

Systematics, distribution, and host specificity of *Amblyopinus* Solsky 1875 (Coleoptera Staphylinidae) in Mexico and Central America

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The Mexican and Central American species of *Amblyopinus* Solsky 1875, adults of which are usually found in the fur of rodents, are revised. All species are fully described, and keys and illustrations of diagnostic features are provided to aid in their identification. A substantial quantity of new host and distributional data is provided. Five species, one of which consists of two subspecies, are known from Mexico and Central America. *Amblyopinus emarginatus* Seevers 1955 (*sanborni* group) occurs in the montane regions of northwestern Panama and Costa Rica where it occurs on *Oryzomys albigularis*. In addition, four species and two subspecies of the *jelskii* group occur in Central America and Mexico: *A. isabellae* Barrera 1966, Sierra Madre del Sur in Mexico (host[s] various species of *Peromyscus* and *Neotoma*); *A. barrerae* Zaragoza Caballero & Sánchez Hernández 1993, Sierra Madre de Oaxaca in Mexico (host[s], *Peromyscus* species, especially *P. melanocarpus*); *A. schmidti schmidti* Seevers 1944, highlands of Chiapas and Guatemala (host, primarily *Peromyscus guatemalensis*); *A. schmidti bolivari* Barrera et al. 1960, Transvolcanic Sierra of Mexico (host, primarily *Microtus mexicanus*); *A. titoni* Barrera 1966, highlands of northwestern Panama and Costa Rica (host[s], *Peromyscus nudipes* and *Reithrodontomys creper*). The hosts of *A. emarginatus* in both Central and South America are complex-penis cricetines, primarily *Oryzomys albigularis*. However, the Mexican and Central American members of the *jelskii* group exhibit two major host transfers: to simple-penis peromyscine rodents (*A. isabellae*, *A. barrerae*, *A. s. schmidti*, *A. tipitoni*); and, to microtine rodents of the genus *Microtus* (*A. s. bolivari*). All five taxa of the *jelskii* group have allopatric ranges in different mountain systems. Only *A. tipitoni* and *A. emarginatus* have sympatric ranges in the montane regions of northwestern Panama and Costa Rica, but these two species are in different species groups and live on different hosts.

KEY WORDS: *Amblyopinus*, systematics, distribution, host relationships, Mexico, Central America.

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INTRODUCTION

Six genera have been described in the staphylinid beetle tribe Amblyopinini, five of which are restricted to the Neotropical region, *Amblyopinus* Solsky 1875, *Amblyopinodes* Seevers 1955, *Chilamblyopinus* Ashe & Timm 1988, *Edrabius* Fauvel 1900, and *Megamblyopinus* Seevers 1955, and a single monotypic genus, *Myotyphlus* Fauvel 1883, is restricted to Australia and Tasmania (SEEVERS 1955, ASHE & TIMM 1988). The most widely distributed genus of amblyopinine, *Amblyopinus*, occurs from the highlands of central Mexico to southern Chile, and contains some 34 described species.

Five species of *Amblyopinus* have been described from Mexico and Central America. These include: *Amblyopinus barrerae* Zaragoza Caballero & Sánchez Hernández from Mexico; *A. bolivari* Barrera et al. from Mexico; *A. emarginatus* Seevers from Panama, Colombia, and Venezuela; *A. isabellae* Barrera from Mexico; *A. schmidti* Seevers from Guatemala; and *A. tiptoni* Barrera from Costa Rica and Panama. In recent years, *A. bolivari* has been treated as a subspecies of *A. schmidti* (MACHADO-ALLISON & BARRERA 1972).

A wealth of new information and specimens of *Amblyopinus* from Mexico and Central America recently have become available to us through our own field efforts and those of colleagues. This material has prompted us to review the systematic status, distribution, and host specificity of all species of *Amblyopinus* known from this region, and provide descriptions and a key to these species.

BIOLOGY OF AMBLYOPINUS

Amblyopinines were, until recently, believed to be obligate, blood-feeding ectoparasites and have been accepted as such in a number of recent parasitology texts and review papers (e.g., ASKEW 1971, MARSHALL 1981, KIM & ADLER 1985). However, we have demonstrated, by studies of these beetles and their hosts in Costa Rica, that at least two species of Central American *Amblyopinus* most likely have a mutualistic relationship with their hosts rather than a parasitic one, and that the conclusion that other amblyopinines are parasitic is not supported by the available evidence (ASHE &

TIMM 1987a, 1987b). Amblyopinines studied fed exclusively on other parasitic arthropods, often in the nests of the host rather than while on the host, and did not bite or molest the host in any way. In addition, the hosts actively tolerated the presence of these beetles, even when they ran across such sensitive regions as the eyes and vibrissae. We also demonstrated that the beetles exhibit a marked diurnal activity pattern, climbing onto the hosts and gripping the hair tightly at night when the host is active, and crawling from the host to feed in the nest when the host is inactive during the day (ASHE & TIMM 1987a). Species of beetles on mice with different nesting biologies show significantly different behaviors (ASHE & TIMM unpublished data), and we hypothesized that the nesting biology of the hosts has played a major role in evolution of this interaction (ASHE & TIMM 1987b, TIMM & ASHE 1987).

Hosts of amblyopinines are primarily cricetine and caviomorph rodents and South American marsupials (SEEVERS 1955). There is substantial evidence that members of each individual species of amblyopinine are quite host specific (TIMM & ASHE 1987), and members of each genus and intrageneric higher taxon have a tendency to be associated with a particular group of mammals. In South America members of *Amblyopinus* are restricted to opossum-like marsupials or various species of complex-penis cricetine rodents. However, in Central America and Mexico, *A. emarginatus* is found on complex-penis cricetines, while all others are either found on simple-penis peromyscine rodents or microtine rodents (WENZEL & TIPTON 1966, also see discussion below).

IDENTIFICATION

All amblyopinines currently known to occur in Mexico and Central America are in the genus *Amblyopinus* Solsky. Adults of the genus *Amblyopinus* can be easily recognized by the following combination of characteristics: body size 7-11 mm; body color uniformly brunneous to rufo-flavate; head subtriangular; eyes small but multifaceted, located distant from antennal fossae and immediately anterior to basal angles of head; gular sutures subparallel medially and broadly divergent anteriorly and posteriorly; labrum small, slightly bilobed, not, or only slightly, visible from above; elytra short, broader than long; hind wings absent; metasternum very short; coxae more or less oval or transverse (rather than triangular); and, their occurrence in the fur of rodents (see also SEEVERS 1955).

Separation of the single species of the *sanborni* group, *A. emarginatus*, from the four species in the *jelskii* group is relatively simple. However, the four species of the *jelskii* group known from Mexico and Central America are extremely similar to each other. We have not been able to discern any reliable way to distinguish them based on external features. Slight differences in body proportions, setation, microsculpture, and other features overlap broadly among species when more specimens are studied. However, features of the male aedeagi are distinctive. These, then, are used extensively in the following key. This means that only males can be identified with certainty, and females must be identified by association with males. Currently, except for the sympatry between species of *A. tiptoni* and *A. emarginatus* in Costa Rica, known ranges of all Mexican and Central American amblyopinines are distinct. Therefore, distribution is also included in the following key.

KEY FOR IDENTIFICATION OF CENTRAL AMERICAN *AMBLYOPINUS*

- 1 Posterior margin of pronotum with six large macrosetae on each side; dorsal cervical region of head distinctly delimited from remainder of head capsule by an abrupt and deep depression across entire width; mesotarsal segment 1 markedly robust and large in comparison with other mesotarsal segments (*sanborni* group) *A. emarginatus*
- Posterior margin of pronotum with one large macroseta on each side near apico-lateral angles; dorsal cervical region of head delimited only by fine carina or bead, without deep depression across entire width; mesotarsal segment 1 not markedly robust or large in comparison with other mesotarsal segments (*jelskii* group) 2
- 2 Apex of paramere of aedeagus relatively long and slender, slightly upturned, with broad shallow sinuation extended from about midway between macrosetae 2 and 3 to proximal to macroseta 4 (Fig. 6); internal sclerotized plate of aedeagus as in Figs 8-9; known from highlands of northern Oaxaca in Mexico *A. barrerai*
- Apex of paramere of aedeagus not as above (Figs 3, 10, 14, 18); internal sclerotized plate of aedeagus not as above (Figs 4-5, 12-13, 16-17, 20-21) 3
- 3 Apex of paramere of aedeagus with large mesolateral shelf extended to near base of macroseta 4, paramere abruptly and deeply sinuate near base of basal macroseta in lateral aspect; spiniform setae numerous from near apex to near, or posterior to, base of most basal macroseta (Fig. 18); internal sclerotized plate of aedeagus as in Figs 20-21; known from the highlands of Costa Rica and northwestern Panama *A. tiptoni*
- Apex of paramere of aedeagus with mesolateral shelf less prominent, extended no farther than base of macroseta 3; paramere slightly sinuate in lateral view between macrosetae 2 and 3 or near base of macroseta 3; spiniform setae extended no farther proximally than macroseta 3 (Figs 2, 10, 14); internal sclerotized plate of aedeagus not as above (Figs 4-5, 12-13, 16-17); known from Mexico and Guatemala 4
- 4 Apex of paramere of aedeagus long and slender, slightly sinuate near base of macroseta 3 in lateral aspect (Fig. 2); spiniform setae extended to near base of macroseta 3; internal sclerotized plate of aedeagus as in Figs 2, 4-5; apex of male sternum IX slightly to moderately emarginate; known from Sierra Madre del Sur in Guerrero, Mexico *A. isabellae*
- Apex of paramere shorter and more stubby, moderately sinuate between macrosetae 2 and 3 in lateral aspect (Figs 10, 14); internal sclerotized plate of aedeagus as in Figs 12-13, 16-17; apex of male sternum IX not emarginate; known from Transvolcanic Sierra of Mexico and highlands of southern Chiapas and Guatemala (subspecies of *A. schmidti*) 5
- 5 Known from Transvolcanic Sierra of Mexico; most commonly found in association with *Microtus mexicanus* or *Neotomodon alstoni* *A. schmidti bolivari*
- Known from highlands of southern Chiapas and Guatemala; most commonly found in association with *Peromyscus guatemalensis* *A. schmidti schmidti*

SYSTEMATICS

Amblyopinus emarginatus Seevers 1955 (Fig. 1, Map 1)

Head. Lateral margins of head similar to other Central American species, except: occipital angles much more distinct; occipital region behind eyes distinctly and moderately concave; concave region extended laterally across dorsal cervical region to near 0.25 width of head; cervical region distinctly delimited from remainder of head capsule dorsally by an abrupt and deep shelf across entire dorsal width. Clypeal margin very slightly and broadly concave to almost straight; 1 very short seta at each

