

A review of the *Blaesiina* (Coleoptera, Scarabaeidae, Cetoniinae, Gymnetini)

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Abstract

The two genera comprising the subtribe *Blaesiina* (Scarabaeidae: Cetoniinae: Gymnetini) are reviewed. Each genus contains two species, with *Blaesia* Burmeister occurring in southern South America and *Halfferinetis* Morón & Nogueira occurring in northern Mexico. Descriptions, keys, distributions, biology, and illustrations are provided. The biogeography of the *Blaesiina* is discussed with a hypothesis to explain the current disjunct distributions. I provide a new state record for *Halfferinetis gonzalo* Morón & Nogueira in San Luis Potosí, Mexico.

Keywords

Scarabaeidae, Cetoniinae, Gymnetini, *Blaesiina*

Who knows not the name, knows not the subject.

– Linnaeus, 1773

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Introduction

The purpose of this paper is to provide a comprehensive review of the gymnetine subtribe *Blaesiina* by re-describing the two genera and four species, providing illustrations and a key for identification, mapping their distributions, and recording observations on life history when known. This review is a continuation of my series of studies on the New World Gymnetini genera (Deloya and Ratcliffe 1988; Morón

and Ratcliffe 1984; Ratcliffe 1978, 2004, 2005; Ratcliffe and Mico 2001). Two species in the genus *Blaesia* occur in southern South America, and one of them (*B. subrugosa* Moser) is uncommon in collections, possibly a result of unusual life history traits that conceals them from general collecting methods. Two other species in the genus *Halffterinetis* are found in northern Mexico, and each is known by several specimens only, again possibly a result of secretive life history traits or limited occurrence in space and time.

Methods

In order to ascertain species limits (both morphological and geographic), I examined (or recorded from the literature) 238 specimens of *Blaesia* and *Halffterinetis* species from the research collections listed below. The collections and their acronyms (as given in Arnett et al. 1993) are as follows. The curators and/or collection managers who provided the material are also indicated.

AMIC	Antonio Martínez Collection, then at Salta, Argentina (currently at the Canadian Museum of Nature, Ottawa, Canada).
AMNH	American Museum of Natural History, New York, NY, USA (Lee Herman).
BCRC	Brett C. Ratcliffe Collection, Lincoln, NE, USA.
BMNH	The Natural History Museum, London, England (Malcolm Kerley, Michael Bacchus).
CASC	California Academy of Sciences, San Francisco, CA, USA (Norman Penny, David Kavanaugh).
CMNC	Canadian Museum of Nature, Ottawa, Canada (François Génier).
FMNH	Field Museum of Natural History, Chicago, IL, USA (Al Newton).
GMNC	Guillermo Nogueira Collection, Zapopan, Jalisco, Mexico.
IEXA	Instituto de Ecología, Xalapa, Mexico (Miguel Morón).
ISNB	Institut Royal de Sciences Naturelles de Belgique, Brussels, Belgium (Alain Drumont).
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (Axel Bachmann).
MCZC	Museum of Comparative Zoology, Cambridge, MA, USA (Phil Perkins).
MGFT	Georg Frey Collection, then at the Zoologische Staatssammlung, Munich, Germany (Gerhard Scherer, Max Kühbandner), now at the Naturhistorisches Museum, Basel, Switzerland (Daniel Burkhardt).
MLPA	Museo de La Plata, La Plata, Argentina (Analia Lanteri).
MNHN	Museum National d'Histoire Naturelle, Paris, France (Jean Menier, Roger-Paul Dechambre).
MXAL	Miguel Morón Collection, Xalapa, Veracruz, Mexico.
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Cleide Costa).

- QBUM** Museu Nacional, Rio de Janeiro, Brazil (Miguel Monné).
RMNH Nationaal Natuurhistorische Museum Leiden, the Netherlands (Jan van Tol).
USNM U. S. National Museum, currently at University of Nebraska State Museum, Lincoln, NE, USA.
WBWC William B. Warner Collection, Chandler, AZ, USA.
ZMHU Museum für Naturkunde der Humboldt Universität, Berlin, Germany (Manfred Uhlig, Joachim Schulze, Hella Wendt).

The generic and species descriptions were based on the following characteristics: length (from apex of clypeus to apex of elytra), color and markings, interocular width (number of transverse eye diameters across the frons), form and sculpturing of the frons, clypeus, antennae, pronotum, mesepimeron, elytra, pygidium, legs, venter (mesometasternal process, abdominal sternites), form of the apex of the metatibia, and parameres.

Geographical localities are arranged alphabetically by province, state, or department within each country and then alphabetically by locality within each province. Temporal data is provided, but these data should be used with caution because many specimens in old collections lack these data.

I use the phylogenetic species concept as outlined by Wheeler and Platnick (2000). This concept defines species as the smallest aggregation of (sexual) populations diagnosable by a unique combination of character states.

Taxonomic history

The cetoniine tribe Gymnetini is currently comprised of 26 genera in the New World (Krikken 1984; Krajcik 1998; Morón and Nogueira 2007) distributed from the eastern and central United States south to Argentina (Blackwelder 1944). Keys to the tribes of Cetoniinae and subtribes of Gymnetini can be found in Krikken (1984). Krikken (1984) recognized the subtribe *Blaesiina* to accommodate the genus *Blaesia* based upon the presence of approximate mesocoxae, the absence of a distinct mesometasternal process, the greatly enlarged metafemora, and the modified apex of the metatibia in the males of *Blaesia* species. *Blaesia atra* Burmeister and *Blaesia subrugosa* Moser occur in Bolivia, Paraguay, Uruguay, Argentina, and southern Brazil.

Morón and Nogueira (2007) established the genus *Halfffierinetis* for their new species, *H. gonzaloi* Morón and Nogueira and *H. violetae* Morón and Nogueira, from arid regions of northern Mexico. The morphological similarities between *Blaesia* and *Halfffierinetis* are obvious, thus leading Morón and Nogueira to place *Halfffierinetis* in the *Blaesiina*.

Specimens of *Blaesiina* are not commonly found in collections, thus suggesting either their relative rarity in nature or our lack of knowledge regarding their habitat. Krikken (1984) suggested that *Blaesia* species are termitophilous, while Monné (1969) described the larvae of *B. atra* from the nest of *Acromyrmex* species (Formicidae) in

Uruguay. Morón and Nogueira (2007) suggested myrmecophily for both genera. If this is so, sampling ant and termite nests might yield additional specimens and reveal more of their life history, which is, at present, completely unknown. In spite of the broad array of collections consulted, I have seen only about two dozen examples of *B. subrugosa*, and specimens of *Halfffierinetis* are known from only 11 specimens.

