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Systematics, distribution, and host specificity of *Edrabius* Fauvel (Insecta: Coleoptera: Staphylinidae)

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Abstract.—Systematics, distribution, and host relations of the amblyopinine genus *Edrabius* (Coleoptera: Staphylinidae) are reviewed. Herein, we recognize 11 species in the genus *Edrabius,* all of which are obligate associates of South American caviomorph rodents of the families Caviidae, Ctenomyidae, and Octodontidae (Mammalia: Rodentia), and restricted to the southern cone of the continent. Three new species are described: *Edrabius grandis* (host: *Ctenomys coyhaiquensis* and *C. haigi*); *Edrabius australis* (host: *Ctenomys maulinus maulinus*); and *Edrabius chilensiformis* (host: *Octodon degus*). New distribution and host records are given for *E. alticolus* Seevers, *E. argentinus* Seevers, *E. chilensis* Scheerpeltz, *E. peruanus* Seevers, *E. philippianus* Fauvel, and *E. weiseri* Seevers. Occurrence of *Edrabius* on octodontid rodents is reported for the first time (*E. chilensis* from *Aconaemys* and *E. chilensiformis* from *Octodon*). The genus *Edrabius* was formerly known to occur in association with various species of *Ctenomys,* with the exception of one species, *E. kuscheli,* associated with *Galea musteloides* (Caviidae).

Resumen.—Se presenta una revisión de la sistemática, la distribución y las relaciones de los hospederos de los amblyopininos del género *Edrabius* (Coleoptera: Staphylinidae). Se reconocen 11 especies de *Edrabius,* todas parásitos obligados de roedores caviomorfos sudamericanos de las familias Caviidae, Ctenomyidae y Octodontidae (Mammalia: Rodentia). Se describen tres nuevas especies: *Edrabius grandis,* hospedador: *Ctenomys haigi*); *Edrabius australis,* hospedador: *Ctenomys maulinus maulinus*); y *Edrabius chilensiformis,* hospedador: *Octodon degus*). Se entregan nuevos registros distribucionales y de hospederos para *E. alticolus* Seevers, *E. argentinus* Seevers, *E. chilensis* Scheerpeltz, *E. peruanus* Seevers, *E. philippianus* Fauvel y *E. weiseri* Seevers. Por primera vez se reporta la presencia de *Edrabius* en roedores octodóntidos (*E. chilensis* en *Aconaemys* y *E. chilensiformis* en *Octodon*). El género *Edrabius* anteriormente se conocía solamente asociado a diferentes especies de *Ctenomys,* con la excepción de una especie, *E. kuscheli,* asociada a *Galea musteloides* (Caviidae).

Perhaps the most interesting and enigmatic of all insect-vertebrate interactions are those of rove beetles of the tribe Amblyopinini (Coleoptera: Staphylinidae) and their mammal hosts. Amblyopinine beetles are unique members of the family Staphylinidae because of their obligate association with mammals; most of the 40,000 described species of staphylinids are free-living predators (Ashe & Timm 1987b). All

known species of amblyopinines have been most often found attached to the fur of mammalian hosts or in the hosts' nests. Six genera and more than 55 species have been described in the tribe Amblyopinini; five genera are restricted to the Neotropical region and one is found in the Australian region (Ashe & Timm 1988). Those restricted to the Neotropical region include: *Amblyopinodes* Seevers, *Amblyopinus* Solsky, *Chilamblyopinus* Ashe and Timm, *Edrabius* Fauvel, and *Megamblyopinus* Seevers; a single monotypic genus, *Myotyphlus* Fauvel, is restricted to Australia and Tasmania (Ashe & Timm 1988, 1995; Seevers 1944, 1955).

Amblyopinines were, until recently, believed to be obligate, blood-feeding ectoparasites. However, the Central American *Amblyopinus* have a mutualistic relationship with their hosts rather than a parasitic one, and the conclusion that other amblyopinines are parasitic is not supported by available evidence. Beetles living on various rodents that have different nesting biologies show significantly different behaviors, and nesting biology of the hosts undoubtedly played a major role in the evolution of this mutualistic relationship (Ashe & Timm 1987a, 1987b, 1988; Timm & Ashe 1987, 1988, 1989).

Hosts of amblyopinines are primarily cricetine and caviomorph rodents and South American marsupials. The evolution of this association is exceptionally interesting, both in terms of the ecology, evolution and biogeography of the beetles themselves, and also of the mammals with which they are associated. Members of each amblyopinine species are host specific, and members of the genera and intergeneric higher taxa have a tendency to be associated with a particular group of mammals. Our concerted field efforts in recent years have uncovered a high degree of host specificity in these rather large, active beetles (Ashe & Timm 1987a, 1995; Timm & Ashe 1987, and see below).