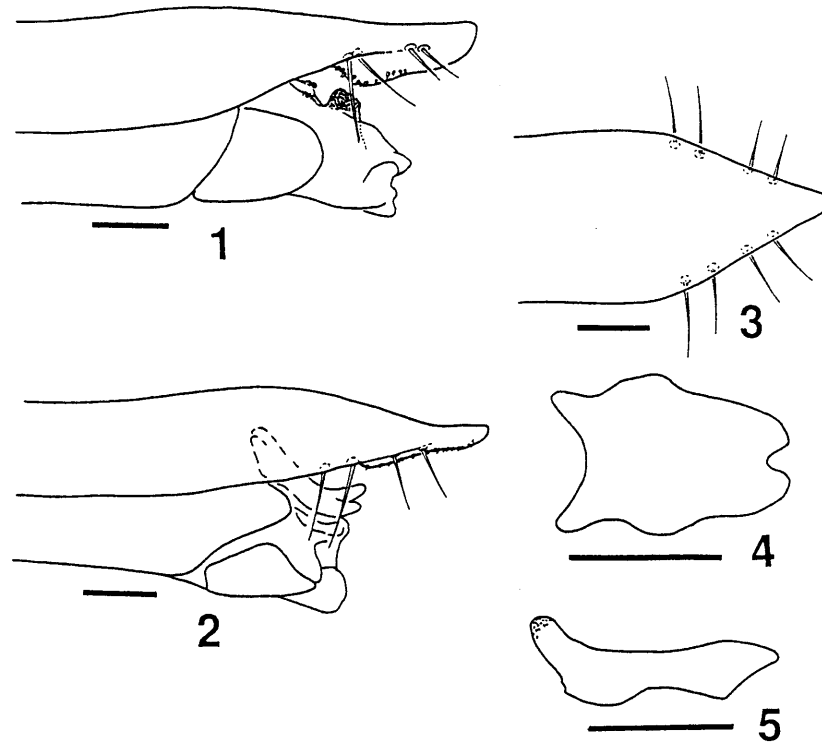
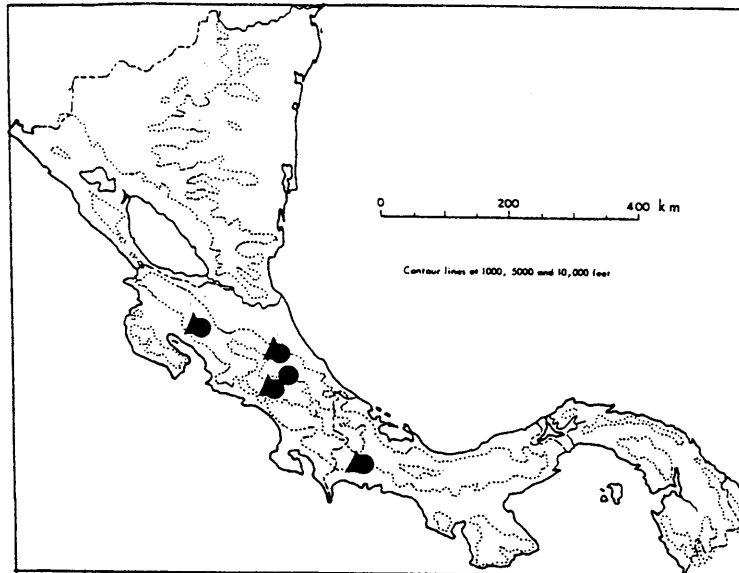


Fig. 1. — *Amblyopinus emarginatus* Seevers, aedeagus, lateral aspect, internal sac partially extended. (Scale line = 0.1 mm).

Figs 2-5. — *Amblyopinus isabellae* Barrera. Fig. 2, aedeagus, lateral aspect, internal sac not extended. Fig. 3, aedeagus, dorsal aspect. Fig. 4, internal sclerotized plate of aedeagus, dorsal aspect, oriented with more ventral margin to right. Fig. 5, internal sclerotized plate of aedeagus, lateral aspect, oriented same as Fig. 4. (Scale lines = 0.1 mm).

fronto-lateral angle. Labrum as in *A. isabellae*. Macrosetae typical for Central American amblyopinines, but with supra- and super-orbital macrosetae only slightly longer than super-antennal macroseta. Eight-nine marginal microsetae in addition to a large macroseta on ocellar margin immediately behind eye; antennal groove with 8-10 microsetae on ventral margin and 1-3 microsetae dispersed in medial longitudinal line anterior to eye. Antennal groove slightly and broadly concave from antennal insertion to near eye. Antennal length moderately long, extended to basal 0.25 of pronotum; article 2 about 0.5 times as long as article 1; all articles more compact and robust than those of other Central American amblyopinines. Microsculpture of head moderately distinct, sculpticells slightly to moderately transverse in most specimens (more reticulate in a few); integument appearing moderately shiny. Punctures of head distinct, moderately deep, and more or less uniformly distributed; distance between punctures 1.0-2.5 times average width of punctures. Eyes with 3-4 (5-6 in some) facets visible from above; supra-ocellar bristle separated from eye by 2.5 times width of puncture. Gena wide, with numerous microsetae, and 1 moderately sized macroseta (noticeably



Map 1. — Distribution of *Amblyopinus emarginatus* Seevers (triangles) and *A. tiptoni* Barrera (circles) in Costa Rica and Panama.

smaller than those of Central American representatives of *jelskii* group) on each side. Submentum wide; anterior margin more or less straight to very slightly arcuate; 1 long, dark macroseta on each side and 12-14 microsetae on each half of midline. Mentum with 1 (or in some 2, differ right to left in some) small dark, more or less blunt seta on each side in lateral 0.3 (larger, darker, and more distinct than those of Central American representatives of *jelskii* group).

Pronotum. Sides moderately converging from greatest width near basal 0.3 to distinct anterior angles. Greatest width 1.3-1.4 times width at anterior margin; 1.6 times as wide as greatest length. Posterior margin slightly but distinctly and broadly emarginate medially. Posterior margin with 6 macrosetae in each half; most lateral macroseta located on margin slightly medial to posterior angle; most lateral macroseta largest, and more medial setae progressively smaller; lateral margin with 1 macroseta. Microsculpture distinct and moderately prominent; sculpticells slightly to moderately transverse in most, to more or less reticulate in some; surface appearing moderately shiny. Punctures small, moderately deep, and uniformly distributed, each puncture more or less distinct, not noticeably surrounded by a shallow depressed area; distances between punctures 1.0-2.5 times average width of punctures.

Elytra. Each elytron about as wide as long; uniformly covered by moderately dense pilosity of fine, flavate microsetae; microsetae not of two different sizes, except longer on sides and near postero-lateral angles. Scutellum broad with sides convergent to distinctly pointed apex, most distal point of apex rounded.

Thorax. Prosternum with 1 pair of long, medial macrosetae, and scattered microsetae on anterior half. Anterior margin of mesosternum broadly concave; apex of mesosternum short but acute. Mesosternum with 8-9 macrosetae on anterior half

and a few scattered microsetae on posterior half. Apical process of metasternum somewhat parallel-sided in apical 0.20-0.25; apex deeply and acutely emarginate (more so than those of all other Central American amblyopinines); depth of emargination about equal to 1.0 times width of emargination; anterior 0.75 of process with numerous, widely scattered microsetae. Tarsal segment 1 of mesothoracic legs longer than 2 and 3 together; segment 1 markedly robust and large in comparison with other tarsal segments; segments decreasing in size from segment 1 to 4, segment 4 very small. White pilosity on mesothoracic legs on distal 0.7 of tarsomere 1 and extended through tarsomeres 2-3.

Abdomen. Tergum II without marginal macrosetae; terga III-VI with 1 large, dark macroseta near lateral 0.25, and with 1 large, distinct but thinner, macroseta lateral to it; tergum VIII evenly rounded, with 2-3 small, thin discal macrosetae in each half. Sterna III-VI with 1 large, darkly pigmented marginal macroseta on each side of midline, and with 4 or 5 thin, less darkly pigmented marginal macrosetae lateral to it; sternum VII with 2 large, darkly pigmented, marginal macrosetae on each side, and 3 or 4 thin, less darkly pigmented, almost whip-like, marginal macrosetae lateral to them.

Female abdomen. Sterna VII-VIII and tergum VIII similar to male; tergum IX fairly broad, more truncate than that of male.

Male abdomen. Posterior margin of sternum VIII deeply emarginate; most specimens with 2, some with 3, large macrosetae on each half (a few specimens with 2 large and 1 very thin, slightly pigmented, macrosetae in each half). Apical margin of sternum IX more or less truncate to broadly rounded. Posterior margin of tergum VIII more or less broadly rounded. Tergum IX broadly trapezoidal, broadly and shallowly emarginate posteriorly.

Aedeagus (Fig. 1). Apex of paramere relatively short and robust, not upturned. Spiniform setae on posterior half of apex, scattered from about midway between macrosetae 2 and 3 to near, or slightly proximal to, macroseta 4. Internal sclerotized plate not present.

Distribution. As in Map 1.

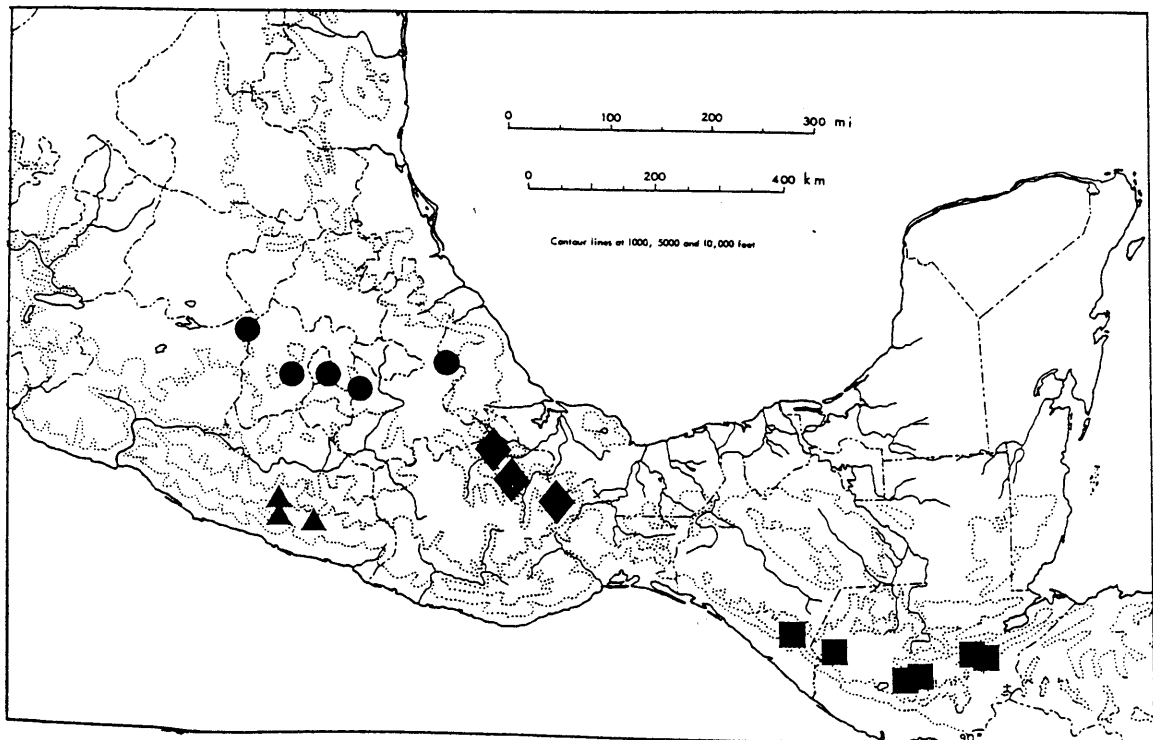
Type material. Holotype: male. Colombia: Huila; San Antonio, San Agustin, VIII-X.1951, coll. P. Hershkovitz, ex. *Thomasomys laniger*. Pinned, genitalia dissected, and placed in glycerin in genitalia vial attached beneath specimen. Deposited at Field Museum of Natural History.

Material examined. Costa Rica: Province Cartago; Refugio Nacional de Fauna Silvestre Tapantí, Río Dos Amigos, ca 22 km from Orosi, 24.I.1987, coll. N. Woodman, ex. *Oryzomys albigularis* (female, NW 41), 1 male and 3 females (FMNH, KSEM). Refugio Nacional de Fauna Silvestre Tapantí, 7 km SSE Río Macho [9°45'N, 83°47'W], coll. C.S. Vaughan, ex. *Oryzomys albigularis* (sex unknown, several hosts), 9 males and 16 females (FMNH, KSEM). Heredia; Parque Nacional Braulio Carrillo, 5 km E Vara Blanca, 2050 m, 18.IV.1986, coll. J.S. Ashe, ex. *Oryzomys albigularis* (male, RMT 3661), 2 females (FMNH). Same locality, elevation, and collector, 20.IV.1986, ex. *Oryzomys albigularis* (female, RMT 3668), 3 males, 6 females (FMNH, KSEM). Same locality, elevation, date, and collector, ex. *Oryzomys albigularis* (male, RMT 3669), 2 males, 2 females (FMNH). Puntarenas; Cerro Amigos, Monteverde, 1780-1840 m, 10-13.V.1986, coll. J.S. Ashe & R.M. Timm, ex. *Oryzomys albigularis* (5 males and 2 females, collection numbers A&T 366, 382, 403, 413, 422, 432, and 475), 14 males and 10 females (FMNH, KSEM). Monteverde, Chavarria Woods, 1700 m, 20.XII.1989, coll. F.A. Reid, ex. *Tylomys watsoni* (male, FAR 60), 1 male, 1 female (KSEM). Province San José; Ojo de Agua [9°34'45"N, 83°48'06"W], 2440 m, 21.V.1986, coll. J.S. Ashe & R.M. Timm, ex. *Oryzomys albigularis* (male, A&T 514), 2 females (FMNH).