Key to the genera of adult *Blaesiina*

1. Clypeal apex broadly rounded, surface slightly longitudinally tumid at middle. Metafemora enlarged in both sexes (Fig. 1). Male with apex of metatibia elongated into stout, acute spine and with 1 articulated spur (Fig. 1). Southern South America *Blaesia*
- 1'. Clypeal apex broadly truncate and weakly to distinctly emarginate at middle, surface concave. Metafemora not enlarged. Male with apex of metatibia with 2 angulate lobes and with 2 articulated spurs. Northern Mexico *Halfffierinetis*

Blaesia Burmeister, 1842

Blaesia Burmeister 1842: 615. Type species: *Blaesia atra* Burmeister, 1842, by monotypy.

Description. Scarabaeidae, Cetoniinae, Gymnetini. *Form:* Rhomboidal, robust, sides slightly tapering toward apex of elytra, dorsum nearly flat. Color on dorsum black to dark reddish brown, venter shiny black. Surface of head, pronotum, elytra, and pygidium with or without distinct setae. *Head:* Shape subrectangular, longer than wide. Clypeus with apex broadly rounded, surface slightly longitudinally tumid at middle. Antenna 10-segmented, club subequal in length to segments 1–7. Eyes small. *Pronotum:* Shape subtrapezoidal, widest near base, gradually convergent to anterior angles, basomedian lobe strongly produced, lobe covering all but tip of scutellum. *Elytra:* Widest at base, post-humeral emargination distinct. *Pygidium:* Surface punctate and/or with transverse strigulae. *Legs:* Protibia tridentate in both sexes, teeth subequally spaced. Metatrochanter with long, acute spur, spur with apex projecting almost perpendicular to posterior margin of metafemur in both sexes (Fig. 2). Metafemur greatly enlarged, broad. Metatibia in male with apex extended into long, thick, acute spine and with 1 long, articulated spur; metatibia at apex in female with short, subtriangular extension and with 2 long, articulated apical spurs. *Venter:* Mesometasternal process short, flat, apex rounded, nearly obsolete.

Diagnosis. Species of *Blaesia* can be easily recognized by the presence of the enlarged metafemora in both sexes. In addition, males have the apex of the metatibia elongated into stout, acute spine and with only one articulated spur, both of which are unique characters in the Gymnetini.

Distribution. Species of *Blaesia* are known from Bolivia, Paraguay, Uruguay, Argentina, and southern Brazil.

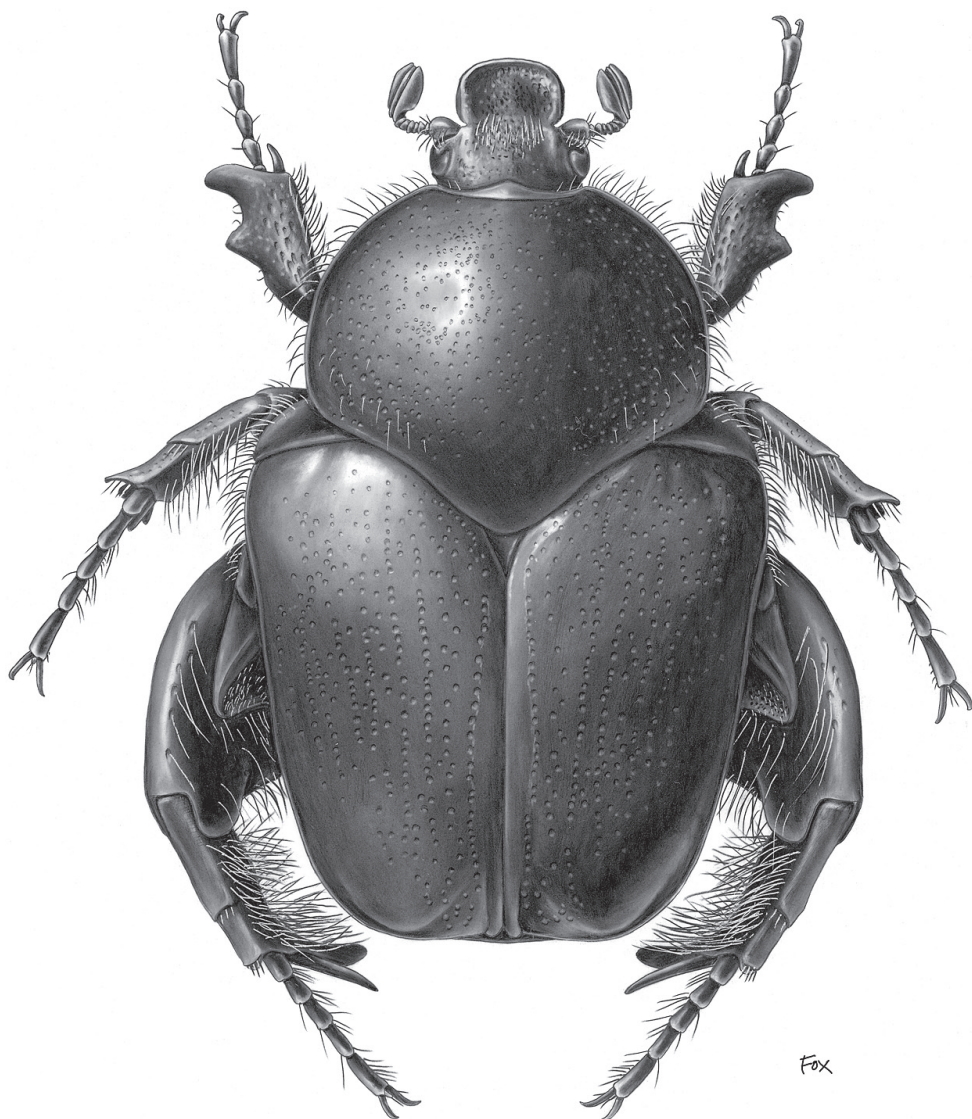


Figure 1. *Blaesia atra*, habitus drawing of male.