One of the most poorly known of the amblyopinine genera is *Edrabius*. Currently, eight species of *Edrabius* are known from southern Peru, Argentina, and Chile. These are: *E. alticolus* Seevers; *E. argentinus* Seevers; *E. chilensis* Scheerpeltz; *E. kuscheli* Scheerpeltz; *E. pearsoni* Seevers; *E. peruanus* Seevers; *E. philippianus* Fauvel; and *E. weiseri* Seevers. Of the species of *Edrabius* currently recognized, most occur on species of *Ctenomys* (Rodentia: Ctenomyidae), the tuco-tucos. However, in this paper we also report their occurrence on two additional genera of rodents, *Aconaemys* and *Octodon* (Octodontidae). Ctenomyids and octodontids are caviomorph rodents that are found throughout southern South America. They occur in Argentina, Chile, southern Bolivia, and Peru and range in elevation from sea level to 4700 m (Mares & Ojeda 1982).

Little information is available about the life history or habits of the species of *Edrabius,* or about the nature of the beetle-mammal interaction. Fauvel (1900) reported the observations of Philippi that adults and larvae of *Edrabius philippianus* were found around the anus of a species of *Ctenomys* and caused damage to the skin. Fauvel received adult beetles that he subsequently described, but he did not mention the larvae in his description, and he may not have actually received them. There have been no subsequent reports of amblyopinine larvae on any host, although hundreds of mammals carrying adult amblyopinines have been examined. Timm & Ashe (1989) described larval *Edrabius* that were found in the nest of *Ctenomys* in Chile.

In this paper we: describe three new species of *Edrabius*; review previously published information about *Edrabius*; and provide new information on host and geographic distributions of *Edrabius.*

Materials and Methods

Recent field work in Chile by one of us (MHG) as part of his ongoing research on the systematics and biogeography of *Cten-*

omys, as well as that of other field workers provide significant new information about, and specimens of, *Edrabius.* The new material prompted us to review the systematic status of all the species of *Edrabius* in Argentina, Bolivia, Chile, and Peru.

In the course of this study, we examined the types and dissected aedeagi of all described species of *Edrabius* except *E. philippianus.* According to Seevers (1955) the holotype, and only known specimen, of *E. philippianus* is a female. He gives a detailed description of this specimen, including illustrations of distinctive pronotal features. None of the species described here match the description of *E. philippianus* given by Seevers. We also examined the specimens that Scheerpeltz (1957) identified as *E. philippianus* and that he used in his comparisons with other species. We are convinced that these specimens are incorrectly identified. They do not have the distinctive pronotal shape that Seevers (1955) described for *E. philippianus,* and other described features also do not fit Scheerpeltz's specimens very well (though these are more qualitative and less distinctive). In addition, all of Scheerpeltz's specimens are from Argentina, whereas the type of *E. philippianus* is from Antofagasta, in the Atacama Desert of Chile.

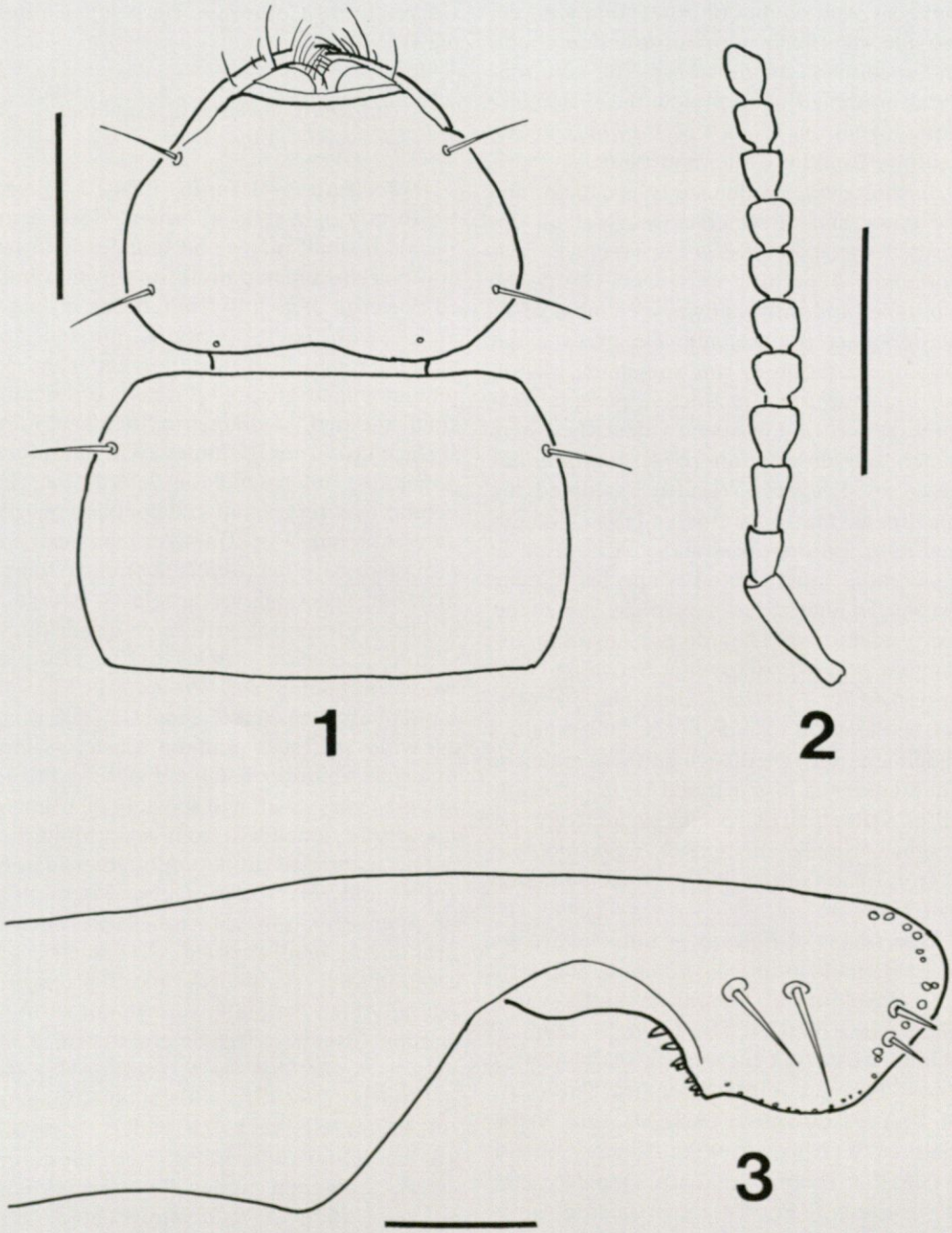
Specimens of *Edrabius* examined are deposited in: Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile (IEEUACH); Field Museum of Natural History, Chicago, Illinois (FMNH); Snow Entomological Museum, University of Kansas, Lawrence (KSEM); and Naturhistorisches Museum Wien, Vienna, Austria (NHMW). The mammal hosts are deposited in: Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile (IEEUACH); American Museum of Natural History, New York (AMNH); Field Museum of Natural History (FMNH); Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico (MSB); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ).

