+	+	-	(northern)			
Bruchidae	*Meibomeus*	2 species	+	+	-	-	(northern)			
Carabidae	*Anisotarsus* *	2 species	+	+	+	-	(northern)			
Carabidae	*Anisotarsus*	1 species	+	+	-	-	(northern)			
Carabidae	*Brachinus*	1 species	+	+	+	+	(northern)			
Carabidae	*Brachinus*	2 species	+	+	+	-	(northern)			
Carabidae	*Brachinus*	6 species	+	+	-	-	(northern)			
Carabidae	*Schizogenius*	1 species	+	+	+	+	(northern)			
Carabidae	*Schizogenius*	2 species	+	+	+	-	(northern)			
Carabidae	*Schizogenius*	3 species	+	+	-	-	(northern)			

Table 3. (concluded). Part 4. North American lineages, endemic species.

Family	Genus	Species	A	B	C	D	E	F	G	H
Bruchidae	*Meibomeus*	*howdeni*	-	+	+	-	+	-	-	-
Bruchidae	*Meibomeus*	*viduus*	-	+	-	-	+	+	+	-
Carabidae	*Schizogenius*	*emdeni*	-	+	+	-	-	-	-	+
Carabidae	*Schizogenius*	n. sp.	-	+	-	-	+	-	-	-

* subgenus of *Notiobia*

with no clear indication of Middle American radiation or of Pleistocene refugial cycles. The South American lineages also express a clear subtraction pattern, south to north, but Middle American radiation probably resulting from Pleistocene cycles is indicated at least for the 2 forms of *Caryedes brasiliensis*, for *Ctenocolum janzeni* and *C. salvini*, and for *Rhinochenus chorrensis* and *R. janzeni.* The subtraction patterns may have been influenced by Chiriqui vulcanism, Pleistocene cycles, both, or neither. None of these lowland groups are highly complex in distribution patterns in Middle America, but I predict that some other, specialist groups will be found to have extremely complex patterns.

The overall plan of high altitude speciation is simple, because extrinsic and, frequently, intrinsic disjunctions are obvious; but interpretation is difficult because of the difficulty of obtaining sufficient data to make the plan apparent. Patterns of dispersal and isolation clearly relate to Pleistocene cycles, but with dispersal phases corresponding to *cool pluvial* periods; isolation phases such as exist at present reflect retraction of suitable habitat. The only high altitude groups considered here are the carabid genera *Cyrtolaus* and *Pelmatellus.* All *Cyrtolaus* are wingless and thus of limited vagility. The subgenus *Cyrtolaus* is essentially endemic to nuclear Middle America (1 Pleistocene derivative is known from Oaxaca): 3 in the Pacific coastal highlands (including an undescribed form from Cerro Tres Picos in southwestern Chiapas), 3 in the central highlands or Cuchumatanes range, and 2 in highlands east of the Rio Chixoy. I suggest that these 3 areas represent high altitude ("cloud forest") refugia in nuclear Middle America. *Pelmatellus* have a more complex pattern: some are alate and some flightless, and some are widespread and some localized. Insufficient material of the subgenus *Thenarellus* was available for detailed geographic analysis; the group is endemic to Middle America, represented by apparently endemic forms in both nuclear and southern Middle America. Five species of the more northern subgenus *Pelmatellus* were reported from nuclear Middle America, including a group of 3 related endemic species. With the substantial fresh material of *Pelmatellus* now available, a re-analysis is needed to confirm the notion that nuclear Middle America includes 3 major high altitude refugia, to identify other major and secondary refugia, and to identify major refugia in southern Middle America. Still better for those purposes would be an analysis of some particularly large genus having large numbers of high altitude species—e.g., *Platynus*—but I am not aware of any such analytic treatment currently available.