Key to the species of adult *Blaesia*

1. Pronotum with small punctures, punctures becoming large on lateral margins. Elytra with several large punctures in incomplete rows. Setae on venter rust colored to tawny ***atra* Burmeister**
- 1'. Pronotum completely punctate, with large, deep, dense punctures. Elytra densely punctate to rugopunctate, punctures moderate to large. Setae on venter black ***subrugosa* Moser**

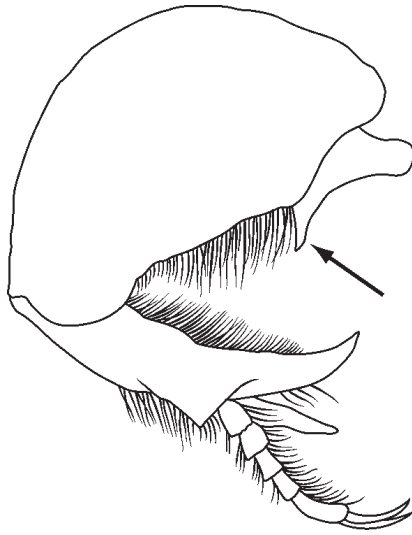


Figure 2. *Blaesia atra*, right posterior leg, ventral view.

***Blaesia atra* Burmeister, 1842**

Figs 1–3, 5

Blaesia atra Burmeister 1842: 615. Type not found; not present in Burmeister collection at Martin-Luther-Universität Halle-Wittenberg, Halle, Germany (Karla Schneider, personal communication, September 2009) or at the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (personal observation, 2003).

Description. Length 13.9–20.5 mm; width 8.5–12.4 mm. Color usually completely black, shining occasionally pronotum and elytra dark reddish brown and only weakly shining. *Head:* Surface densely punctate; punctures moderate to large, deep, nearly confluent to rugose on clypeus and between eyes. Frons and clypeus with distinct, median, longitudinal ridge. Frons with sparse, rust colored to tawny setae. Clypeus with apex evenly, broadly rounded, thickened, slightly reflexed, subapex slightly wider than base, surface slightly longitudinally tumid at middle. Interocular width equals 5.5–6.0 transverse eye diameters. Antenna black, with 10 segments, club slightly shorter than antennomeres 1–7. *Pronotum:* Most of surface moderately densely punctate; punctures small in males, slightly larger in females, round to slightly transverse, becoming large, setigerous and dense on sides; setae long, rust colored to tawny; base at center not modified. Apex at center with margin thickened. Sides margined. Mesepimeron with dense, large, setigerous punctures anteriorly, setae long, rust colored to tawny. *Elytra:* Surface finely shagreened, usually with; 3–4 distinguishable punctate, incomplete striae; punctures round to \cap -shaped, moderate to large, some setigerous in unworn specimens; setae sparse, long, rust colored to tawny. Intervals with sparse, irregularly spaced punctures similar to those of striae. Bead present on lateral margin. Apical umbone

pronounced. Apices rounded into right-angles. *Pygidium*: Surface varies from moderately densely punctate with small to slightly transverse punctures to densely, transversely strigulate. Base usually with sparse, long, rust colored to tawny setae. In lateral view surface weakly convex in male, nearly flat in female. *Venter*: Setae rust colored to tawny. Mesometasternal process short, flat, apex rounded, nearly obsolete. Abdominal sternites with transverse, irregular row of large punctures; punctures mostly large with rust colored to tawny setae. *Legs*: Femora and tibiae with dense fringe of mostly short, rust colored (most common) to tawny (less common) setae on both median and lateral surfaces. Protibia tridentate, apical tooth longer, narrower, slightly curving. Metafemur greatly enlarged, broad (Fig. 2). Metatibia in male with apex extended into long, thick, acute spine and with 1 long, articulated spur with acute apex; metatibia at apex in female with short, subtriangular extension and with 2 long, articulated apical spurs with apices rounded. Metatrochanter with long, acute spur, spur with apex projecting almost perpendicular to posterior margin of metafemur in both sexes (Fig. 2). *Parameres*: Fig. 3.

Distribution (Fig. 5). 200 specimens examined from AMIC, BCRC, BMNH, CASC, CMNC, FMNH, ISNB, MACN, MGFT, MLPA, MNHN, MZCZ, MZSP, QBUM, RMNH, USNM, WBWC, ZMHU.

ARGENTINA (30). BUENOS AIRES (14): Buenos Aires, La Plata; CORRIENTES (2): Santo Tomé; MISIONES (1): Loreto; SAITA (1): No data; SANTA FÉ (4): Rosario; NO DATA (9).

BRAZIL (28). PARANÁ (1): No data; RIO GRANDE DO SUL (21): Porto Alegre; SÃO PAULO (5): Campinas, Itatiba, Pres. Epitácio; NO DATA (1).

PARAGUAY (7). GUAÍRA (2) Sapucay, Villarrica; NO DATA (5).

URUGUAY (107). CANELONES (3): La Tuna; DISTRITO FEDERAL (80): Montivideo; TACUAREMBÓ (2): Pozo Honso; TRIENTA Y TRES (17): Santa Clara de Olimar; NO DATA (5).

NO DATA (28).

Temporal Distribution. January (7), February (3), June (1), September (2), October (3), November (4), December (6 adults, 11 larvae). Too few specimens have label data with the month of collection to indicate a reliable temporal distribution.

Biology. Monné (1969) described the larvae of *B. atra* from the nest of *Acromyrmex* species (Formicidae) in Uruguay, thus demonstrating myrmecophily for this species. Krikken (1984) suggested, without any supporting commentary, the possibility that this species is termitophilous.

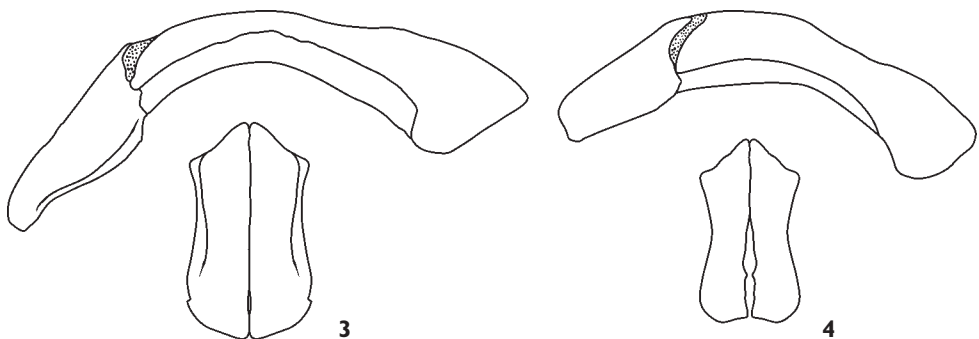
Blaesia subrugosa Moser, 1905

Figs 4–5

Blaesia subrugosa Moser, 1905: 211. Lectotype female (Fig. 9) at ZMHU, labeled: S. Cruz de la Sierra, Bolivia / *Blaesia subrugosa* Moser, Type / *Blaesia subrugosa* Moser, Type, G. Ruter det. 1966 / Type / with my red lectoallotype label. Paralecto-

totype female at ZMHU with same locality label as lectotype and with my yellow paralectotype label (Ratcliffe 2004).