Edrabius grandis, new species
Figs. 1–3

Description.—Length 9.0–10.5 mm. Uniformly light reddish-brown. Head shape variable, small males and females with lateral margins tapered uniformly from rounded posterior angles to front, heads of larger males with lateral margins inflated and broadly rounded in posterior half (Fig. 1); integument of head with dense, prominent, small-meshed, isodiametric microsculpture, surface not strongly shining; without micropunctures; microsetae on lateral margins behind eye very small and sparsely distributed. Antenna (Fig. 2) longer than head and pronotum together, article 2 slightly longer than, or subequal to, article 3, article 4 slightly elongate; article 5 quadrate to slightly elongate; articles 6-10 slightly to moderately elongate. Pronotum (Fig. 1), moderately transverse, about 1.5–1.6 times as wide as long; without postero-lateral macroseta; microsetae on antero-lateral margins very small and sparsely distributed, microsetae extended from near middle of lateral margin of pronotum to antero-lateral angles and very sparsely along lateral third of anterior margin; integument with dense, prominent, small-meshed, isodiametric microsculpture, sculpticells more prominent laterally than medially, surface not strongly shining (except in specimens in which the microsculpture has been eroded away due to abrasion); surface without micropunctures. Elytra with very fine, widely dispersed, golden-yellow microsetae, punctures very small. Abdomen uniformly covered with silky vestiture of moderately dense, very fine, yellowish microsetae.

Male.—Posterior margin tergum VIII emarginate. Posterior margin of sternum VIII broadly and evenly emarginate, maximum depth of emargination about 0.5 times width of emargination.

Aedeagus.—As in Fig. 3.



Figs. 1–3. *Edrabius grandis* n. sp. 1. Head and prothorax, dorsal (scale = 1.0 mm); 2. Antenna (scale = 1.0 mm); 3. Apex of aedeagus, lateral (scale = 0.1 mm).

Holotype.—Male, with labels as follows: "Argentina: Prov. Río Negro; 13 km WSW Comallo, el. 1150 m, 15 Nov 1987, A. K. and O. P. Pearson #OPP 7435, ex. *Ctenomys haigi* (MVZ 175156)." "HOLOTYPE, *Edrabius grandis* Ashe, Timm, & Gallardo, Designated J. S. Ashe, R. M. Timm, and M. L. Gallardo 1995." Deposited in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Paratypes.—6, from the following localities. Argentina: Río Negro Prov., 3-V-1986, M. H. Gallardo #833, ex. *Ctenomys haigi* (IEEUACH 1535) ♀, 2 males 2 females. Same locality, date, and collector, MHG #837, ex. *Ctenomys coyhaiquensis* (IEEUACH 1539), 1 male. Chile: Coyhaique Prov.; 4.5 km SE Coyhaique Alto, Fundo Los Flameneos, 750 m; M. H. Gallardo #1092, ex. *Ctenomys coyhaiquensis* ♂ (IEEUACH 4233), 1 male. Paratypes deposited in IEEUACH and KSEM.