Panama: Bocas del Toro; 25 km NNE San Felix, 1425-1525 m, 22.V-11.VI.1980, coll. R.J. Izor & R.H. Pine, ex. *Oryzomys albigularis* (8 males and 1 female, RJI 23 and RHP 8062, 8063, 8080, 8083, 8146, 8258, 8259, 8279, and 8287), 13 males and 17 females (FMNH). Chiriquí-Bocas del Toro boundary; 3.5 km E Escopeta, 1800-1856 m, 7.VII.1980, coll. R.J. Izor, ex. *Oryzomys albigularis* (male, RJI 159), 1 female (FMNH) (see TIMM & ASHE 1987 for more details).

Amblyopus isabellae Barrera 1966 (Figs 2-5, Map 2)

Head. Lateral margins of head divergent posteriorly to eyes, sharply convergent behind eyes. Occipital lobe of head with concave sinus immediately behind eyes. Clypeal margin very slightly and broadly concave; 1 short seta at each fronto-lateral angle. Labrum moderately bilobed; 7 setae along anterior margin in each half, setae 3 and 5 from midline noticeably larger than others, with 5 significantly larger than 3. Macrosetae typical for species group. Seven-eight marginal microsetae in addition to a large macroseta on ocellar margin immediately behind eye; antennal groove with about 6 microsetae on ventral margin and 1 anterior to eye. Antennal groove moderately concave posterior to antennal insertion. Antenna length moderately long, extended to near base of pronotum; article 1 about 1.5 times as long as article 2. Microsculpture of head very prominent, dense, reticulate throughout, with sculpti-



Map 2. — Distribution of *Amblyopus isabellae* Barrera (triangles), *A. barrerae* Zaragoza Caballero & Sánchez Hernández (diamonds), *A. schmidti schmidti* SeEVERS (squares) and *A. schmidti bolivari* Barrera et al. (circles) in southern Mexico and Guatemala.

cells well defined; integument appearing granulate, not strongly shining. Punctures of head small, distinct, shallow; distance between punctures 1.0-3.0 times average width of punctures. Eyes with 4-6 facets visible from above; supra-ocellar bristle at upper rear angle of eye, and separated from eye by distance less than the width of the puncture. Gena broad, with numerous microsetae, and 1 large macroseta on each side. Submentum wide; anterior margin arcuate; 1 long macroseta on each side and 13-14 microsetae on each half of midline. Mentum with 1 very small blunt seta on each side.

Pronotum. Sides markedly converging from greatest width near basal third to distinct anterior angles. Greatest width 1.6 times width at anterior margin; 1.5 times as wide as greatest length. Posterior margin nearly straight, or, at most, slightly concave medially. Posterior margin with one prominent macroseta slightly medial to postero-lateral angles; lateral margin with one macroseta. Microsculpture dense, prominent and reticulate throughout; surface appearing granular, not strongly shining. Punctures small, shallow, and uniformly distributed; distances between punctures 1.5-3.0 times average width of punctures.

Elytra. Each elytron slightly wider than long; covered by moderately dense pilosity of mixed long and short microsetae. Scutellum wide and broad, broadly rounded posteriorly.

Thorax. Prosternum with 1 pair of long, medial macrosetae, and scattered microsetae on anterior half. Anterior margin of mesosternum straight, with lateral sides converging to more or less acute apex. Mesosternum with 13 macrosetae and 6 scattered microsetae on anterior half, none on posterior half. Apical process of metasternum nearly pentagonal; apex broadly and shallowly emarginate, depth of emargination about equal to 0.5-1.0 times width of emargination; process with numerous microsetae throughout except on apical margin. First mesotarsal segment as long as 2-4 together, not noticeably robust, 2-4 subequal in length. Tarsal segments 1-3 of mesothoracic legs with white pilosity.

Abdomen. Tergum II with 1 large, darkly pigmented marginal macroseta near lateral margin, and with smaller and thinner weakly pigmented marginal seta lateral to it; terga III-VIII with 1 large, dark macroseta near each postero-lateral margin and 1 much thinner, less pigmented, long, whip-like macroseta lateral to it; tergum VIII evenly rounded, with 1 very thin, more or less whip-like, discal seta on each side near lateral margin; tergum IX trapezoidal, with several long, slender marginal bristles. Sterna IV-VI with 1 large, darkly pigmented, marginal macroseta on each side, and 1 thin, whip-like, less darkly pigmented macroseta lateral to it; sternum VII with 2 large, darkly pigmented, marginal macrosetae on each side, and 2 thin, whip-like, less darkly pigmented marginal macrosetae lateral to them.

Female abdomen. Sternum VII with 2 large, dark, marginal macrosetae on each side, and 2 or 3 thin, less darkly pigmented marginal macrosetae lateral to them; sternum VIII with 2-3 (4 in a few specimens) large, dark macrosetae on each side.

Male abdomen. Posterior margin of sternum VIII deeply emarginate; macrosetae of sternum VIII variable, range 2-4, 2 on each half in most specimens (holotype has 2 on left side and 3 on right). Apical margin of sternum IX slightly to moderately emarginate. Posterior margin of tergum VIII evenly rounded. Tergum IX trapezoidal, truncate posteriorly, and with several long, slender marginal bristles.

Aedeagus (Figs 2-3). Apex of paramere long and slender, not greatly upturned, scarcely sinuate anterior to third macroseta. Spiniform setae most abundant anterior

to most distal macroseta, other spiniform setae small and scattered. Internal sclerotized plate as in Figs 4-5.

Distribution. As in Map 2.

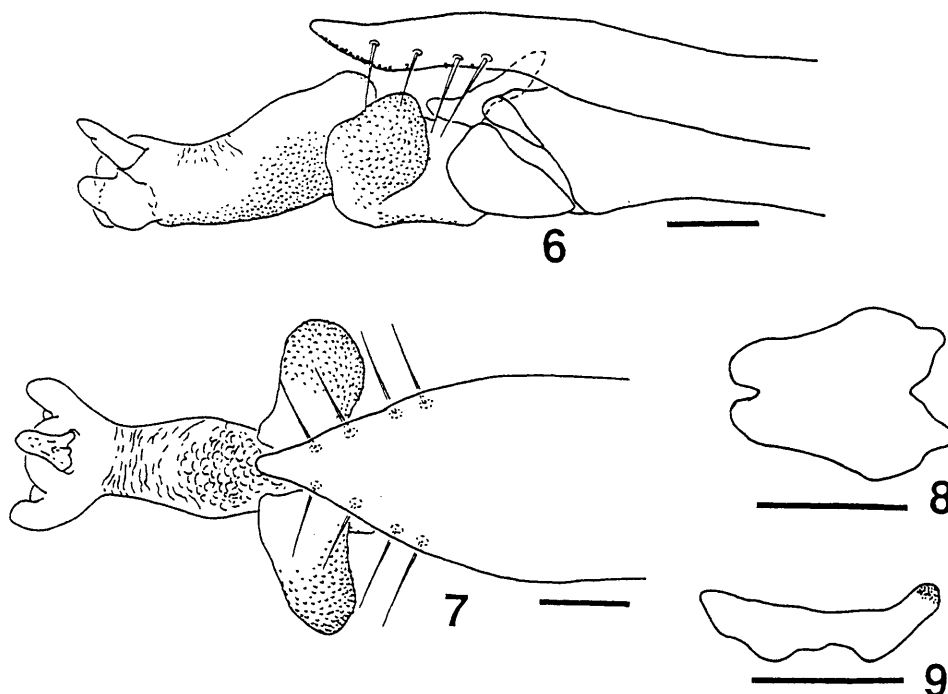
Type material. Holotype: male. Mexico: Guerrero; Omiltemi, 2300 m, 29.XII.1954, coll. A. Barrera & D. Pelaez, ex. *Peromyscus megalops auritus*. Deposited in the Museo de Zoología "Alfonso L. Herrera" de la Facultad de Ciencias de la Universidad Nacional Autónoma de México. Holotype cleared and dissected and mounted on three separate microslides: body on slide MZFC 43; aedeagus on slide MZFC 43a; and, terminal abdominal segments on slide MZFC 43b. Locality data provided in original description by BARRERA (1966a) does not include elevation or host. BARRERA & MACHADO-ALLISON (1965) stated the host to be *Peromyscus melagops*. The elevation and host data provided above are included in MUÑIZ et al. (1981).

Material examined. Mexico: Guerrero; Omiltemi, 2600 m, 26.VII.1986, coll. M.D. Engstrom, ex. *Peromyscus megalops* (female, MDE 4988), 1 female (FMNH). Same locality, 18.II.1985, coll. F.D. Romano, ex. *Peromyscus thomasi* (FRR 211), 1 female (UNAM). Omiltemi, Cañada de Agua Fria, 2500 m, 6.VII.1985, coll. J. Juárez, ex. *Peromyscus thomasi* (JJG 1432), 1 male (UNAM). Same locality, elevation, and date, coll. A. Jiménez, ex. *Peromyscus thomasi* (JJG 1435), 1 female (UNAM). Guerrero; Pto del Gallo, Mpio Tlacotepec, 2540 m, 30.VII.1983, coll. J. Juárez, ex. *Peromyscus* species? (JJG 314), 1 female (UNAM). Guerrero; El Iris, Mpio Tlacotepec, 2300 m, 2.IX.1983, coll. A. Jiménez, ex. *Peromyscus* species? (JJG 367), 2 males (UNAM, KSEM). Guerrero; Bosque de Lauráceas, Mpio Atoyac, 1950 m, 26.XI.1983, coll. J. Juárez, ex. *Peromyscus* species? (JJG 673), 1 female (UNAM). Guerrero; Pto del Gallo, Mpio Atoyac, 30.VII.1983, coll. A. Jiménez, ex. *Neotoma mexicana* (JJG 312), 2 females (UNAM, KSEM).

Amblyopinus barrerae Zaragoza Caballero & Sánchez Hernández 1993 (Figs 6-9, Map 2)

Head. Lateral margins of head divergent posteriorly to eyes, sharply convergent behind eyes. Occipital lobe of head hardly sinuate. Clypeal margin very slightly and broadly concave; 1 short seta at each fronto-lateral angle. Labrum moderately bilobed; 7 setae along anterior margin in each half, setae 3 and 5 from midline noticeably longer than others, with 5 significantly larger than 3. Macrosetae typical for species group. Seven-eight marginal microsetae in addition to a large macroseta on ocellar margin immediately behind eye; antennal groove with 7-8 microsetae on ventral margin and with or without 1 microseta anterior to eye. Antennal groove moderately concave posterior to antennal insertion. Antenna length moderately long extended to base of pronotum; article 2 about 0.6 times as long as article 1. Microsculpture distinct, sculpticells moderately to slightly transversely elongate, to almost reticulate in some specimens; integument appearing slightly to moderately shiny. Punctures of head small and well-defined; distance between punctures 1.0-3.0 times average width of punctures. Eyes with 4-6 facets slightly visible from above; supra-ocellar bristle at upper rear angle of eye, and separated from eye by less than or equal to the length of the puncture. Gena broad, with numerous microsetae, and 1 large macroseta on each side. Submentum wide; anterior margin arcuate; 1 long macroseta on each side and 9-11 microsetae on each half of midline.