Description. Length 12.0–19.5 mm; width 7.5–11.8 mm. Color completely black, shining. *Head:* Surface densely punctate; punctures moderate to large, deep, nearly confluent to rugose on clypeus and between eyes. Frons and clypeus with weak, median, longitudinal ridge. Frons with sparse, dark brown setae. Clypeus with apex evenly, broadly rounded, thickened, slightly reflexed, subapex slightly wider than base, surface slightly longitudinally tumid at middle. Interocular width equals 5.0 transverse eye diameters. Antenna black, with 10 segments, club slightly shorter than antennomeres 1–7. *Pronotum:* Surface densely punctate; punctures large, deep, round to slightly transverse, becoming confluent or rugose on sides; base at center narrowly depressed, impunctate or with numerous small, shallow punctures. Apex at center with small, broad, flattened, opaque tumosity. Sides margined. Mesepimeron with a few large, setigerous punctures anteriorly, setae long, black. *Elytra:* Surface densely punctate to rugopunctate, punctures moderate (on sides) to large (on disc), round to \cap -shaped. Bead present on lateral margin. Apical umbone pronounced. Apices nearly right-angled. *Pygidium:* Surface with short, transverse strigae (on disc) (often reduced) to transversely strigose (on base and sides). Base usually with sparse, short, black setae. In lateral view surface weakly convex. *Venter:* Setae black. Mesometasternal process short, flat, apex rounded, nearly obsolete. Abdominal sternites with transverse, irregular row of large punctures; punctures mostly large with short, black setae. *Legs:* Femora and tibiae with fringe of mostly short, black setae on both median and lateral surfaces. Protibia tridentate, apical tooth longer, narrower, curving slightly. Metafemur greatly enlarged, broad. Metatibia in male with apex extended into long, thick, acute spine and with 1 long, articulated spur with acute apex; metatibia in female with short, subtriangular extension and with 2 long, articulated apical spurs with apices rounded. Metatrochanter with long, acute spur, spur with apex projecting almost perpendicular to posterior margin of metafemur in both sexes. *Parameres:* Fig. 4.



Figures 3–4. Parameres, caudal and lateral views, of **3** *B. atra* and **4** *B. subrugosa*.

Distribution (Fig. 5). 27 specimens examined from AMIC, BMNH, CASC, CMNC, FMNH, ISNB, MACN, MLPA, MNHN.

ARGENTINA (23). BUENOS AIRES (8): Buenos Aires; SALTA (4): Tobatirenda, No data; TUCUMAN (1): Buruyacú; NO DATA (10): Gran Chaco region.

BOLIVIA (4). SANTA CRUZ (2): Santa Cruz de la Sierra; NO DATA (2).

Temporal Distribution. March (5), December (1). Too few specimens have label data with the month of collection to indicate a reliable temporal distribution.

Biology. Nothing is known of the biology of this species. Krikken (1984) suggested the possibility that this species is termitophilous, while Morón & Nogueira (2007) suggested myrmecophily.



Figure 5. Distribution map of *Blaesia* and *Halffterinetis* species. Open symbol is state record only.

***Halffterinetis* Morón & Nogueira, 2007**

Halffterinetis Morón & Nogueira 2007: 52. Type species: *Halffterinetis gonzaloi* Morón & Nogueira, by original designation.

Description. Scarabaeidae, Cetoniinae, Gymnetini. *Form:* Rhomboidal, robust, sides slightly tapering toward apex of elytra, dorsum nearly flat. Color shiny black, males of *H. gonzaloi* with chalky white marks on lateral margin of pronotum (Fig. 6) and sides of 4th sternite; males of *H. violetae* and females lacking cretaceous marks (Fig. 7). Surface of frons densely punctate to rugopunctate, usually with short setae. *Head:* Shape subrectangular, longer than wide. Clypeus with apex broadly truncate, distinctly emarginate at middle, surface distinctly concave (Fig. 8). Antenna 10-segmented, club in males longer than antennomeres 1–7 (Fig. 8), club in females subequal in length to antennomeres 2–7. Eyes small. *Pronotum:* Shape subtrapezoidal, widest near base, gradually convergent to anterior angles, basomedian lobe with margin arcuate, weakly to moderately produced, most of scutellum visible. *Elytra:* Widest at base, posthumeral emargination distinct. *Pygidium:* Surface varies from moderately densely punctate to having strong, concentric, vermiform strigulae (Fig. 9). *Legs:* Protibia tridentate in both sexes, teeth subequally spaced. Metatrochanter triangular, elongated, flush with posterior margin of metafemur in both sexes, not projecting as a spur. Metafemur slightly enlarged. Metatibia at apex with 2 broad lobes and with 2 long, articulated, apical spurs. *Venter:* Mesometasternal process short, nearly obsolete, flat, apex rounded.