Distribution.—Known from the Río Negro Valley in Argentina and adjacent Coyhaique in Chile.

Hosts.—Collected from *Ctenomys coyhaiquensis* in Coyhaique, Chile, and *C. haigi* in Río Negro Province, Argentina.

Discussion.—Specimens of this species are among the largest of any described species of *Edrabius.* They can be recognized by: large size; relatively elongate antenna with elongate antennomeres; head and pronotum densely reticulate with isodiametric sculpticells; integument of head and pronotum without micropunctures; microsetae on lateral margins of head and pronotum very small and sparsely distributed; and, the distinctive aedeagus.

Edrabius australis, new species
Figs. 4–6

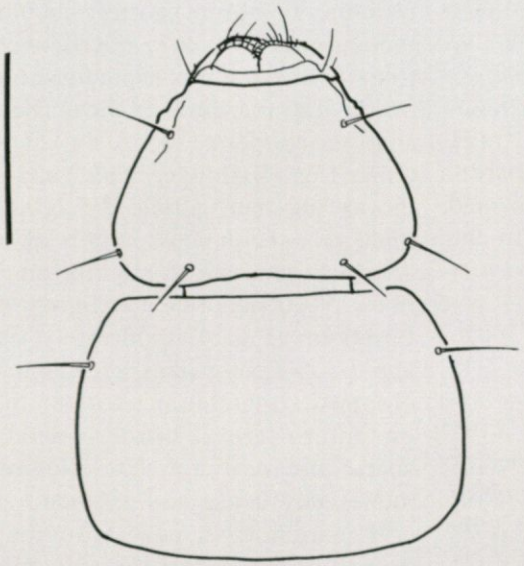
Description.—Length 7.0–9.0 mm. Uniformly light reddish-brown. Head shape (Fig. 4) with lateral margins uniformly tapered from rounded posterior angles anteriorly; integument of head with faint, isodiametric microsculpture, microsculpture obsolete to absent postero-medially, surface strongly shining; micropunctures extremely fine and inconspicuous; microsetae on lateral margins of head behind eye sparse to moderate in size and number. Antenna (Fig. 5) longer than head and prothorax together; article 2 slightly shorter than, to subequal to, length of article 3, article 4 quadrate to slightly elongate, articles 5–10 quadrate to slightly elongate. Pronotum (Fig. 4) moderately transverse, about 1.4–1.5 times as wide as long; without postero-lateral macroseta; microsetae on antero-lateral border variable from sparse and located in antero-lateral half, to moderately dense and extended along lateral margin from near posterior third of pronotum to antero-lateral angles and along lateral third of anterior margin; integument with faint microsculpture, sculpticells isodiametric laterally but slightly elongate medially, surface strongly shining; micropunctures extremely fine and inconspicuous. Elytra with moderate sized, uniformly distributed, yellowish microsetae, punctures small. Abdomen uniformly covered with silky vestiture of moderately dense yellowish microsetae.

Male.—Posterior margin of tergum VIII broadly and moderately emarginate. Posterior margin of sternum VIII broadly and deeply emarginate, emargination broadly rounded internally, width of emargination about 2.3 times depth.

Aedeagus.—As in Fig. 6.

Holotype.—Male, with labels as follows: "Chile: Bío-Bío Prov.; Laguna Laja, 21-III-1987, M. H. Gallardo 1011 & 1012, ex. *Ctenomys maulinus maulinus* (IEEUACH 1640 & 1641)." "HOLOTYPE, *Edrabius australis* Ashe, Timm, & Gallardo, Designated J. S. Ashe, R. M. Timm, and M. H. Gallardo 1995." Deposited in Zoological Collections of the Universidad Austral de Chile, Valdivia, Chile.

Paratypes.—12, same data as holotype; 11, Chile: same locality, date, and collector, MHG #1017, ex. *Ctenomys maulinus mau-*



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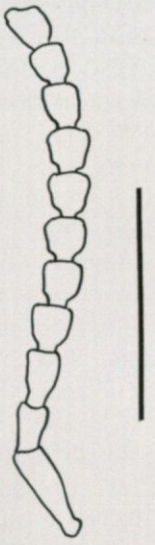