Pronotum. Sides slightly rounded and slightly converging to anterior angles. Greatest width near posterior 0.3; about 1.6 times as wide as greatest length. Posterior margin very slightly and broadly emarginate. Posterior margin with 1 prominent macroseta medial to postero-lateral angles; lateral margin with 1 macroseta. Microsculpture dense and prominent; sculpticells reticulate throughout in most to



Figs 6-9. — *Amblyopinus barrerai* Zaragoza Caballero & Sánchez Hernández. Fig. 6, aedeagus, lateral aspect, internal sac fully extended. Fig. 7, aedeagus, dorsal aspect, internal sac fully extended. Fig. 8, internal sclerotized plate of aedeagus, dorsal aspect, oriented with more ventral margin to left. Fig. 9, internal sclerotized plate of aedeagus, lateral aspect, oriented same as Fig. 8. (Scale lines = 0.1 mm).

slightly transverse medially in some specimens; integument appearing slightly to moderately shiny. Punctures small, distinct, and uniformly distributed; distances between punctures 2.0-4.0 times average width of punctures.

Elytra. Each elytron slightly wider than long; covered by moderately dense pilosity of mixed long and short flavate microsetae. Scutellum moderately broad, obtusely rounded posteriorly.

Thorax. Prosternum with 1 pair of long, medial macrosetae, and scattered microsetae on anterior half. Apical process of metasternum more or less pentagonal; apex narrowly and slightly emarginate, depth of emargination about equal to 0.5-0.9 times width of emargination; process with numerous uniformly distributed microsetae except for posterior margin. Mesothoracic tarsal segment 1 about as long as 2 and 3 together, not markedly robust; 2 and 3 subequal, 4 minutely shorter.

Abdomen. Tergum II with 1 large, darkly pigmented marginal seta near lateral margin, and with much smaller and thinner, weakly pigmented (not whip-like) marginal macroseta lateral to it; terga III-VII with 1 large, dark macroseta near lateral 0.25 and 1 thin, less pigmented, long, whip-like macroseta lateral to it; tergum VIII evenly rounded; tergum IX trapezoidal, truncate posteriorly, with numerous long, slender, marginal bristles. Sterna V-VI with 1 large, darkly pigmented, marginal

macroseta on each side, and with 3 (4 in some) small, thin, lightly pigmented macrosetae lateral to it; sternum VII with 2 large, darkly pigmented, marginal macrosetae on each side and 2 thin, whip-like, less darkly pigmented macrosetae lateral to them.

Female abdomen. Sternum VII with 2 large, dark, marginal macrosetae on each side, and 3 or 4 thin, weakly pigmented marginal macrosetae lateral to them. Sternum VIII broadly rounded, with 3 or 4 large, dark, discal macrosetae (variable right to left sides in some specimens).

Male abdomen. Posterior margin of sternum VIII deeply emarginate; 2-3 macrosetae on each half. Apical margin of sternum IX truncate, not at all emarginate. Posterior of tergum VIII evenly rounded. Tergum IX truncate posteriorly, broader than that of *A. isabellae*, and with numerous long slender marginal bristles.

Aedeagus (Figs 6-7). Apex of paramere relatively long and slender, slightly upturned, and with broad, shallow sinuation extended from about midway, slightly macrosetae 2 and 3 to proximal to macroseta 4. Spiniform setae fairly numerous, extended between seta 3, or about medially between setae 2 and 3, to near apex; spiniform setae between macrosetae 2 and 3 few and widely scattered. Internal sclerotized plate as in Figs 8-9.

Distribution. As in Map 2.

Type material. Holotype: male. Mexico: Oaxaca; 4.5 km NW Campamento a Santa María Totontepec, 2480 m, 15.I.1993, coll. ?, ex. *Peromyscus melanocarpus*. Deposited at Colección Entomológica del Instituto de Biología, Universidad Nacional Autónoma de México.

Material examined. Mexico: Oaxaca; 27.5 km NNE Llano de las Flores, Hwy 175, 2500 m, 21.VII.1986, coll. L.J. Barkley, ex. *Peromyscus thomasi* (female, LJB 3014), 2 males (FMNH); same locality, date, and collector, ex. *Peromyscus thomasi* (female, LJB 3020), 1 male, 2 females (FMNH); same locality, date, and collector, ex. *Peromyscus melanocarpus* (male, LJB 3024), 3 males (FMNH, KSEM); same locality, date, and collector, ex. *Peromyscus oaxacensis* (male, LJB 3028), 1 female (FMNH); same locality, 20.VII.1986, coll. M.D. Engstrom, ex. *Peromyscus melanocarpus* (male, MDE 4955), 1 female (FMNH); same locality, date, and collector, ex. *Peromyscus melanocarpus* (male, MDE 4961), 2 females (FMNH); same locality, date, and collector, ex. *Peromyscus melanocarpus* (male, MDE 4964), 1 male (FMNH); same locality, VII.1986, coll. M.D. Engstrom, ex. *Peromyscus* species?, 1 male, 2 females (FMNH, KSEM); 11 km SW La Esperanza, Municipio Santiago Comaltepec, 2000 m, 8.XII.1989, coll. J.M. Vázquez, ex. *Peromyscus thomasi* (female, JMV 437), 1 female (KSEM). Same locality and collector, 7.XII.1989, ex. *Peromyscus melanocarpus* (male, JMV 393), 1 male (KSEM). Eight km N La Esperanza, 2000 m, 10.XI.1989, coll. J.M. Vázquez, ex. *Peromyscus melanocarpus* (female, JMV 262), 1 female (KSEM). 1 km N La Esperanza, 2000 m, 8.XII.1989, same collector, ex. *Peromyscus melanocarpus* (male, JMV 426), 1 female (KSEM). Rancho Tarabundi, 5 km SE Vista Hermosa, 1100 m, 21.X.1989, ex. *Peromyscus melanocarpus* (male, JMV 230), 3 males, 3 females (KSEM, UNAM). Camino Lodosa, 11 km SW La Esperanza, 2000 m, 23.III.1990, coll. J.M. Vázquez, ex. *Peromyscus melanocarpus* (female, JMV 799), 1 female (KSEM). Same locality, date, and collector, ex. *Oryzomys alfaroi* (male, JMV 795), 1 male. Same locality and collector, 8.XII.1989, ex. *Peromyscus melanocarpus* (inside trap), 1 male, 3 females (KSEM, UNAM). Distrito Teotitlán, Mpio. San José Tenango, near San Martín Caballero, 18°06.721'N, 96°38.426'W, 1470 m, 25-27.V.1994, coll. N. Woodman, ex. *Peromyscus* sp. (1 female, NW 902, 1 male, NW 910), 2 males, 2 females (KSEM).

Comments. The three specimens collected from *Peromyscus* in Distrito Teotitlán, near San Martín Caballero (1500 m elev.) are slightly different in that the apex of the paramere of the aedeagus is slightly longer and more slender than that of more typical *A. barrerae* (Fig. 6). Also, one male specimen has the apex of sternum IX emarginate.

They are otherwise indistinguishable from typical *A. barrerai*. These slight differences seem insufficient to warrant assigning these specimens to a new taxon (subspecies or species). Therefore, we have included them as *A. barrerai*, but with some reservation. Additional material is required, most especially from the region between the Teotitlán population and the populations north of Oaxaca City, to assess the status of these populations.

We have not examined the holotype and other specimens of *A. barrerai* described by ZARAGOZA CABALLERO & SÁNCHEZ HERNÁNDEZ (1993), but it is clear from their descriptions and figures that the specimens listed here are correctly placed in this species. However, the differences that they listed between *A. barrerai* and *A. bolivari* were variable in our specimens and did not prove to be reliable for species discrimination.

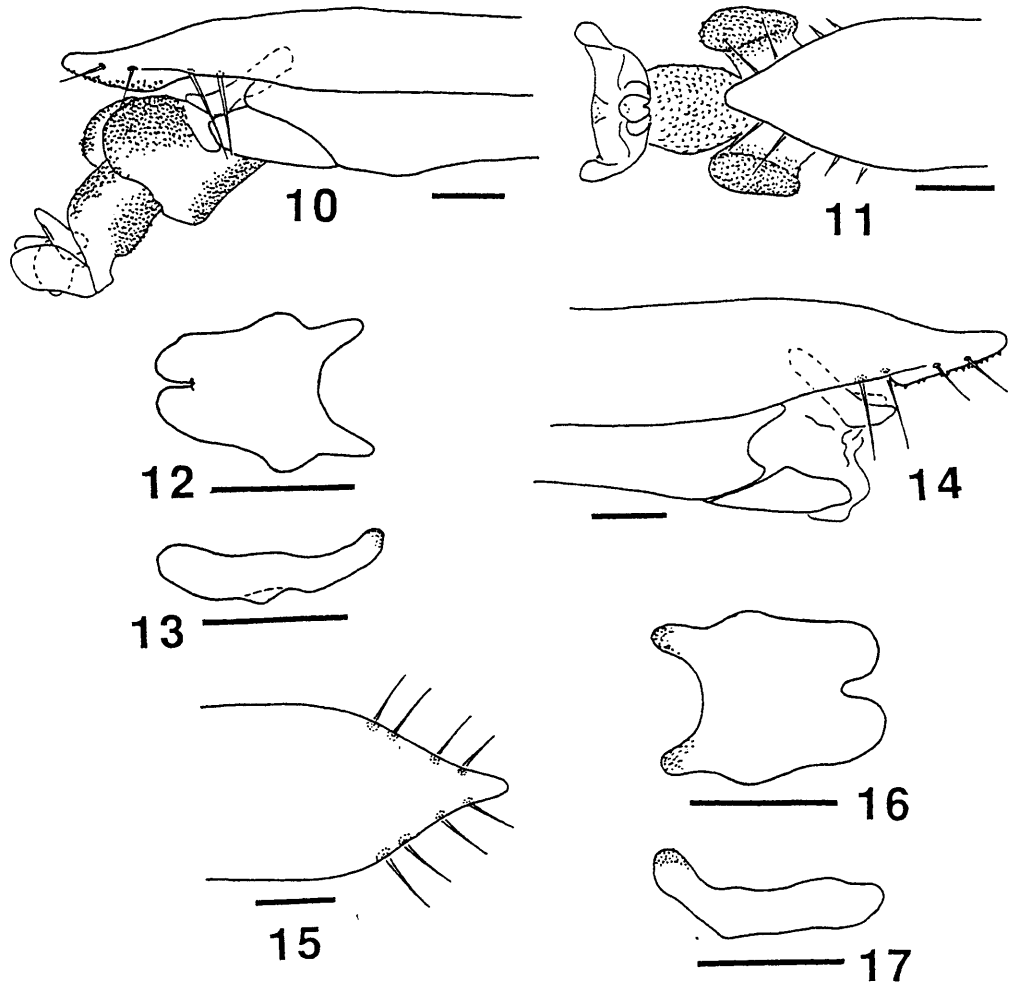
Amblyopinus schmidti SeEVERS 1944 (Figs 10-17, Map 2)

Head. Shape similar to *A. isabellae* except lateral margins not as divergent posterior to eyes, anterior margin wider. Occipital lobe of head without, or with weak, shallow, broad sinus behind eyes. Clypeal margin very slightly and broadly concave; 1 short seta at each fronto-lateral angle. Labrum bilobed; 7 setae along anterior margin in each half, setae 3 and 5 from midline noticeably larger than others, with 5 significantly larger than 3. Macrosetae typical for species group. Seven-eight marginal microsetae in addition to a large macroseta on ocellar margin immediately behind eye; antennal groove with 5-8 microsetae on ventral margin, without microseta anterior to eye. Antennal groove moderately concave posterior to antennal insertion. Antennal length moderately long, extended to basal 0.25 of pronotum; article 1 about 1.5 times as long as article 2. Microsculpture distinct to slightly obsolete in some specimens, with sculpticells slightly to moderately transverse; integument appearing moderately shiny. Punctures of head small and uniformly distributed; distance between punctures 1.5-3.0 times average width of punctures. Eyes with 4-5 facets partially visible from above; supraocellar bristle at upper rear angle of eye, and separated from eye by less than the width of puncture. Gena broad, with numerous microsetae uniformly distributed, and 1 large macroseta on each side. Submentum wide; anterior margin straight; 1 very long slender macroseta on each side and 8-12 microsetae on each half of midline. Mentum with 1 very small to minute seta on each side.