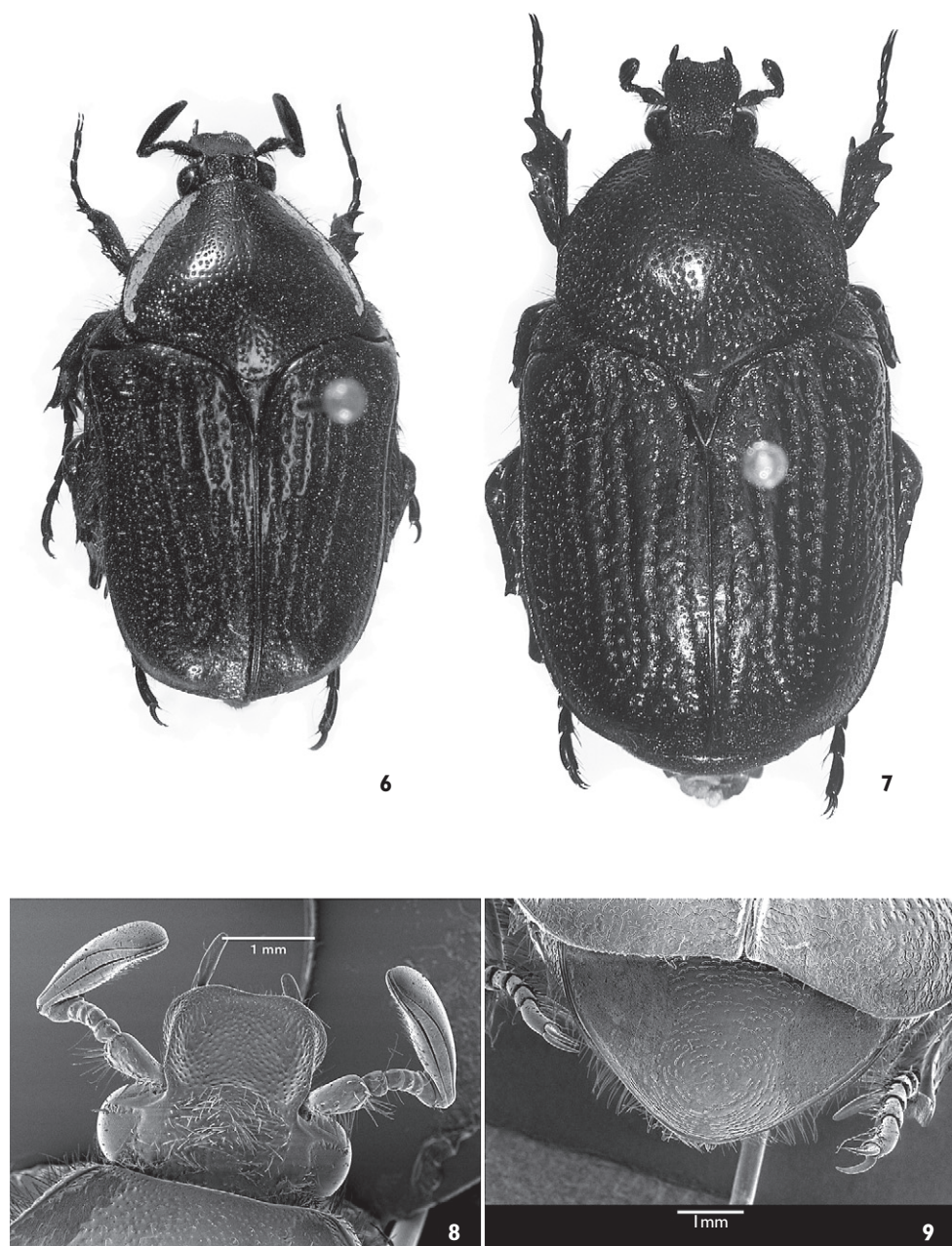
Diagnosis. The genus *Halffterinetis* is unique among the American Gymnetini, because the basomedian lobe of the pronotum is only arcuate to moderately produced (not covering most of the scutellum) instead of strongly produced posteriorly (covering all but the extreme tip of the scutellum) as in the other genera of the tribe. Morón and Nogueira (2007) proposed *Halffterinetis* as a member of the Blaesiina pending further studies, and I am in agreement with their placement. I have a single female (AMNH) collected in August from Guadalupe in the state of Coahuila (a NEW STATE RECORD for the genus) that I am unable to assign to the species level; characteristics of the specimen do not coincide with the description of *H. gonzaloi*, and the female of *H. violetae* remains unknown.

Distribution. *Halffterinetis* species are known from northern Mexico only.

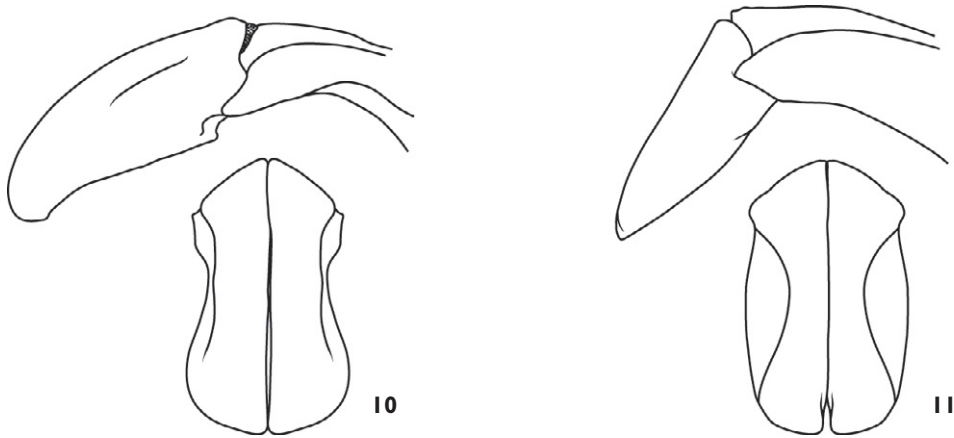
Key to the species of adult Male *Halffterinetis*

(females of *H. violetae* are unknown)

1. Frontoclypeal region with transverse carina. Clypeal apex weakly emarginate. Cretaceous marking present on lateral margins of pronotum and pygidium. Parameres as in Fig. 10..... ***gonzaloi* Morón & Nogueira**
- 1'. Frontoclypeal region without transverse carina. Clypeal apex strongly emarginate. Cretaceous markings absent. Parameres as in Fig. 11 ***violetae* Morón & Nogueira**



Figures 6–9. *Halffterinetis gonzaloi*: **6** male, dorsal view **7** female, dorsal view **8** head of male, dorsal view **9** pygidium of male. Images courtesy of M. Morón, Instituto de Ecología, Xalapa, Mexico (Figs 6–7 taken by R. Woodruff and Figs 8–9 taken by P. Skelley, both Florida State Collection of Arthropods, Gainesville, FL).



Figures 10–11. Parameres, caudal and lateral views, of **10** *H. gonzaloi* and **11** *H. violeetae*.

***Halffterinetis gonzaloi* Morón & Nogueira, 2007**

Figs 5–10

Halffterinetis gonzaloi Morón & Nogueira 2007: 52.

Holotype male and allotype female at MXAL. Holotype labeled MEXICO: Tamaulipas, Palmillas, 1130 m, 23-VII-2005, G. Nogueira; allotype with same data but 19-VII-2005 and 1030 m. Five paratypes with same data deposited at IEXA (2), CMNC (1), and GNGC (2).