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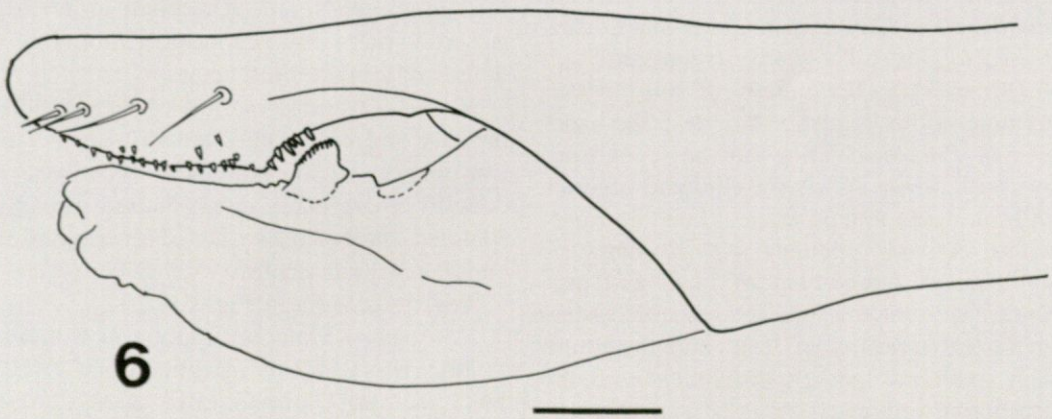

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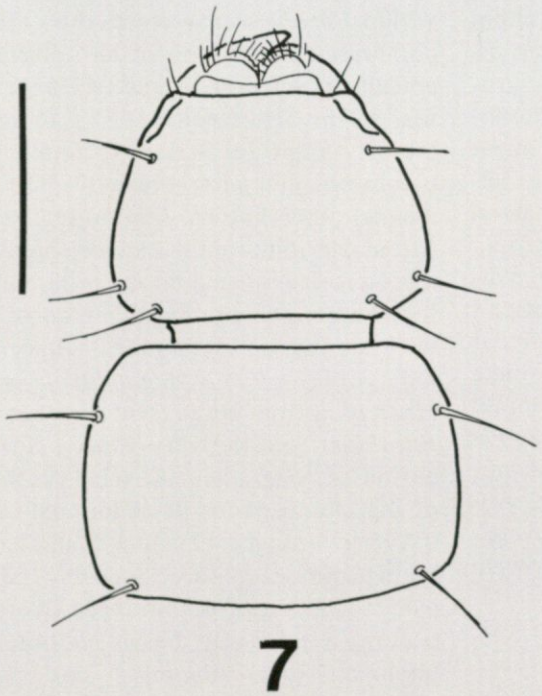
Figs. 4–6. *Edrabius australis* n. sp. 4. Head and prothorax, dorsal (scale = 1.0 mm); 5. Antenna (scale = 1.0 mm); 6. Apex of aedeagus, lateral (scale = 0.1 mm).

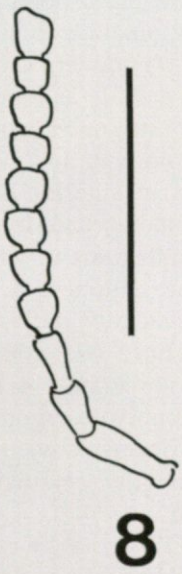
linus (IEEUACH 1646). Paratypes deposited in IEEUACH and KSEM.

Distribution.—Known only from Petronquines, Laguna Laja, Bío-Bío Province, Chile.

Host.—Collected only from *Ctenomys maulinus maulinus.*

Discussion.—This species can be distinguished by the relatively faint reticulation of the head and prothorax with extremely





Figs. 7–9. *Edrabius chilensiformis* n. sp. 7. Head and prothorax, dorsal (scale = 1.0 mm); 8. Antenna (scale = 1.0 mm); 9. Apex of aedeagus, lateral (scale = 0.1 mm).

fine and inconspicuous micropunctures, and the distinctive aedeagus.

Edrabius chilensiformis, new species
Figs. 7–9

Description.—Length 5.0–6.0 mm. Reddish-brown. Head shape (Fig. 7) rounded and tapered from broadly-rounded posterior angles to anterior margins; integument with moderate, elongate, irregularly wavy microsculpture, sculpticells obsolete to absent medially, integument strongly shining; micropunctures numerous, very minute; microsetae on lateral margins behind eye

moderately dense. Antenna (Fig. 8) about as long as head and pronotum together; article 2 subequal in length to article 3, articles 4–10 quadrate to subquadrate. Pronotum (Fig. 7) moderately transverse, about 1.4 times as wide as long; with postero-lateral macroseta; microsetae on antero-lateral margin prominent and more or less densely distributed in anterior half of lateral margins and along anterior third of anterior margins, integument with faint, irregular wavy microsculpture, sculpticells obsolete to absent medially, surface strongly shining; micropunctures numerous, very minute. Elytra with moderately dense, yellowish microsetae, punctures moderate in size. Abdomen uniformly covered with silky vestiture of very densely distributed, yellowish microsetae.

Male.—Posterior margin of tergum VIII very shallowly and broadly emarginate. Posterior margin of sternum VIII broadly and deeply emarginate, emargination broadly rounded; width of emargination about 2.0 times depth.

Aedeagus.—As in Fig. 9.