Pronotum. Sides slightly rounded and moderately converging to anterior angles, greatest width in posterior 0.2. Greatest width 1.5 times width at anterior margin; 1.5 times as wide as greatest length. Posterior margin almost straight, or at most very slightly concave medially. Posterior margin with 1 prominent macroseta medial to postero-lateral angle. Lateral margin with 1 macroseta. Microsculpture moderately strong to slightly obsolete, sculpticells reticulate to slightly transverse; integument moderately shiny. Punctures small, somewhat shallow, and uniformly distributed; distances between punctures 2.0-4.0 times average width of punctures.

Elytra. Each elytron 1.1-1.2 times wider than long; uniformly covered with a uniform pilosity of mixed long and short flavate microsetae. Scutellum moderately broad and obtusely rounded posteriorly.

Thorax. Prosternum with 1 pair of long medial macrosetae, and scattered microsetae on anterior half. Metasternum more transverse than that of *A. isabellae*; apex



Figs 10-13. — *Amblyopinus schmidti schmidti* Seevers. Fig. 10, aedeagus, lateral aspect, internal sac partially extended. Fig. 11, aedeagus, dorsal aspect, internal sac partially extended. Fig. 12, internal sclerotized plate of aedeagus, dorsal aspect, oriented with more ventral margin to left. Fig. 13, internal sclerotized plate of aedeagus, lateral aspect, oriented same as Fig. 12. (Scale lines = 0.1 mm).

Figs 14-17. — *Amblyopinus schmidti bolivari* Barrera et al. Fig. 14, aedeagus, lateral aspect, internal sac not extended. Fig. 15, aedeagus, dorsal aspect, internal sac not extended. Fig. 16, internal sclerotized plate of aedeagus, dorsal aspect, oriented with more ventral margin to right. Fig. 17, internal sclerotized plate of aedeagus, lateral aspect, oriented same as Fig. 16. (Scale lines = 0.1 mm).

acutely emarginate medially, depth of emargination about equal to width; process uniformly covered with recumbent microsetae except for posterior margin. Mesotarsal segment 1 slightly longer than 2 and 3 together, not noticeably robust, segments 2-4 subequal in length. White pilosity of mesothoracic legs on distal 0.7 of tarsomere 1 and extending through tarsomeres 2-3.

Abdomen. Tergum II with 1 large, darkly pigmented, marginal macroseta in lateral 0.25, and smaller and thinner, weakly pigmented marginal seta lateral to it (not whip-like); terga III-VII with 1 large, dark, marginal macroseta near lateral 0.25, and with 1 thin, less pigmented, whip-like macroseta lateral to it; tergum VIII evenly rounded, with 1 thin, whip-like (in some), discal macroseta on each side near lateral margin (broken in many specimens); tergum IX truncate posteriorly, broader than that of *A. isabellae*, with numerous long, slender marginal bristles. Sterna III-VI with 1 large, darkly pigmented marginal macroseta on each side, and 3 small weakly pigmented, thin, macrosetae lateral to it; sternum VII with 2 or 3 large, darkly pigmented, marginal macrosetae on each side, and 2 or 3 thin, whip-like, less darkly pigmented marginal macrosetae lateral to them.

Female abdomen. Sternum VII with 2 larger and 1 smaller, dark, marginal macrosetae on each side, and 2 thin, slender macrosetae more lateral to them; sternum VIII with 3 large, dark macrosetae on each side (one specimen has 2 on one side and 3 on the other). Tergum IX fairly broad, more or less truncate with numerous long, thin, golden setae.

Male abdomen. Posterior margin of sternum VIII deeply emarginate; most specimens with 3 macrosetae on each half (holotype of *A. s. schmidti* has 2 macrosetae on each half). Apical margin of sternum IX truncate in most, not or only slightly emarginate. Posterior margin of tergum VIII evenly rounded. Tergum IX truncate posteriorly, broader than that of *A. isabellae*, and with numerous long slender marginal bristles.

Aedeagus (Figs 10-11, 14-15). Apex of paramere short and stubby, not upturned, moderately sinuate anterior to third macroseta. Spiniform setae numerous, extended 0.5-0.7 distance between seta 2 and 3 to near apex. Internal sclerotized plates as in Figs 12-13, 16-17.

Distribution. As in Map 2.

Two subspecies of *A. schmidti* are known. They are not distinguishable by external characteristics, and the differences in the male aedeagi are very slight. They can primarily be distinguished by the very distinct ranges occupied by the two forms, and by differences in their primary host.

Amblyopinus schmidti schmidti SeEVERS 1944 (Figs 10-13, Map 2)

Very similar to *A. schmidti bolivari* but spiniform setae of mesolateral shelf of paramere of aedeagus distributed more or less uniformly to near situation (Fig. 10); internal sclerotized plate as in Figs 12-13. Known from highlands of southern Chiapas and Guatemala (Map 2). Primary host *Peromyscus guatemalensis*.

Type material. Holotype: male. Guatemala: Chimal, Santa Elena, 22.I.1934, L. Mandel-F.M. Guat. Exped., K.P. Schmidt, ex. *Peromyscus guatemalensis*. Pinned, genitalia dissected and placed in genitalia vial attached beneath specimen. Deposited at Field Museum of Natural History.

Material examined. Mexico: Chiapas; El Triunfo, 10 km SSE Finca Prussia, 1900 m, ex. *Peromyscus* sp., 4 males, 2 females (FMNH, KSEM). Same locality, 09.VIII.1986, coll. L.J. Barkley, ex. *Peromyscus guatemalensis* (female, LJB-0397), 2 females (FMNH, KSEM). Same locality, date, and collector, ex. *Peromyscus guatemalensis* (male, LJB-3096), 3 males (FMNH, KSEM). Same locality and date, coll. M.D. Engstrom, ex. *Peromyscus guatemalensis* (female, MDE-5032), 1 female (FMNH). Same locality, date, and collector, ex. *Peromyscus guatemalensis* (female, MDE-5031), 1 female (FMNH). Same locality, date, and collector, ex. *Peromyscus guatemalensis* (male, LJB-3098), 1

male (FMNH). Same locality, date, and collector, ex. *Peromyscus guatemalensis* (female, MDE-5041), 1 male (FMNH). Same locality, date, and collector, ex. *Peromyscus guatemalensis* (female, LJB-3100), 1 female, 1 male (FMNH). Same locality, date, and collector, ex. *Peromyscus guatemalensis* (male, LJB-3091), 1 male (FMNH). Same locality, date, and collector, ex. *Peromyscus* sp., 1 male (FMNH).

Guatemala: Chimal, Santa Elena, 26.I.1934, K.P. Schmidt, ex. *Peromyscus guatemalensis*, 1 male (paratype) (FMNH). Same locality and collector, 23.I.1934, ex. *Peromyscus guatemalensis*, 2 females (paratypes) (FMNH, MCZ). Sacatepéquez, Finca San Rafael, 6 km W of Mixco, 6900 ft, 1.VI.1948, ex. *Peromyscus guatemalensis*, 1 male, 1 female (FMNH). V. Tajumulco, 6000-8000 ft, 18.II.1934, coll. K.P. Schmidt, 1 female (paratype) (FMNH). El Progreso, Arriba de Albores, Cerro Pinalon, 1-7.III.1993, coll. E. Cano & EER, 6 males, 1 female (KSEM, UDVG). Zacapa, 2 km N San Lorenzo, Sierra de las Minas, 2150 m, 10.I.1992, coll. M.D. Engstrom, ex. *Peromyscus guatemalensis* (F34216 and F34224), 1 male, 1 female (KSEM); Sierra de las Minas, Finca Montes de Morán [15°09'N, 89°31'W], 1500-2000 m, coll. R.G. McLean & S.R. Ubico, ex. *Peromyscus guatemalensis* (GT862, 874, 875, 883, 895, 898, 903), 4 females, 5 males (KSEM).

Amblyopinus schmidti bolivari Barrera et al. 1960 (Figs 14-17, Map 2)

Very similar to *A. schmidti schmidti*, but spiniform setae of mesolateral shelf of paramere of aedeagus more concentrated in apical 0.6 than in basal 0.4 of shelf before sinuation (Fig. 14), internal sclerotized plate as in Figs 16-17. Known from the Transvolcanic Sierra of Mexico (Map 2). Primary hosts *Microtus mexicanus* and *Neotomodon alstoni*.

Type material. Holotype: male. Mexico: D.F., Estación Piscícola, El Zarco, 3000 m, 27.VI.1959, coll. C.E. Machado-Allison, ex. nido de *Microtus m. mexicanus*. Entire beetle cleared and mounted in Canadian balsam on a microscope slide. Slide number MZFC 30. In collection of Museo de Zoología, UNAM, Mexico City.

Material examined. Mexico: same locality, date, collector, and host, 1 female (allotype, whole mount of beetle on microscope slide, slide number MZFC 31) (UNAM). Same locality, date, collector, and host, 1 male (paratype, aedeagus on microscope slide, slide number MZFC 32a) (UNAM). Michoacan, nr Angango on Sierra Chincua, 3000 m, 28.III.1986, coll. J.I. Glendinning, ex. *Microtus mexicanus* (between ears), 1 male (FMNH). Same locality [19°41'N, 100°18'W], 3050 m, 13.I.1988, coll. J.I. Glendinning, no host, 1 male (KSEM).

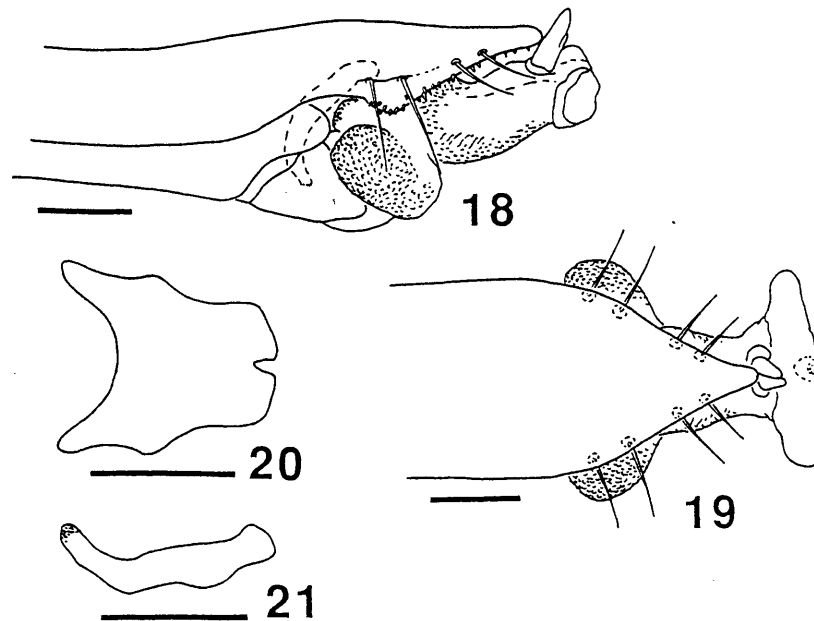
Specimens of uncertain placement. BARRERA & MACHADO-ALLISON (1965) report a specimen of *Amblyopinus* species near *A. bolivari* from Cerro Potosí (Nuevo León, Mexico). They give no further details, and we were not able to locate this specimen. Therefore, we are not able to determine the identity of the *Amblyopinus* species found on Cerro Potosí.

Discussion. In spite of the great similarity between specimens of *A. s. schmidti* and *A. s. bolivari* we accept their subspecific status with some reservations. The great distance which separates the two populations, and the presence of other, clearly distinct, species of *Amblyopinus* between them, suggests that these two populations must have been separated for a considerable period of time. It seems unlikely that the populations of these two subspecies could have been in contact more recently than either was to one of the other Mexican species. In addition, the remarkable host change from *Peromyscus* to *Microtus* in the *A. s. bolivari* population suggests substantial behavioral, physiological and ecological diversification. It seems possible that these two populations have simply failed to diverge from the plesiomorphic condition in spite of long separation, so that, in spite of a high degree of morphological similarity, they may not be sister taxa. If so, the subspecific status for the two populations would be inappropriate. Demonstration of the true patterns of relation-

ship among the two subspecies of *A. schmidtii* and the other Mexican members of the *jelskii* group will probably require molecular studies. While we currently accept the subspecific status of the Transvolcanic Sierra populations and those from southern Chiapas and northern Guatemala, based solely on morphology, we believe there is good reason to question this interpretation.