Description. Length 14.9–18.5 mm; width 8.4–10.1 mm. Color black, shining; male with lateral margins of pronotum (Fig. 6), sides of 4th sternite, and usually a spot on pygidium cretaceous; female lacking cretaceous marks. *Head:* Surface densely punctate to rugopunctate; punctures small to large, deep. Frontoclypeal region with weak, transverse ridge in male, ridge absent in female. Frons with dense, moderately long, black setae in male (Fig. 8), setae absent in female. Clypeus with apex broadly truncate, weakly emarginate at middle in male, more so in female, thickened, slightly reflexed, subapex slightly wider than base, surface concave in male, slightly less so in female. Interocular width equals 5.0 transverse eye diameters. Antenna black, with 10 segments, club in male slightly longer than antennomeres 1–7 (Fig. 8), club in female subequal in length to antennomeres 2–7. *Pronotum:* Surface densely punctate; punctures moderate to large, deep, round to slightly transverse, punctures becoming larger to rugopunctate on sides (more pronounced in female), and with short, black setae. Sides margined. Mesepimeron completely punctate to rugose, with sparse, black setae. *Elytra:* Surface superficially and irregularly striate, rugopunctate, punctures moderate to large, round to mostly \cap -shaped. Bead present on lateral margin. Apical umbone pronounced. Apices nearly right-angled in male, rounded in female. *Pygidium:* Surface in male with oval punctures or with short, transverse strigae (on disc) (often reduced) to transversely strigose (on base and sides) (Fig. 9); surface in

female densely, concentrically strigulate. Base usually with sparse, short, black setae. In lateral view surface in male weakly convex, female with surface usually strongly convex. *Venter*: Setae black. Mesometasternal process short, nearly obsolete, flat, apex rounded. Abdominal sternites with transverse, irregular field of large punctures; punctures sparser in central third, mostly large, shallow, with short, black setae. *Legs*: Meso- and metaemora and meso- and metatibiae with sparse fringe of mostly long, black setae on median surface. Protibia tridentate, apical tooth longer, slightly narrower. Metafemur normal, not enlarged. Metatibia at apex with 2 broad lobes and with 2 long, articulated apical spurs with apices rounded. Metatrochanter triangular, elongate, flush with posterior margin of metafemur, acuminate apex not projecting perpendicularly. *Parameres*: Fig. 10.

Distribution (Fig. 5). 8 specimens recorded (7 from Morón & Nogueira 2007). The San Luis Potosí specimen is a NEW STATE RECORD.

MEXICO (8): SAN LUIS POTOSÍ (1): km 200 carretera SLP a Ciudad del Maíz TAMAULIPAS (7): Palmillas.

Temporal Distribution. July (8).

Biology. Morón & Nogueira (2007) reported that the seven specimens were crepuscular, that some were collected in flight, while others were found on dead trunks of mesquite trees (*Prosopis juliflora* [Swartz]) (Mimosaceae), all near the nests of *Atta* ants at elevations ranging from 1030–1130 meters. A search of the *Atta* nest found no larvae or pupae, but these authors surmised there might be some association with the ants. The habitat was semiarid with an annual precipitation of 500–600 mm and an average annual temperature of 20–22°C. Dominant plants consisted of *Prosopis* species (Mimosaceae), *Acacia* species (Leguminosae), *Hechtia* species (Bromeliaceae), *Yucca* species (Lilaceae), *Opuntia* species (Cactaceae), *Agave* species (Amarilidaceae), and *Helietta* species (Rutaceae). Adults were not attracted to banana traps.

Halffterinetis violetae Morón & Nogueira, 2007

Figs 5, 11

Halffterinetis violetae Morón & Nogueira 2007: 56.

Holotype male at CMNC and one paratype male at MXAL. Types labeled MEXICO: Durango, 40 mi SW Torreón, Hwy 40, 18-VI-1961, D. H. Janzen.

Description. Male (female unknown). Length 14.6–15.3 mm; width 7.9–8.4 mm. Color black, shining, lacking cretaceous marks. *Head*: Surface densely punctate to rugopunctate; punctures small to large, deep. Frontoclypeal region lacking transverse ridge. Frons with short, moderately dense, black setae. Clypeus with apex broadly truncate, strongly emarginate at middle, slightly reflexed, subapex distinctly wider than base, surface weakly concave. Interocular width equals 3.9 transverse eye diameters. Antenna black, with 10 segments, club almost twice as long as antennomeres 2–7. *Pronotum*: Surface densely punctate; punctures moder-

ate to large, deep, round to slightly transverse, punctures becoming larger to rugopunctate on sides, and with short, tawny setae. Sides margined, bead reduced in anterior fifth. Mesepimeron completely punctate, with sparse, black setae. *Elytra*: Surface superficially and irregularly striate, rugopunctate, punctures moderate to large, round to mostly \cap -shaped, setigerous; setae short, sparse, black. Bead present on lateral margin. Apical umbone pronounced. Apices nearly right-angled. *Pygidium*: Surface with oval punctures or with short, transverse strigae (often reduced) to transversely strigose. Base usually with sparse, short, black setae. In lateral view surface weakly convex. *Venter*: Setae black. Mesometasternal process short, nearly obsolete, flat, apex rounded. Abdominal sternites with transverse, irregular field of large punctures; punctures sparser in central third, mostly large, shallow, with short, black setae. *Legs*: Femora and tibiae with sparse fringe of mostly short, black setae on median surface. Protibia tridentate, apical tooth longer, slightly narrower. Metafemur normal, not enlarged. Metatibia at apex with 2 broad lobes and with 2 long, articulated apical spurs with apices rounded. Metatrochanter triangular, elongate, flush with posterior margin of metafemur, acuminate apex not projecting perpendicularly. *Parameres*: Fig. 11.

Distribution (Fig. 5). Two specimens recorded from Morón and Nogueira (2007).

MEXICO (2): DURANGO (2): Torreón (40 mi SW on Hwy 40).

Temporal Distribution. June (2).

Biology. Morón & Nogueira (2007) indicated the habitat where this species was collected is semiarid with an average annual temperature of 12–18°C and located at 1287–1300 meters above sea level. Dominant plants consisted of *Parthenium* species (Asteraceae), *Fouquieria* species (Fouquieriaceae), *Larrea* species (Zygophiliaceae), *Hechtia* species (Bromeliaceae), *Opuntia* species (Cactaceae), *Agave* species (Amarillidaceae), and *Euphorbia* species (Euphorbiaceae).

Biogeography

The distribution of blaesiine species (Fig. 5) nearly mirrors that of *Hologymnetis* species, another genus within the Gymnetini. The biogeography of *Hologymnetis* species was reviewed by Ratcliffe and Deloya (1992) and is reviewed here to understand the similar distribution of the Blaesiina. Lacking fossil evidence for the Gymnetini, it is necessary to rely upon data from plate tectonics, present and paleodistribution of other plants and animals, and ecological factors to formulate a hypothesis to best explain the current distribution of these insects.