Holotype.—male, with labels as follows: "Chile: Coquimbo Prov.; 10 km N Puente Los Molles, 32°09′S, 71°31′W, 26-VII-1976, R. E. Martin #1470, ex. *Octodon degus* ♀ (FMNH 119659)." "HOLOTYPE, *Edrabius chilensiformis* Ashe, Timm, & Gallardo, Designated J. S. Ashe, R. M. Timm, and M. L. Gallardo 1995." Deposited in the Field Museum of Natural History, Chicago, Illinois.

Paratypes.—3, same data as holotype. Paratypes deposited in FMNH and KSEM.

Distribution.—Known only from Coquimbo Province, Chile.

Host.—Collected from *Octodon degus* (Octodontidae).

Discussion.—This species is closely related to *Edrabius chilensis* Scheerpeltz from which it can be distinguished by the denser abdominal setation and distinctive aedeagus of *E. chilensiformis. Edrabius chilensis* and *E. chilensiformis* appear to form a distinctive monophyletic group within *Edrabius* characterized by the synapomorphous condition of an upturned and apically pointed aedeagus (see Fig. 9, and fig. 2C in Scheerpeltz 1957). In contrast, these two species appear to retain several plesiomorphic characteristics not found among other known *Edrabius.* These apparent plesiomorphies include: presence of a postero-lateral seta on the pronotum (also found among many free-living quediines, as well as the amblyopinines—*Amblyopinodes, Amblyopinus, Megamblyopinus,* and *Myotyphlus,* but not present on other known *Edrabius*), and the very weakly developed cluster of long aciculate setae on the apex of the lateral plates of abdominal segment 9 (very strongly developed among other known *Edrabius*—see Seevers 1955, fig. 44G). This suggests that these two species occupy a relatively basal position in the phylogeny of *Edrabius.*

It is also interesting that both of these species are known from caviomorph rodents other than *Ctenomys* in the family Octodontidae: *Edrabius chilensis* from the rock rat, *Aconaemys fuscus* and *E. chilensiformis* from the degu, *Octodon degus.* In contrast, most other *Edrabius* are known from *Ctenomys* (the only exception is *E. kuscheli* from the nest of a cui, *Galea musteloides* (Caviidae), but see below).

New Records

Edrabius alticolus Seevers. Bolivia: Dept. Oruro; 3.5 km E Huancaroma, 6-VIII-1984, ex. *Ctenomys opimus opimus* ♀, NK 11550 (MSB 55377), 1 male. Oruro; 2.5 km NE Huancaroma, 3720 m, 6-VIII-1984, ex. *Ctenomys opimus opimus* ♀, NK 11566 (AMNH 260837), 2 males. Oruro; 1 km N, 5 km W Pomata Ayte, Río Barros, 11-IX-1986, ex. *Ctenomys opimus opimus* ♂, NK 14549 (AMNH 263040), 1 male 1 female. Oruro; Huancaroma, 2-X-1986, ex. *Ctenomys opimus opimus* ♀, NK 14765 (MSB 57197), 2 males. Chile: Parinacota Prov.; D. Reise #2710, ex. *Ctenomys opi-*

mus (IEEUACH 4332), 2 males 2 females (KSEM and IEEUACH).

Edrabius argentinus Seevers. Argentina: Mendoza Prov.; 5.7 km NW Villavicencio, 2800 m, 31 December 1981, Richard D. Sage #10656, ex. *Ctenomys haigi* (MVZ 162936), 1 male (KSEM). Seevers (1955: 258) described *E. argentinus* from "ex nido de *Ctenomys*" from Argentina: Catamarca; Hualfin (near Tucumán). On the basis of the locality, we believe the host to be *Ctenomys tucumanus.*

Notes.—This specimen differs from the type series of *Edrabius argentinus* in having a slightly longer antenna with longer articles 4–10, more uniformly rounded lateral margins of the pronotum and mostly isodiametric microsculpture on pronotum (more wavy on specimens in type series). However, the aedeagus is highly distinctive and cannot be distinguished from the aedeagus of the holotype of *E. argentinus.* Therefore, we have chosen to assign the specimen from Mendoza Province to *E. argentinus* in spite of the minor differences noted above. It is possible that a new subspecies should be established for the Mendoza population; however, until more specimens of *E. argentinus* are known from the original population, the Mendoza Province population, and other intervening populations, it would be premature to describe such a subspecies.

Edrabius chilensis Scheerpeltz. Chile: Cautín Prov.; Quetropillán; F. Mondaca #439, ex. *Aconaemys porteri* (IEEUACH 4119), 1 male 1 female. Malleco Prov.; Parque Nacional Nahuelbuta, 10-I-1976, Robert E. Martin #1339, ex. *Aconaemys fuscus,* 1 male (IEEUACH and KSEM).

Notes.—The specimen from Malleco Province has an aedeagus that is slightly more robust apically than that of the specimens from Cautín and that shown in Scheerpeltz's (1957) figure. However, this slight difference does not seem sufficient to assign this specimen to a new species.