***Amblyopinus tiptoni* Barrera 1966 (Figs 18-21, Map 1)**

Head. Shape similar to *A. isabellae* except lateral margins not as divergent posterior to eyes, anterior margin wider. Occipital region behind eyes only slightly concave, concave region not extending laterally across neck. Clypeal margin very slightly and broadly concave to almost straight; 1 small, stubby seta near each fronto-lateral angle. Labrum as in *A. isabellae* and *A. schmidtii*. Macrosetae typical for species group; supra- and super-orbital setae longer than super-antennal seta. Six-seven marginal microsetae in addition to a large macroseta on ocellar margin immediately behind eye; antennal groove with 9-11 (occasionally 12) microsetae on ventral margin, with or without (most) microseta anterior to eye. Antennal groove slightly and broadly concave throughout length, more deeply concave near antennal insertion. Antennal length moderately long, extended to near base of pronotum. Microsculpture of head moderately prominent with isodiametrically reticulate to more or less transverse sculpticells. Punctures of head distinct and shallow; distance between punctures 1.0-4.0 times average width of punctures. Eyes with 6-7 facets visible from above.



Figs 18-21. — *Amblyopinus tiptoni* Barrera. Fig. 18, aedeagus, lateral aspect, internal sac extended. Fig. 19, aedeagus, dorsal aspect, internal sac extended. Fig. 20, internal sclerotized plate of aedeagus, dorsal aspect, oriented with more ventral margin to right. Fig. 21, internal sclerotized plate of aedeagus, lateral aspect, oriented same as Fig. 20. (Scale lines = 0.1 mm).

Supra-ocellar bristle at upper rear angle of eye, and separated from eye by less than or equal to length of puncture. Gena broad, with numerous microsetae, and 1 large macroseta on each side. Submentum wide; anterior margin slightly arcuate to almost straight; 1 long, dark macroseta on each side and 13-14 microsetae on each half of midline. Mentum with 1 short, blunt seta on lateral third of each side.

Pronotum. Sides moderately converging from greatest width near basal third to distinct anterior angles. Greatest width 1.5 times width at anterior margin; about 1.4 times as wide as long. Posterior margin slightly and broadly emarginate to almost straight in some specimens. Posterior margin with 1 prominent macroseta slightly medial to postero-lateral angles; lateral margin with 1 macroseta. Microsculpture distinct, moderately strong and reticulate throughout; integument moderately shining. Punctures, small, shallow, uniformly distributed; each puncture distinct and craterform and surrounded by a shallow depression resulting in appearance of broad, shallow punctures; distances between punctures 1.5-3.0 times average width of punctures.

Elytra. Proportions of elytra similar to *A. isabellae*; covered by dense pilosity of mixed long and short microsetae. Scutellum broad, bluntly and obtusely pointed posteriorly.

Thorax. Prosternum with 1 pair of long, medial macrosetae and scattered microsetae on anterior half. Mesosternum similar to that of *A. isabellae* (see BARRERA 1966a: fig. 31). Mesotarsal segment 1 slightly longer than 2 and 3 together, not markedly robust or larger in comparison to other articles; tarsi not greatly shortened or dilated. White pilosity of mesothoracic legs on distal 0.7 of tarsomere 1 and extended through tarsomere 2-3.

Abdomen. Terga II-VII with 1 large, dark, marginal macroseta in lateral 0.25 and 1 much thinner, less pigmented, long, whip-like macroseta lateral to it; tergum VIII broadly rounded, with at least 2, and 3 or 4 in some specimens, thin, almost whip-like, macrosetae. Tergum IX more or less trapezoidal, with several long, thin, marginal setae. Sterna III-VI with 1 large, darkly pigmented, marginal macroseta on each side and with 5 (or 4) thin, less darkly pigmented, marginal macrosetae lateral to it; sternum VII with 2 (or 3 in some) large, darkly pigmented, marginal macrosetae on each side, and 3 (or 2 in some) thin, less darkly pigmented (almost whip-like), marginal macrosetae lateral to it.

Female abdomen. Sternum VII with 2 (or 3 in some) large, dark, marginal setae on each side, and 2 (or 3 in some?) thinner, less pigmented macrosetae lateral to them; sternum VIII with 3 large, dark macrosetae on each side (2 on each side in some, and some with 2 on one side and 3 on the other). Tergum IX fairly broad, more or less truncate with numerous long, thin, golden setae.

Male abdomen. Posterior margin of sternum VIII deeply emarginate; macrosetae of sternum VIII variable, most with 3 large macrosetae on each side (range 2-4, holotype has 2 on left and 4 on right). Apical margin of sternum IX broadly rounded to truncate, or very slightly, and broadly, emarginate in some specimens. Posterior margin of tergum VIII evenly rounded. Tergum IX truncate to slightly and broadly emarginate posteriorly.

Aedeagus (Figs 18-19). Apex of paramere relatively wide in dorsal aspect. Spiniform setae numerous from near apex to basal to most proximal macroseta. Internal sclerotized plate as in Figs 20-21.

Distribution. As in Map 1.

Type material. Holotype: male. Panama: Chiriquí; Bambito, 5800 ft, 9.II.1960, coll. V.J. Tipton, ex. *Peromyscus nudipes nudipes*, T-5967. Undisseminated male on microslide. Reported in MUÑIZ et al. (1981) as deposited in the Barrera collection [catalog number MZFC 47] at Museo de Zoología "Alfonso L. Herrera", Universidad Nacional Autónoma de México, Mexico City; has been permanently transferred to the Field Museum of Natural History in accordance with the type deposition indicated in the original description thanks to the efforts and generosity of Jorge Llorente Bousquets.

Material examined. Costa Rica: Province Cartago; Cordillera de Talamanca, Villa Mills, Pensi3n La Georgina, 3000 m, 10.VIII.1984, coll. R.M. Timm, ex. *Peromyscus nudipes* (female, RMT 3509), 1 female (FMNH). Same locality, elevation, date, and collector, ex. *Peromyscus nudipes* (RMT 3510), 1 female (FMNH). Cordillera de Talamanca, Villa Mills, upper R3o Mache watershed, 2750 m, 24.II.1989, coll. C.A. Langtimm, ex. *Peromyscus nudipes* (male, CAL 2738), 1 male (KSEM). Same locality, elevation, date, and collector, ex. *Peromyscus nudipes* (female, CAL 230), 1 female (KSEM). Same locality, elevation, and collector, 25.II.1989, ex. *Peromyscus nudipes* (female, CAL 232), 1 male (KSEM). Same locality, elevation, date, and collector, ex. *Peromyscus nudipes* (male, CAL 233), 1 male (KSEM). One km N of Villa Mills, 2750 m, early III.1991, coll. H. Korn, ex. *Peromyscus nudipes* (several hosts), 5 females, 8 males (KSEM). Province Heredia; Parque Nacional Braulio Carrillo, 2 km N, 500 m E Sacramento, 2600 m, 2.V.1986, coll. C.S. Vaughan, ex. *Peromyscus nudipes* (CSV 23), 1 female (FMNH). Parque Nacional Braulio Carrillo, 5 km E Vara Blanca, 2050 m, 17.IV.1986, coll. J.S. Ashe, ex. *Peromyscus nudipes* (male, RMT 3654), 1 female (FMNH). Same locality and elevation, 18.IV.1986, coll. J.S. Ashe, ex. *Peromyscus nudipes* (male, RMT 3655), 1 female (FMNH). Same locality, elevation, date, collector, ex. *Peromyscus nudipes* (male, RMT 3657), 1 female (FMNH). Same locality and elevation, 19.IV.1986, coll. J.S. Ashe, ex. *Reithrodontomys creper* (male, RMT 3663), 2 males (FMNH). Same locality and elevation, 20.IV.1986, coll. J.S. Ashe, ex. *Reithrodontomys creper* (female, RMT 3667), 1 male and 2 females (FMNH). Province Puntarenas; Cerro Amigos, Monteverde, 1790-1800 m, 11-13.V.1989, coll. J.S. Ashe & R.M. Timm, ex. *Peromyscus nudipes* (35 hosts), 46 males, 49 females (FMNH, KSEM). Monteverde, Campbell's Woods, 17.VII.1980, coll. S. Anderson, ex. *Peromyscus nudipes* (SA 86), 1 male (LACM). Same locality, date, and collector, ex. *Peromyscus nudipes* (SA 87), 2 males (LACM). Same locality and collector, 13.IX.1980, ex. *Peromyscus nudipes* (SA 102), 1 male and 1 female (LACM). Monteverde, 1520 m, VII.1984, coll. D.H. Clayton, ex. *Peromyscus nudipes* (sex ?), 1 male and 1 female (FMNH). Monteverde, Campbell's Woods, 1-7.V.1986, coll. J.S. Ashe & R.M. Timm, ex. *Peromyscus nudipes* (8 hosts), 5 males, 6 females (FMNH). Province San Jos3; 4 km S, 2 km E Ojo de Agua [9°34'45"N, 83°48'06"W], 2440-2650 m, 19-21.V.1986, coll. J.S. Ashe & R.M. Timm, ex. *Peromyscus nudipes* (13 males and 13 females, A&T 487-543), 60 males and 65 females (FMNH, KSEM). San Gerardo de Sta Mar3a de Dota, 1850-2000 m, XI.1982, coll. L.D. G3mez, ex. *Reithrodontomys creper* (11 unsexed hosts), 31 males and 27 females (FMNH, KSEM). San Gerardo de Dota, 20.VII.1984, coll. J. Monge, ex. *Peromyscus nudipes* (JM 15), 1 female (FMNH). Same locality, 21.VII.1984, coll. J. Monge, ex. *Peromyscus nudipes* (JM 18), 1 female. Same locality, date, and collector, ex. *Peromyscus nudipes* (JM 25), 1 male and 1 female (FMNH). Same locality, date, and collector, ex. *Peromyscus nudipes* (JM 26), 2 females (FMNH).

Panama: Chiriquí-Bocas del Toro boundary; Cerro Bollo, 3.5 km E Escopeta, 1800-1856 m, 15-22.VI.1980, coll. R.J. Izor & R.H. Pine, ex. *Reithrodontomys creper* (2 males and 3 females, RHP 8314, 8358, 8376, 8385, and 8396), 4 males and 3 females (see TIMM & ASHE 1987 for more details).

OTHER MATERIAL

Two specimens of *Amblyopinus* sp. are known from "Honduras: Cortes, 8/10 km. E. Santo Domingo, 470 m, 9 August 1988, coll. T.J. McCarthy, ex. *Peromyscus mexicanus*". Unfortunately, both are females. They are clearly members of the *jelskii* group and are very similar to other members of this group that occur in Mexico and Central America. Because of the great similarity among females of this group it is not possible to determine the status of these specimens until males are discovered. These specimens are deposited in the Snow Entomological Museum, University of Kansas.

DISTRIBUTION AND HOST RELATIONSHIPS

Amblyopinus barrerae. *A. barrerae* has been collected only in the Oaxacan highlands north and east of Oaxaca City at elevations ranging from 1100-2600 m (Map 2). Sixty-five have been collected from at least 18 individual hosts. Seventeen of these hosts are various species of *Peromyscus* (*P. melanocarpus*, *P. oaxacensis*, *P. thomasi*, and *Peromyscus* spp.) with most beetles from *P. melanocarpus* [at least 10 hosts, 21 specimens; ZARAGOZA CABALLERO & SÁNCHEZ HERNÁNDEZ (1993) do not give specific numbers of hosts or beetles]. A single specimen of *A. barrerae* has been found on *Oryzomys alfaroi* (Table 1).

Table 1.
Summary of available host records for Mexican and Central American species of *Amblyopinus*
(* = literature records).