As with most other genera of New World Gymnetini, the ancestral Blaesiina were present in South America prior to the establishment of the Panamanian land bridge in the Miocene. Given the current distribution and ecological requirements of Blaesiina species, it is assumed that they evolved in drier habitats. Drier habitats have been present in South America since middle Tertiary time (Webb 1978). The Quaternary (*i.e.*, the last two million years) is characterized by great environmental instability (Bigarella and

Andrade-Lima 1982; Whitmore & Prance 1987). These climatic changes caused, in relatively short geologic time, successive expansions and contractions of either forest or open, drier vegetation. Forest and nonforest biomes broke up into isolated blocks or expanded and coalesced depending on varying humid or arid climatic conditions (Haffer 1969, 1982; Vuilleumier 1971; Müller 1973; Prance 1973, 1982; Brown et al. 1974; Brown 1977; Tricart 1974; Simpson and Haffer 1978). With the reduction of forest vegetation during drier periods, there was a corresponding increase in nonforest formations that penetrated into the Amazon region from both north and south. Such formations consisted of large blocks or corridors connecting the open vegetation associations of the Central Brazilian Plateau with those of Venezuela and the Guianas (Eden 1974; Sarmiento 1975; Bigarella and Andrade-Lima 1982; Marshall 1985).

Present day *Blaesia* species inhabit the mesic to semiarid, relatively open vegetation habitats of Bolivia, Paraguay, Uruguay, Argentina, and southern Brazil. The broad, continuous band of present-day Amazonian rainforest is a barrier preventing further dispersal northward. Ancestral *Blaesiina* would have been afforded suitable avenues for traversing previously inhospitable lowland forested regions in Amazonia by the extensions of savanna-like habitat (Fig. 12). With the establishment or re-establishment of rain forest in the Amazon basin, populations of ancestral *Blaesiina* became divided and isolated both to the north and south of the Amazon region. The northern lineage (today's *Halffterinetis* species) ultimately dispersed to nuclear northern Mexico, and the southern lineage (today's *Blaesia* species) became isolated in the woodland savannas south of the Amazon basin. As habitats changed through time, ancestral *Blaesiina* disappeared entirely from between northern Mexico and southern South America.

Pre-Miocene dispersal of the biota between North and South America was probably rare, and a small amount of biotic interchange agrees with the geologic evidence suggesting a relatively wide separation of the Americas in Cretaceous through Oligocene times (Raven and Axelrod 1974; Smith and Briden 1977; Gose et al. 1980). Consideration of climate is important both before and after establishment of a land connection (Stehli and Webb 1985b). For example, the existence of clear evidence of mountain glaciation along the continental divide in Guatemala suggests that simply extending present-day conditions back in time will not suffice to allow a real understanding of the physical nature of the link between the two Americas or of its effect on biotic interchange. After Mesoamerica coalesced during the Pliocene 3.0 MYBP (Marshall 1988) to 5.7 MYBP (Lloyd 1963; Kaneps 1979), an extensive faunal exchange began (Webb 1978; Stehli & Webb 1985a). Formation of the Panamanian isthmus dispersal route permitted separate invasions of plants and animals at widely separated periods when climates and topographic features were different than today.

After the formation of the isthmus of Panama, members of the Gymnetini began their northward dispersal from South America into Central America, Mexico, and the United States. Webb (1978, 1985) provided an excellent analysis of the interamerican biotic exchange, pertinent parts of which are described here. The interval from 2.5–1.5 MYBP shows an extensive movement of savanna-adapted mammal faunas from south temperate to north temperate latitudes and vice versa. All of the animals that



Figure 12. Maps showing approximate distribution of savannas (gray areas) in South America at **a** about 4.0 MYBP, **b** during glacial maxima, and **c** today. Arrow in **b** shows most likely dispersal route of taxa living in savanna habitats (after Marshall 1985).

are known to have dispersed between the Americas in the late Tertiary were tolerant of, or specifically adapted to, savanna woodland habitats. The savanna elements were not incidental parts of the interchange but represent the vast majority of the taxa involved. Notable among them were horses, llamas, armadillos, and ground sloths. The extent of savanna adaptations among the land mammals of the interchange indicates the presence of a uniformly nonforested corridor or a moving mosaic of such habitats between South America and North America. The more arid conditions that must be postulated for the isthmian region during its early history probably supported seasonal forests grading into thorn scrub savannas. Similar habitats exist today in northern Venezuela and eastern Colombia and on the Pacific slopes of Central America from western Panama northward. Less mesic conditions in the isthmian corridor were a result of a combination of factors having to do with climatic fluctuations associated with northern hemisphere glaciations, lowering of sea levels (with a concomitant increase in land area), regional uplift with large-scale volcanic extrusion, and creation of rain shadow regions.

The glacial maxima at and following the emergence of the Panamanian land bridge, combined with the presence of a north-south corridor over the bridge, occurred only twice in the late Tertiary (Shackelton and Opdyke 1977; Cronin 1981). These times (2.5 and 1.8 MYBP) represent “optimal ecological windows” that permitted dispersal of taxa living in savanna habitats between the Americas (Marshall 1985). The earliest known South American mammals to disperse to North America across the Panamanian land bridge occur in rocks dated at 2.8–2.6 MYBP. This reciprocal event favoring savanna-adapted forms could not have occurred earlier due to absence of a suitable corridor, habitat, and climate. Subsequent opportunities did not exist until the next glacial maxima at about 2.0–1.9 MYBP (Marshall 1985). “Thus, two synchro-

nous and reciprocal dispersal events of late Tertiary age are recognized. The first event (2.8–2.6 Ma) included dispersal of *Erethizon* Cuvier, *Nechoerus* Hay, *Glyptotherium* Osborn, *Glossotherium* Owen, *Othrotheriops* Hoffstetter, *Kraglievichia* Casatellanos, and *Dasyops* L. (and the ground bird *Titanis* Brodkorb) to North America, and *Conepatus* Gray, *Hippidion* Roth, and *Platygonus* LeConte to South America. The second event (2.0–1.9 Ma) included dispersal of *Hydrochoerus* Brisson, *Eremotherium* Spillmann, and *Holmesina* Simpson to North America, and *Arctodus* Leidy, *Galictis* Bell, *Felis* L., *Smilodon* Lund, *Tapirus* Brünnich, *Hemiauchenia* Gervais and Ameghino, *Onohippidium* Moreno, and *Cuvieronius* Osborn (and possibly *Stipanicia* Reig, *Dusicyon* Smith, and *Protocyon* Giebel) to South America. Only one dispersal event of early Pleistocene age is evident, and this occurred at about 1.4 Ma. It corresponds to the earliest of the Pleistocene glacial maxima recognized by Cronin (1981) and follows the one at 2.0–1.9 Ma. During this event, *Canis* L., *Lutra* Brisson, *Chrysocyon* Hamilton-Smith, *Cerdocyon* Hamilton-Smith, *Leo* (= *Panthera* Oken), and *Stegomastodon* Pohlig dispersed to South America, and *Didelphis* L. and *Palaeolama* Gervais dispersed to North America” (Marshall 1985). The last glacial maximum permitting dispersal of savanna biotas over the land bridge occurred 12,000–1,000 years B.P. (Bradbury 1982; Markgraf and Bradbury 1982). A savanna corridor formed along the eastern side of the Andes connecting the now disjunct habitats in South America (Fig. 12).