Edrabius peruanus Seevers. Chile: Parinacota Prov.; ex. *Ctenomys opimus,* 3 males 4 females (IEEUACH and KSEM).

Edrabius philippianus Fauvel. Fauvel (1900) described *E. philippianus* from *Ctenomys* sp. from Antofagasta, Chile. We herein correct the type host identification to be *C. fulvus* as that is the only species of tuco-tuco occurring in Antofagasta (Gallardo 1991).

Edrabius weiseri Seevers. Bolivia: Dept. Oruro; 7 km S, 4 km E Cruce Ventilla, 3450 m, 30-IX-1986, ex. *Ctenomys opimus opimus* ♀, NK 14748 (MSB 57194), 1 male. Dept. Potosí; 2 km E ENDE Camp, Laguna Colorado, 4280 m, 16-IX-1986, ex. *Ctenomys opimus opimus* ♀, NK 14571 (AMNH 263051), 1 male. Potosí; 2 km E ENDE Camp, Laguna Colorado, 4278 m, 16-IX-1986, ex. *Ctenomys opimus opimus* ♀, NK 14572 (MSB 57204), 7 males 20 females (KSEM).

Discussion

Two major groups of *Edrabius* are apparent. One, represented by *E. chilensis* and *E. chilensiformis,* is found on *Aconaemys* and *Octodon* respectively, both in the family Octodontidae (Table 1). These two small species of *Edrabius* share the synapomorphy of a sharply pointed and upturned apex to the aedeagus. However, they share a number of plesiomorphic features not found in other *Edrabius* (see discussion under *E. chilensiformis*).

The second major *Edrabius* lineage is made up of those species that have the apomorphic conditions of the following characteristics: that is, pronotum without a postero-lateral macroseta, and a very distinct and prominent "pencil" of aciculate setae on the apices of the lateral styli of abdominal tergum IX. This lineage includes all the other known species of *Edrabius.* Members of this second lineage are found primarily on various species of the genus *Ctenomys,* the sole genus in the family Ctenomyidae, though all known specimens of *E. kuscheli*

Table 1.—Summary of known general distribution and hosts of *Edrabius* species (Staphylinidae, Amblyopinini).

General distribution	Host	Reference
E. alticolus Seevers		
Peru: Tacna Prov.	*Ctenomys fulvus*	Seevers, 1955
Bolivia: Oruro Prov.	*Ctenomys opimus*	this paper
Chile: Parinacota	*Ctenomys opimus*	this paper
E. argentinus Seevers		
Argentina: Catamarca	"nest of *Ctenomys*" [*Ctenomys tucumanus*]	Seevers, 1955
Argentina: Mendoza Prov.	*Ctenomys mendocinus*	this paper
E. australis Ashe, Timm, & Gallardo		
Chile: Bío-Bío Prov.	*Ctenomys maulinus maulinus*	this paper
E. chilensiformis Ashe, Timm, & Gallardo		
Chile: Coquimbo Prov.	*Octodon degus*	this paper
E. chilensis Scheerpeltz		
Chile: Curicó	"An Ratten"	Scheerpeltz, 1957
Chile: Malleco Prov.	*Aconaemys fuscus*	this paper
Chile: Cautín Prov.	*Aconaemys porteri*	this paper
E. grandis Ashe, Timm, & Gallardo		
Argentina: Río Negro Prov.	*Ctenomys haigi*	this paper
Chile: Coyhaique Prov.	*Ctenomys coyhaiquensis*	this paper
E. kuscheli Scheerpeltz		
Chile: Arica-Lipiche	"nest of *Galea musteloides*"	Scheerpeltz, 1957
E. pearsoni Seevers		
Peru: Puno Prov.	*Ctenomys opimus nigriceps*	Seevers, 1955
E. peruanus Seevers		
Peru: Puno Prov.	*Ctenomys peruanus*	Seevers, 1955
Chile: Parinacota Prov.	*Ctenomys opimus*	this paper
E. philippianus Fauvel		
Chile: Antofagasta	*Ctenomys fulvus*	Seevers, 1955
E. weiseri Seevers		
Argentina: Jujuy	host unknown	Seevers, 1955
Bolivia: Dept. Oruro	*Ctenomys opimus opimus*	this paper
Bolivia: Dept. Potosí	*Ctenomys opimus opimus*	this paper

were found in the nest of a cui, *Galea musteloides* (but see below) (Table 1).

Scheerpeltz (1957), illustrated specimens of *Edrabius kuscheli, E. philippianus,* and *E. chilensis* showing a posterolateral seta on the pronotum. However, our examination of the holotype of *E. chilensis,* all paratypes of *E. kuscheli,* and specimens labeled *E. philippianus* (almost certainly misidentified, see above) from Scheerpeltz's collection clearly show that specimens of both species lack posterolateral pronotal setae, whereas all three specimens of the type series of *E. chilensis* have such setae.