Host	No. hosts with beetles	No. beetles	Locality	Reference
<i>A. barrerae</i>				
* <i>Peromyscus melanocarpus</i>	?	29?	Mex.: Oaxaca	ZARAGOZA CABALLERO & SÁNCHEZ HERNÁNDEZ (1993)
<i>Peromyscus melanocarpus</i>	10	21	Mex.: Oaxaca	this paper
* <i>Peromyscus mexicanus</i>	?	?	Mex.: Oaxaca	ZARAGOZA CABALLERO & SÁNCHEZ HERNÁNDEZ (1993)
<i>Peromyscus oaxacensis</i>	1	1	Mex.: Oaxaca	this paper
<i>Peromyscus thomasi</i>	3	6	Mex.: Oaxaca	this paper
<i>Peromyscus</i> sp.	3	7	Mex.: Oaxaca	this paper
<i>Oryzomys alfaroi</i>	1	1	Mex.: Oaxaca	this paper
<i>A. emarginatus</i>				
* <i>Oryzomys albigularis</i>	9	30	Panama: San Felix	TIMM & ASHE (1987)
<i>Oryzomys albigularis</i>	1	4	Costa Rica: Cartago P.	this paper
<i>Oryzomys</i> sp.	?	25	Costa Rica: Cartago P.	this paper
<i>Oryzomys albigularis</i>	3	15	Costa Rica: Heredia P.	this paper
<i>Oryzomys albigularis</i>	7	24	Costa Rica: Puntarenas P.	this paper
<i>Oryzomys albigularis</i>	1	2	Costa Rica: San José P.	this paper
* <i>Peromyscus (Isthmomys) flavidus</i>	1	?	Panama: Chiriquí	MACHADO-ALLISON & BARRERA (1964)
<i>Tylomys watsoni</i>	1	2	Costa Rica: Puntarenas P.	this paper
<i>A. isabellae</i>				
* <i>Peromyscus megalops auritus</i>	1	1	Mex.: Guerrero	BARRERA & MACHADO-ALLISON (1965)

(continued)

Table 1 (continued)

Host	No. hosts with beetles	No. beetles	Locality	Reference
<i>Peromyscus megalops</i>	1	1	Mex.: Guerrero	this paper
<i>Peromyscus thomasi</i>	2	2	Mex.: Guerrero	this paper
<i>Peromyscus</i> sp.	3	4	Mex.: Guerrero	this paper
<i>Neotoma mexicana</i>	1	2	Mex.: Guerrero	this paper
<i>A. schmidti schmidti</i>				
* <i>Peromyscus guatemalensis</i>	?	14	Guatemala	SEEVERS (1944)
<i>Peromyscus guatemalensis</i>	7	9	Guatemala: Zacapa	this paper
<i>Peromyscus mexicanus</i>	2	2	Guatemala	this paper
<i>Peromyscus guatemalensis</i>	8	12	Mex.: Chiapas	this paper
<i>Peromyscus</i> spp.	?	6	Mex.: Chiapas	this paper
<i>Peromyscus</i> sp.	2	2	Guatemala: Zacapa	this paper
<i>A. schmidti bolivari</i>				
* <i>Microtus mexicanus</i> (nest of...)	1	2	Mex.: D.F.	BARRERA et al. (1960)
* <i>Microtus mexicanus</i>	1	1	Mex.: D.F.	BARRERA et al. (1960)
* <i>Microtus mexicanus</i>	?	?	Mex.: Mex.	MACHADO-ALLISON & BARRERA (1964)
* <i>Microtus mexicanus</i>	?	?	Mex.: Mex.	MACHADO-ALLISON & BARRERA (1964)
* <i>Neotomodon alstoni</i>	?	?	Mex.: Puebla	MACHADO-ALLISON & BARRERA (1964)
* <i>Peromyscus</i> sp.	?	?	Mex.: Mex.	MACHADO-ALLISON & BARRERA (1964)
* Under rotten tree trunk	—	1	Mex.: Vol. Orizaba	BARRERA et al. (1960)
<i>Microtus mexicanus</i>	1	1	Mex.: Michoacan	this paper
<i>A. tiptoni</i>				
* <i>Peromyscus nudipes</i>	20	several "long series"	Panama: Chiriquí P.	BARRERA (1966a)
* <i>Peromyscus nudipes</i>	?	5	Costa Rica: Cartago P.	BARRERA (1966b)
* <i>Reithrodontomys creper</i>	1	1?	Panama: Chiriquí	BARRERA (1966a)
* <i>Reithrodontomys creper</i>	1	"several"	Costa Rica: San José P.	VAUGHAN (1982)
* <i>Reithrodontomys creper</i>	5	7	Panama: Cerro Bollo	TIMM & ASHE (1987)
<i>Peromyscus nudipes</i>	2	2	Costa Rica: Cartago P.	this paper
<i>Peromyscus nudipes</i>	?	16	Costa Rica: Cartago P.	this paper
<i>Peromyscus nudipes</i>	5	5	Costa Rica: Heredia P.	this paper
<i>Reithrodontomys creper</i>	2	5	Costa Rica: Heredia P.	this paper
<i>Peromyscus nudipes</i>	45	114	Costa Rica: Puntarenas P.	this paper
<i>Peromyscus nudipes</i>	26	125	Costa Rica: San José P.	this paper
<i>Reithrodontomys creper</i>	11	58	Costa Rica: San José P.	this paper

These data provide strong evidence that species of *Peromyscus*, especially *P. melanocarpus*, are the preferred host of *A. barrerai*.

Amblyopinus emarginatus. In Central America *A. emarginatus* has been found in the montane areas of Chiriquí Province in western Panama and throughout the montane regions of Costa Rica at elevations of 1400-2500 m (Map 1). *A. emarginatus* is also known from numerous collections in the highlands of Colombia and Venezuela (BARRERA & MACHADO-ALLISON 1968, MACHADO-ALLISON & BARRERA 1972). The populations of *A. emarginatus* from Central America are isolated from those of South America by about 900 km of lowlands in northwestern Colombia and Panama (TIMM & ASHE 1987).

At least 22 collections, representing 100 individuals of *A. emarginatus* have been taken from *Oryzomys albigularis*, Tomes' rice rat, in Panama and Costa Rica (Table 1). In Central America only a single collection of two specimens has been taken from another host, *Tylomys watsoni* (Table 1). This is consistent with other host records for *A. emarginatus* in South America reviewed by TIMM & ASHE (1987). We (TIMM & ASHE 1987) point out that of 135 hosts of *A. emarginatus* in the literature, 124 have been from species of *Oryzomys* and most of these have either been from *O. albigularis* (n = 86, 69.4%) or *O. caliginosus* (n = 35, 28.2%). All other hosts reported, including others from various *Oryzomys* species, represent single records, and some may represent contaminations.

These data provide convincing evidence that *Oryzomys albigularis* is the primary host of *A. emarginatus* in Central America.

Amblyopinus isabellae. *A. isabellae* has been collected only in the montane regions of the Sierra Madre del Sur in Guerrero at elevations of 1900-2600 m (Map 2).

Specimens of *A. isabellae* have been collected from eight individual hosts (10 amblyopinine specimens). Seven of these hosts are various species in the *Peromyscus mexicanus* complex (*P. megalops*, *P. thomasi*, *Peromyscus* spp.) and one record is from *Neotoma mexicana* (Table 1). The evidence suggests that the various species of *Peromyscus* form the primary host for *A. isabellae* in the Sierra Madre del Sur, but additional collecting is necessary to determine the full host range of this species and if it shows any host preferences among available hosts.

Amblyopinus schmidti bolivari. *A. s. bolivari* has been found throughout the Transvolcanic Sierra of Mexico at elevations of about 3000 m (Map 2). The tentative occurrence of this subspecies on Cerro Potosí as reported by BARRERA & MACHADO-ALLISON (1965) requires confirmation.

Amblyopinus schmidti bolivari has been collected from six hosts (number of specimens uncertain) as well as from the nest of *Microtus mexicanus* and under a rotten tree trunk. While *A. s. bolivari* has been most commonly collected in association with *Microtus mexicanus* (five out of eight collections) (Table 1), it has also been taken in association with *Neotomodon alstoni* and *Peromyscus* sp. The numerous associations of this species with *Microtus mexicanus* from several different localities are striking and suggest that *M. mexicanus* may be a preferred host of *A. s. bolivari*. If this is confirmed by additional collecting, then the preferred host of *A. s. bolivari* would stand in marked contrast to the other Central American members of the *jelskii* group which are found primarily on the *Peromyscus mexicanus* complex or the closely related *Reithrodontomys creper*.

Additional information on the host relationships of *A. s. bolivari* was provided to us by John I. Glendinning. Glendinning trapped small mammals on Sierra Chincua, near Angangeo, Michoacan, Mexico over a 4-year period as part of his study of rodent predation upon the overwintering populations of monarch butterflies (*Danaus plexippus*). The trapping locality was at 3050 m in a pure stand of the Mexican fir, *Abies religiosa*. His trapping period was from January through March during the years 1985 through 1988. During his mark-recapture study over the 4-year period, he captured six species of rodents and two species of shrews at this site. Species of mammals handled (number of individuals trapped at least once in parentheses) include: Goldman's small-eared shrew, *Cryptotis goldmani* (1); Saussure's shrew, *Sorex saussurei* (24); Mexican vole, *Microtus mexicanus* (49); diminutive wood rat, *Nelsonia neotomodon* (1); volcano mouse, *Neotomodon alstoni* (10); black-eared mouse, *Peromyscus melanotis* (435); Aztec mouse, *P. aztecus hylocetes* (73); and Sumichrast's harvest mouse, *Reithrodontomys sumichrasti* (51). Of these potential hosts, he found *Amblyopinus schmidti bolivari* only on *Microtus mexicanus*. Of the 49 *M. mexicanus* trapped, beetles were found on 11, always located between their ears. The numbers of beetles on Mexican voles ranged from 1 to 3 ($x = 1.5$) (J.I. GLENDINNING pers. comm.). These data further confirm that *Microtus mexicanus* is a primary host for *A. s. bolivari*.

Amblyopinus schmidti schmidti. This species has been collected in the highlands of southern Chiapas in Mexico and in several localities in the montane regions of Guatemala at elevations of 1900-2500 m (Map 2).

Amblyopinus schmidti schmidti has been found only on *Peromyscus* species with the great majority (35 of 45 specimens) having been collected from *P. guatemalensis* in both Chiapas and Guatemala (Table 1). Most other specimens are from unidentified *Peromyscus* species. These data provide strong evidence that *Peromyscus guatemalensis* is the primary host of *Amblyopinus schmidti schmidti*.

Some appreciation of the host specificity of *A. schmidti schmidti* can be gained by comparing the hosts from which amblyopinines were collected, with the diversity of mammals collected on the K.P. Schmidt expedition to Guatemala in 1934 (compiled from K.P. Schmidt field notes located at the Field Museum of Natural History).

At the type locality of Santa Elena, Chimaltenango Department, Karl P. Schmidt and F.J.W. Schmidt collected small mammals from 22 through 30 January 1934. Species of mammals taken (numbers of specimens in parentheses) include: *Cryptotis goodwini* (4), *Sciurus aureogaster* (1), *Sciurus deppei* (1), *Peromyscus guatemalensis* (14), *Peromyscus levipes* (2), and *Reithrodontomys sumichrasti* (1), in addition to one species of bat, *Anoura geoffroyi* (13). Of these potential hosts, Schmidt's field notes and the published type description of *A. s. schmidti* by SEEVERS (1944), clearly record that all beetles (six males and seven females) were collected from only one species of host, *Peromyscus guatemalensis*.

At Volcán Tajumulco, San Marcos Department, F.J.W. Schmidt collected from 13 through 27 February 1934 obtaining: *Sorex veraepacis* (5), *Sciurus aureogaster* (4), *Sciurus deppei* (2), *Heteromys nelsoni* (3), *Neotoma mexicana* (2), *Peromyscus guatemalensis* (5), *Peromyscus levipes* (7), *Reithrodontomys sumichrasti* (3), *Reithrodontomys tenuirostris* (3), and *Mustela frenata* (1). SEEVERS (1944) reported a single female *A. schmidti schmidti* obtained by Schmidt at this locality from *Peromyscus guatemalensis*.