In contrast to the relatively simple, essentially wholly low or high altitude patterns, there also are some highly intricate patterns. Here, trenchant data are largely lacking. Ekis (1976) dealt with one such group, the clerid genus *Perilypus,* but unfortunately was unable to detail relationships among the diverse and crucially important *reventazon* group. These are chiefly mid-altitude beetles, and hence liable to be subject to components of Pleistocene cycles affecting both high and low altitudes; thus, a pattern of moderate elevation endemism emerges, involving not only major mountains but also minor peaks such as Cerro Campana and Cerro Azul in Panama. Ball (1975) dealt with another complex group, *Phloeoxena,* in which an analogue of the "taxon cycle" (Wilson 1959, 1961) has forced lowland forms into high altitude refugia. Here, the *picta* group of *Phloeoxena s. str.* is instructive. The oldest element, the *megalops* complex, is high-adapted, but inferred to have evolved from a low-adapted ancestor; the subspecies of *P. megalops* are distributed, 1 in nuclear Middle America and 2 in southern Middle America, in a way suggesting influence of the 2 latest Pleistocene cycles. Its sister group includes the low altitude sister pair *P. limbicollis* and *P. nigricollis* plus the high altitude *picta* complex. The 2 lowland forms are not disjunctive, but may represent a Tacaná-Tajumulco element, *P. nigricollis,* plus a Chiriqui element, *P. limbicollis,* with the latter having subsequently redispersed into the range of the former. The *picta* complex includes 5 subspecies, distributed in a linear pattern from the slopes of Mount Orizaba to Guatemala. Phylogenetic interpretations suggest a Pleistocene pattern of dispersal and fragmentation: a source in the Tacaná-Tajumulco area, isolation across the Rio Chixoy, dispersal across the Isthmus of Tehuantepec, isolation into trans-Isthmian ancestors, and subsequent subdivision of each.

One pattern obviously missing from this discussion is that of a Middle American lowland group with extensive radiation. I predict that this pattern does exist, and commonly; in the discussion on arboreal carabids earlier—e.g., *Agra, Calleida, Lebia*— I made just this prediction, and I here extend it to include specialist animals in general.

T. L. Erwin (pers. comm.) cites Middle American members of the carabid genus *Loxandrus* as an example of still higher complexity—i.e., one combining extensive radiation with altitudinal diversification—noting phylogenetic trends from wetlands to lowland forest and thence upward to higher elevations, and even predicting eventual movement from forest floor to understory to canopy. Other carabid genera, notably *Platynus*, represent all of these trends, and more. Hence, clearly, causes of observed patterns of diversity and divergence other than isolation in Quaternary refugia are important and common. G. E. Ball (pers. comm.) notes for example, that the taxon cycle provides a mechanism for altitudinal shift upward into zones with more and stronger extrinsic barriers, thus enhancing the prospect of diversification independently of refugia. It is not my purpose to explore such other causes of observed patterns here; my purpose is to emphasize the refugium hypothesis as a vehicle with the potential to unify important blocks of biological data.

The synthesis

In summary, we come to a synthesis with the power to generate hypotheses and predictions. The synthesis is that: (1) the Middle American fauna is comprised (a) of endemic ancestral complexes, (b) old South American ancestral complexes, and (c) recent arrivals from North and South America; (2) species differentiation patterns are (a) continental or (b) islandic; (3) islandic patterns predominate (a) in high altitude faunas generally and (b) in low altitude specialists; and (4) islandic patterns tend to reflect (a) Pleistocene climatic cycles and/or (b) results of altitudinal shifts induced by the taxon cycle.

Without the power to generate hypotheses and predictions, this synthesis would be valueless. Predictions? Specific predictions should be based on specific problems and derived from generalized hypotheses. Thus, if *Agra,* for example, is a genus of specialists, with few species in Mexico, many in Central America, and huge numbers in South America, I would predict that (1) the Central American species derive mainly from a combination of South American ancestral complexes and recent arrivals, (2) species differentiation patterns are islandic, and (3) these patterns reflect Pleistocene events. As a more concrete example, predictions that arise from the hypothesis that there are 3 major high altitude refugia in nuclear Middle America currently in isolation phase are (1) that a strongly developed pattern of endemism should exist but (2) that since these areas are varied topographically there should be some sister pairs within each refugium and (3) that since the current isolation phase is recent there should be some instances of shared, undifferentiated taxa. Prediction (1) is exemplified by distributional data for *Cyrtolaus*; (2) by the vicarious pair *Phloeoxena picta franiae* and *P. p. unicolor* in the Cuchumatanes-central Chiapas highlands; and (3) by the presence of *P. herculeano* in both Pacific coastal highlands and central Chiapas-Cuchamatanes highlands. Such predictions as these may be devised to test the following hypotheses: (1) that the patterns described herein will be found to be repetitive; (2) that complex patterns, exhibiting island-type differentiation in a sense narrower than the broad forest refugia alone, will be found to be a frequent phenomenon among both low and mid altitude organisms; (3) that these complex patterns will have components of the "taxon cycle" complications referred to above–e.g., the altitudinal displacement found in some *Phloeoxena*; and of course (4) that patterns will *not* commonly be found to refute or contraindicate the overall pattern described herein.

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