Furthermore, Seevers (1955), in a quote from O. P. Pearson (page 254), notes that *Galea musteloides* frequently use old *Ctenomys* burrows. If true, then movement of individuals of *Galea* into *Ctenomys* burrows that already had a population of *Edrabius* could account for this unusual host record.

Members of the genus *Ctenomys,* the tuco-tucos, are small to mid-sized (100–

1500 g), strictly fossorial rodents forming a complex assemblage of species with fairly uniform morphology, but extremely variable in chromosome number (Gallardo 1991, Reig et al. 1990). The genetic variation found in the family Ctenomyidae is nearly as great as is found in all other mammals (Gallardo & Köhler 1992, Gallardo & Palma 1992). Although there are 56 available species names of *Ctenomys,* the number of valid species recognized by recent authors ranges from 32 to 44 (Kelt & Gallardo 1994, Mares & Ojeda 1982, Nowak 1991, Reig et al. 1990, Woods 1993). There is consensus that the genus is in need of revision. Tuco-tucos, being strictly fossorial, subterranean dwellers, are restricted to particular soil types and are poor at long distance dispersal and dispersal over water, as is true for other groups of fossorial rodents occupying grasslands on other continents (i.e., the pocket gophers of North America (Geomyidae); the African mole-rats (Bathyergidae); and the mole-rats of Eurasia (Spalacidae)). The subterranean ecotype limits dispersal and produces a population structure characterized by demic fragmentation that facilitates extensive chromosomal variation (Gallardo 1991). In the few species of tuco-tucos studied to date, all maintain extensive underground tunnel systems and have a well-formed, grass-lined nest chamber (Gallardo & Anrique 1991). Reig et al. (1990) suggested that the extensive distribution of tuco-tucos in the southern cone of South America and the lack of morphological differentiation, suggested that the major radiation of the genus was almost certainly post-Pleistocene, although the geologic age of the family goes back to the Pliocene; however, given the diversity, the time of divergence must certainly have been longer. The ctenomyids are believed to be the sister group to the Octodontidae, and it has been suggested that they are more properly classified as a subfamily of the Octodontidae (Reig et al. 1990).

The caviomorph family Octodontidae contains six genera and 11 living species, all with very restricted Andean or pre-Andean ranges. Their habits are diverse. *Octodon degus* is similar to a ground squirrel in behavior, diet, and ecology. *Aconaemys fuscus* is fossorial and similar in size and shape to *Ctenomys,* though less specialized for burrowing (Gallardo & Reise 1992). Other octodontids (*Octomys*) have habits that are similar to woodrats or are strictly fossorial (*Spalacopus*). The biology, ecology, and geographical distributions of most species of octodontids are very poorly known and phylogenetic relationships among the genera are uncertain (Mares & Ojeda 1982, Nowak 1991). Contreras et al. (1987) discussed known aspects of the ecology, distribution, and biogeography of the Octodontidae.

Reig et al. (1990) note that the families Ctenomyidae and Octodontidae (they treated these taxa as subfamilies rather than families) are sister taxa. The Octodontidae are known from the Oligocene of Argentina (Mares & Ojeda 1982, Nowak 1991, Contreras et al. 1987), and it seems possible that the association of *Edrabius* with this lineage of caviomorph rodents may date to at least this time period.

The relatively recent differentiation of *Ctenomys* (Reig et al. 1990) is reflected in evolution of the *Edrabius* found on *Ctenomys* into a number of poorly differentiated species. It is virtually impossible to separate the species of *Edrabius* based exclusively on external characteristics. Aedeagal characteristics are more distinctive, but some (*E. peruanus, E. pearsoni,* and *E. alticolus*) are also only weakly differentiated by aedeagal features. A clear understanding of patterns of species limits and geographic variation of *Edrabius* species associated with *Ctenomys* will require much more extensive collecting.

Few other amblyopinines are known from caviomorph rodents. The only two known species of *Megamblyopinus* are found on *Ctenomys—M. germaini* Fauvel on *C. peruanus* Sandborn & Pearson and

M. mniszechi on *C. opimus nigriceps* Thomas. In addition, *Amblyopinus fuegensis* Seevers occurs on *Ctenomys magellanicus, A. pacae* Seevers is known from *Agouti taczanowskii,* and *Amblyopinodes caviae* Martínez & Prosen is known from *Cavia* species (Caviidae) (Seevers 1955, Machado-Allison 1963).

Given the extensive radiation of *Ctenomys* in southern South America and the relatively few collections of *Edrabius* from these rodents, we strongly suspect that numerous new species of *Edrabius* remain to be collected. In addition, other species of *Edrabius* may be associated with other genera of the Octodontidae. Because of the relatively basal phylogenetic position of those *Edrabius* currently known to be associated with octodontids, it is likely that additional collections of *Edrabius* from octodontids will prove pivotal to understanding the phylogeny and evolution of association of *Edrabius* with caviomorph rodents.

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