Amblyopinus tiptoni. *A. tiptoni* has been found in the montane areas of Chiriquí Province in Panama and throughout the montane regions of Costa Rica at elevations

ranging from 1500-3000 m (Map 1). *A. tiptoni* is sympatric with *A. emarginatus* at many sites in this region.

Throughout this region *A. tiptoni* has been frequently collected on two species of mice, *Peromyscus nudipes* (104 hosts, 251 amblyopinine specimens) and *Reithrodontomys creper* (19 hosts, 70 amblyopinine specimens) (Table 1). *A. tiptoni* has been found associated with both of these rodent species at some sites (e.g., Monteverde, Costa Rica and 5 km E Vara Blanca, Costa Rica). Both of these rodents appear to be preferred hosts of *A. tiptoni*. Considering the numbers of host records, specimens of beetles, number of collecting sites, and the very substantial amount of mammal collecting that has produced these specimens, the level of host fidelity displayed by *A. tiptoni* for *P. nudipes* and *Reithrodontomys creper* is remarkable (see, for example, ASHE & TIMM 1987a).

Discussion. *Amblyopinus emarginatus* is the only member of the *sanborni* group of SEEVERS (1955) that occurs in Central America. SEEVERS (1955) listed six species as members of this group. Members of the *sanborni* group have been collected from various species of *Thomasomys*, *Oryzomys*, and *Chilomys*, all complex-penis cricetine rodents. The preferred host of *A. emarginatus* in Central America, *Oryzomys albigularis*, is consistent with the association of members of this lineage with complex-penis cricetines in South America. In addition, the association of *A. emarginatus* with *Oryzomys albigularis* in both South and Central America suggests that *A. emarginatus* may have dispersed into Central America at the same time as its host. The lack of significant divergence in the Central American population of *A. emarginatus* suggests that this occurred fairly recently. HERSHKOVITZ (1966: 737-738) includes *Oryzomys albigularis* among his "Stratum IV" cricetine rodents, species that only recently spread over the Panamanian land bridge from South America to Central America and Mexico.

All other Mexican and Central American *Amblyopinus* are members of the *jelskii* group which includes 14 South American species (SEEVERS 1955, BARRERA & MACHADO-ALLISON 1968, MACHADO-ALLISON & BARRERA 1972). Although the *jelskii* group has not been rigorously shown to be monophyletic, most of the members of this group have a distinctive internal sclerotized plate in the aedeagus (as in Figs 2, 4-6, 8-10, 12-14, 16-17, 20-21) which may be a synapomorphy for the group. The Mexican and Central American species are extremely similar to each other, in both external morphology and genitalic features, and they probably represent a monophyletic lineage. However, confirmation of the monophyly of the *jelskii* group members of Mexican and Central American *Amblyopinus* would require a complete analysis of the *jelskii* group and is outside the scope of this paper.

In South America, members of the *jelskii* group have been captured on a diversity of complex-penis cricetines including *Akodon* spp., *Rhipidomys* spp., *Thomasomys* spp., *Phyllotis* spp., *Oryzomys* spp. and *Oxymycterus* spp. (SEEVERS 1955, MACHADO-ALLISON & BARRERA 1972). In addition, one species, *A. monticolus* Seevers, has been collected from *Ctenomys*, a caviomorph rodent (SEEVERS 1955). However, *A. monticolus* lacks an internal sclerotized plate in the aedeagus and may not be correctly placed in the *jelskii* group (ASHE unpublished data).

In contrast the members of the *jelskii* group in Central America and Mexico are all found on peromyscine or microtine rodents, primarily northern groups that do not occur in South America (HERSHKOVITZ 1966). If amblyopinines evolved in South

America as is suggested by presence of the greatest amblyopinine diversity and most "generalized" forms in the South American fauna (WENZEL & TIPTON 1966), then the presence of members of the *jelskii* group in Central America and Mexico must represent a relatively recent invasion of this region. All members of the Central American *jelskii* group are found on members of the *Peromyscus mexicanus* complex (including *Reithrodontomys creper*, all are simple-penis cricetines) except for *A. s. bolivari* which occurs on *Microtus mexicanus* (a microtine rodent). Perhaps most remarkable is that this invasion of Central America and Mexico involves two major host changes, onto peromyscine and microtine rodents, respectively. WENZEL & TIPTON (1966) commented on the host transfer to peromyscine rodents, but they failed to recognize the additional, and even more dramatic, host transfer to microtine rodents by *Amblyopinus schmidti bolivari*.

Whether host transfer to peromyscine or to microtine rodents occurred first cannot be determined with any confidence without a phylogeny of the Central American members of the *jelskii* group. However, a greater diversity of middle American amblyopinines is found on peromyscine rodents, and simple-penis peromyscines are phylogenetically close to the South American complex-penis cricetines. In contrast a single *Amblyopinus* subspecies occurs on a microtine rodent at the northern periphery of the range of *Amblyopinus*, and microtines are phylogenetically more distant from the South American cricetines. These facts suggest the hypothesis that the host transfer was initially to peromyscine rodents. A small radiation of members of the *jelskii* group in Mexico followed this initial host transfer. A later host transfer to *Microtus* occurred at the periphery of the range. This tentative hypothesis of the evolution of host relationships among the Mexican and Central American members of the *jelskii* group can only be tested by an independent reconstructed phylogeny of the members of this group, perhaps by use of molecular characters.

Distributional patterns. Amblyopinines are known from all the major mountain systems in Mexico and Central America from the Transvolcanic Sierra to the Costa Rica-Panama highlands. Except for one reference to "*Amblyopinus* sp. near *A. bolivari*" (BARRERA & MACHADO-ALLISON 1965) from Cerro Potosí, amblyopinines have not been found in Mexico's Sierra Madre Occidental or Oriental. Each mountain system appears to have a distinctive amblyopinine fauna: Transvolcanic Sierra, *Amblyopinus schmidti bolivari*; Sierra Madre del Sur, *A. isabellae*; Sierra Madre de Oaxaca, *A. barrerai*; Chiapas-Guatemala highlands, *A. schmidti schmidti*; Costa Rica-Panama highlands, *A. tiptoni*, *A. emarginatus*.

Amblyopinus tiptoni and *A. emarginatus* are broadly sympatric in the mountain systems of Costa Rica and northwestern Panama. *A. tiptoni* and *A. emarginatus* are in different species groups and have different hosts throughout the areas of sympatry. In contrast, the five species and subspecies of the *jelskii* group have allopatric ranges.

The broad hiatus in the known range of Central American *Amblyopinus* extending from northern Costa Rica to Guatemala can be attributed to the fact that Nicaragua and much of the Honduras are primarily lowland areas, with few regions of the montane habitat that amblyopinines apparently require. However, discovery of two specimens of *Amblyopinus* in Honduras suggests that the pockets of higher montane habitats within the area of hiatus in the distribution of *Amblyopinus* may have isolated populations of *Amblyopinus*.

The origins of distributional patterns of *Amblyopinus* in Mexico and Central America cannot be addressed until the phylogeny of amblyopinine species is more fully understood.

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REFERENCES

- ASHE J.S. & TIMM R.M. 1987a. Predation by and activity patterns of 'parasitic' beetles of the genus *Amblyopinus* (Coleoptera: Staphylinidae). *Journal of Zoology, London* 212 (3): 429-437.
- ASHE J.S. & TIMM R.M. 1987b. Probable mutualistic association between staphylinid beetles (*Amblyopinus*) and their rodent hosts. *Journal of Tropical Ecology* 3 (2): 177-181.
- ASHE J.S. & TIMM R.M. 1988. *Chilamblyopinus piceus*, a new genus and species of amblyopinine (Coleoptera: Staphylinidae) from southern Chile, with a discussion of amblyopinine generic relationships. *Journal of the Kansas Entomological Society* 61 (1): 46-57.
- ASKEW R.R. 1971. Parasitic insects. *New York: American Elsevier Publishing Company*, 316 pp.
- BARRERA A. 1966a. New species of the genus *Amblyopinus* Solsky from Panama and Mexico (Coleoptera: Staphylinidae), pp. 281-288. In: Wenzel R.L. & Tipton V.J., Edits. Ectoparasites of Panama. *Chicago: Field Museum of Natural History*, 861 pp.
- BARRERA A. 1966b. Hallazgo de *Amblyopinus tiptoni* Barrera, 1966 en Costa Rica, A.C. (Col.: Staph.). *Acta Zoologica Mexicana* 8 (5): 1-3.
- BARRERA A. & MACHADO-ALLISON C.E. 1965. Coleopteros ectoparasitos de mamíferos. *Ciencia, México* 23 (5): 201-208.
- BARRERA A. & MACHADO-ALLISON C.E. 1968. *Amblyopinus* de Colombia (Coleoptera Staphylinidae [sic]). *Neotropica* 14 (45): 89-98.
- BARRERA A., MACHADO-ALLISON C.E. & MUÑOZ R. 1960. Un nuevo coleoptero parasito de roedores: *Amblyopinus bolivari* sp. nov. (Col., Staph.). *Ciencia, México* 20 (5-6): 127-130.
- HERSHKOVITZ P. 1966. Mice, land bridges and Latin American faunal interchange, pp. 725-751. In: Wenzel R.L. & Tipton V.J., Edits. Ectoparasites of Panama. *Chicago: Field Museum of Natural History*, 861 pp.

- KIM K.C. & ADLER P.H. 1985. Patterns of insect parasitism in mammals, pp. 157-196. In: Kim K.C., Edit. Coevolution of parasitic arthropods and mammals. *New York: John Wiley & Sons*, 800 pp.
- MACHADO-ALLISON C.E. & BARRERA A. 1964. Sobre *Megamblyopinus*, *Amblyopinus* y *Amblyopinodes* (Col., Staph.). *Revista de la Sociedad Mexicana de Historia Natural* 25: 173-191.
- MACHADO-ALLISON C.E. & BARRERA A. 1972. Venezuelan *Amblyopinini* (Insecta: Coleoptera; Staphylinidae). *Brigham Young University Science Bulletin Biological Series* 17 (2): 1-14.
- MARSHALL A.G. 1981. The ecology of ectoparasitic insects. *New York: Academic Press*, 459 pp.
- MUÑOZ-S. A.M., MORALES-M. J.C., BARAJAS R.A. & LLORENTE-BOUSQUETS J. 1981. Primera lista de tipos depositados en el Museo de Zoología "Alfonso L. Herrera" de la Facultad de Ciencias de la Universidad Nacional Autónoma de México: colección de insectos ectoparásitos "Alfredo Barrera". *Folia Entomológica Mexicana* 49: 155-168.
- SEEVERS C.H. 1944. A new subfamily of beetles parasitic on mammals. Staphylinidae, *Amblyopininae*. *Field Museum of Natural History Zoology Series* 28 (3): 155-172, 12 pls.
- SEEVERS C.H. 1955. A revision of the tribe *Amblyopinini*: staphylinid beetles parasitic on mammals. *Fieldiana: Zoology* 37: 211-264.
- TIMM R.M. & ASHE J.S. 1987. Host and elevational specificity of parasitic beetles (*Amblyopinus* Solsky) (Coleoptera: Staphylinidae) in Panama. *Proceedings of the Biological Society of Washington* 100 (1): 13-20.
- TIMM R.M. & ASHE J.S. 1988. The mystery of the gracious hosts. *Natural History* 9/88: 6, 8-9.
- VAUGHAN C. 1982. Parasitism of harvest mice by staphylinid beetles. *Brenesia* 19-20: 615.
- WENZEL R.L. & TIPTON V.J. 1966. Some relationships between mammal hosts and their ectoparasites, pp. 677-723. In: Wenzel R.L. & Tipton V.J., Edits. *Ectoparasites of Panama*. *Chicago: Field Museum of Natural History*, 861 pp.
- ZARAGOZA CABALLERO S. & SÁNCHEZ HERNÁNDEZ C. 1993. Una especie nueva de *Amblyopinus* Solsky, 1875 (Coleoptera: Staphylinidae; *Amblyopininae*) de México. *Universidad Ciencia y Tecnología* 3 (1): 27-33.