The major obstacles to such dispersal events were distance and potential competitive exclusion. Given that cetoniines are capable of such powerful flight, distance may not have been such a deterrent to long distance dispersal. The Japanese beetle (*Popillia japonica* Newman) (Scarabaeidae: Rutelinae), for example, has spread from the east coast of North America (where it was introduced) to the central states (1,900 km away) in only 70 years; that averages 27 km/year. *Aphodius fimetarius* (L.) (Scarabaeidae: Aphodiinae), introduced into North America from Europe probably in colonial times, is now found over much of the continent. *Digitonthophagus gazella* (Fabr.) has dispersed from 43 to 808 (!) km/year in Mexico and the U.S. (Barbero and López-Guerrero 1992). The tussock moth, monarch butterfly, European corn borer, and honeybee all represent contemporary examples of long distance dispersal by insects in short periods of time. The Africanized honeybee, *Apis mellifera scutellata* Lepeletier, has dispersed 300–500 km per year from southern Brazil to northern Mexico in only 30 years (Camazine & Morse 1988). The rapid and historically near-instantaneous colonization of the Australian continent by the European hare, *Lepus europaeus* Pallas, highlights the phenomenal dispersal ability of a small mammal (Marshall 1985). The opossum, *Didelphis marsupialis* L., had an average dispersal rate of 50 km/year during the 26 years following its introduction into California (Tyndale-Biscoe 1973). At such a rate this species could extend its range 25,000 km in only 500 years (Savage and Russell 1983). Martin (1973) noted that a conservative dispersal rate of 16 km/year would have permitted prehistoric humans to spread from Canada to Tierra del Fuego in less than 1,000 years. The dispersal of insects between the mid-continental regions of North and South America may have occurred in only a few thousand years with the availability of suitable habitat. The vertebrate fossil evidence clearly indicates

that dispersal of savanna-adapted animals occurred twice in the late Tertiary. South American ancestral *Blaesiina*, adapted to dry habitats, was part of that dispersal. Webb (1978) observed that it may be difficult for some biologists to accept so short a time scale for such evolutionary change, but the paleontological record of the interamerican interchange demonstrates that two or three million years is sufficient time to produce fundamental evolutionary reorganization of a major biota.

The late Pleistocene shift to more humid conditions in lower Central America produced a major set of savanna disjunctions spanning the isthmian gap (Webb 1978). The disjunct distribution across the American tropics shared by many present-day organisms provides additional evidence of a previous woodland savanna corridor. Within the temperate to subtropical *Areodina* (Scarabaeidae: Rutelinae), six genera are found ranging from the United States to Guatemala, and three genera are found in South America (Jameson 1990). None of these genera occur in the remainder of Central America, which, for the most part, has been historically covered by tropical rainforest. This Central American gap might seem like a paradox until, noticing its occurrence in other groups, we recognize a pattern. Many birds adapted to savanna or thorn scrub show a wide interamerican disjunction. These include the Green Jay, Military Macaw, Melodious Blackbird, Homed Lark, Vermillion Flycatcher, small woodpeckers, and the Grasshopper Sparrow (Griscom 1950; Mengel 1970). Cricetid rodents such as *Reithrodontomys* Giglioli skip from semiarid habitats in Nicaragua to similar habitats in the Andes, and *Crotalus* L. vipers (preferring scrub habitats) now have a large gap across the rainforest of the isthmus (Webb 1985). The distributional gap across the isthmian region is well known for many plants as well as many bees that specialize on these plants (Raven 1963; Solbrig 1972; Rzedowski 1973; Simpson and Neff 1985). Webb (1985) observed that one of the most convincing indications of former continuity is a string of relict populations of *Larrea* Cav. in Peru and Bolivia partly connecting its main south temperate and north temperate ranges. This idea is strengthened by the fact that one of the principal foods of the extinct ground sloth (*Nothrotheriops* Hoffstetter species), as indicated by its dung, was *Larrea*, and that both genera clearly came to North America from temperate South America (Martin et al. 1961; Hunziker et al. 1973). By the late Pleistocene, as now, woodland savanna taxa were excluded from the isthmian region due to the dissolution of savanna habitats and replacement by tropical rainforest. Late Pleistocene pollen samples from Lake Gatun in Panama reveal a forest flora much like that of present lowland Panama (Webb 1978). About 1,700 km of tropical wet forest extending from Costa Rica and Panama through northern Colombia now separates the nearest areas of savanna and thorn forest (Sarmiento 1976). Consequently, ancestral *Blaesiina* were also excluded from this region because they could not survive in tropical wet forests. Northern Central America retained a woodland savanna fauna as evidenced by the present biota and Pleistocene samples from Guatemala, Honduras and El Salvador (Stirton and Gealey 1949; Carr 1950; Duellman 1966; Savage 1966; Woodburne 1969; Howell 1969). Species of *Halffterinetis* are today found in mesic to xeric habitats in north central Mexico.

Based on his analysis of the entomofauna, Halffter (1976) formulated several different dispersal patterns to explain the present distribution of taxa in the Mexican Transition Zone. The distribution of *Halffterinetis* species coincides well with Halffter's "Typical Neotropical Dispersal Pattern". In this pattern, South American elements penetrated into the Mexican Transition Zone after the formation of the Panamanian land bridge and after most of the elevation of the Mexican Plateau. As ancestral *Blaesiina* spread northward, they used as their principal expansion route from Central America the mountains of Oaxaca and the Sierra Madres, which funneled the dispersal of *Blaesiina* to the west and north, respectively, where *Halffterinetis* species occur today.

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