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WHAT CAN SCARABAEOIDEA CONTRIBUTE TO THE KNOWLEDGE OF THE BIOGEOGRAPHY OF GUATEMALA?

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Abstract

Scarabaeoidea is one of the biogeographically best known groups of organisms for Nuclear Central America, especially Guatemala. They have been used to determine areas of endemism for cloud forests of the region and to analyze relationships among these endemic areas. A major north-south division of these areas is described. Lowland scenarios are also given. This information was used for justifying the establishment of biological reserves in the area and is a tool available for prioritization of reserve establishment that could be adapted to other parts of the world as well.

Resumen

Scarabaeoidea es uno de los grupos mejor conocidos biogeográficamente en Centroamérica Nuclear, especialmente Guatemala. Han sido usados para establecer áreas de endemismo en bosques nubosos de la región y para analizar relaciones entre esas áreas. Una división mayor norte-sur de estas áreas endémicas está descrita. Escenarios de tierra de baja elevación también se presentan. Esta información fue usada para justificar el establecimiento de reservas biológicas en el área y como una valiosa herramienta para priorizar el establecimiento de reservas, lo cual podría ser adaptado también a otras partes del mundo.

After the publication of the *Biologia Centrali-Americana* (1881–1915), the principal biogeographical works were primarily on amphibians and reptiles (e.g., Schmidt and Stuart 1941; Stuart 1943, 1950, 1954, 1964; Wake and Lynch 1976; Campbell and Vannini 1989; Johnson 1989). Extensive studies of scarabaeoid distributions in Guatemala began with works by Schuster (e.g., 1985, 1988, 2000, 2005), followed by studies of *Chrysina* Kirby, *Phyllophaga* Harris, and Scarabaeinae by Cano (e.g., Cano and Morón 1998; Kohlmann *et al.* 2003) and Monzón (e.g., Warner and Monzón 1993; Monzón 1995, 2006).

What can Scarabaeoidea contribute to the knowledge of the biogeography of Guatemala? Biogeographically, the scarabaeoid beetles are the best known group of insects in the country; in fact, more well-known than most organisms. Two aspects of biogeography are of summary importance to conservation: biodiversity (e.g., number of species in a given area) and endemism. Reserves are often designed to include the most species possible, or they are designed to include rare, often endemic, species. Because of the infrastructure that we helped to create within Guatemala, biogeographic information concerning scarabaeoid beetles (especially Passalidae) has been used in the prioritization of protected areas in Guatemala (Schuster *et al.* 2000).

Guatemalan topography is characterized by various isolated mountain ranges (Fig. 1). A series of ranges in the middle of the country begin in Huehuetenango

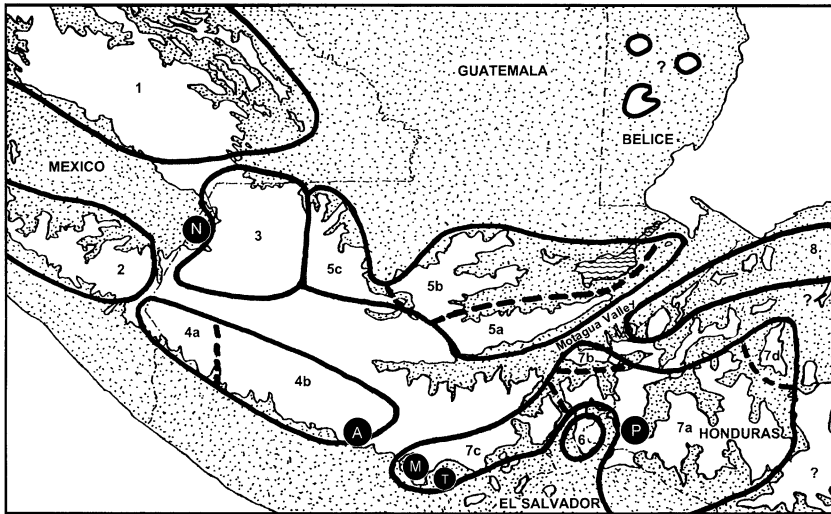


Fig. 1. Map of areas of endemism of the north of Nuclear Central America (after Schuster *et al.* 2000). Numbers indicate areas of endemism: 1=northern Chiapas, 2=southern Chiapas, 3=west Sierra de los Cuchumatanes, 4a=west volcanoes, 4b=east volcanoes, 5a=Sierra de las Minas, 5b=south Sierra de Chamá, 5c=east Sierra de los Cuchumatanes, 6=Trifinio (Cerro Montecristo), 7a=El Portillo region (Honduras), 7b=La Unión, Zacapa, 7c=Tecuamburro region, 7d=Santa Bárbara (Honduras), 8=Sierra del Merendón. La Tigra region (area 9), north of Tegucigalpa, is not included. Black circles indicate volcanoes: A=Agua volcano, M=Miramundo volcano, N=Nentón, P=El Portillo, T=Tecuamburro volcano. White indicates areas above 800 m altitude.

and divide in two, one passing to the north and the other to the south of Lake Izabal. This series of ranges is separated from another series to the south by a dry valley (pine-oak forest to the west and thorn scrub forest to the east, except far eastern Izabal which was, until recently, covered by rainforest) which reaches 1,900 m elevation in Huehuetenango and is near sea level in Izabal. The southern altiplano above 2,000 m from San Marcos, near the Mexican border, extends almost to Guatemala City and continues with isolated areas above 2,000 m east of Guatemala City to the Honduran and El Salvadoran borders. Extending further south of these ranges is the line of coastal volcanoes that run from Chiapas to Panamá. Those in Guatemala are primarily Quaternary age (Weyl 1980). The northern lowlands (50–300 m elevation) of Petén are to the west of the Maya Mountains of Belize, a northeast-southwest range that has various peaks above 900 m elevation. The areas of the Caribbean and Pacific coasts, as well as the area around Lake Izabal, are from 0 to 50 m elevation. This highly variable topography has resulted in many habitat types, including thorn scrub forest, pine-oak forest, cloud forest, rainforest, savanna, various coniferous forests, and mangrove forest (Steyermark 1950).

This topographic diversity contributes greatly to the patterns of endemism. We have determined six areas of endemism for cloud forests in the country on the basis of passalid distributions (Fig. 1) (Schuster *et al.* 2000). Of the three groups (Passalidae, *Phyllophaga*, and *Chrysina*) we have studied most closely, passalids are the least vagile. With few exceptions, endemic passalids do not occur outside

of cloud forest habitat (Table 1) (e.g., *Heliscus yucatanus* Bates occurs only in the Yucatan Peninsula south to Lake Izabal in Guatemala). Endemism in the *Phyllophaga* "schizhorina" group and *Chrysina* is shown in (Tables 2 and 3).

Here we discuss the relationships among these endemic areas based on analyses of the faunal assemblages of Passalidae, *Chrysina*, the *Phyllophaga* "schizhorina" group, and complementary data of *Phanaeus* MacLeay, *Copris* Geoffroy, and *Geotrupes* Latreille. This information, together with phylogenetic analyses of *Proculus* Kaup (Schuster *et al.* 2003), allows us to infer possible migration routes and, together with geological information, possible vicariance events and/or times of colonization. Analyses of these relationships and similarity among endemic areas will provide information that could be decisive in determining priorities for conservation.

Materials and Methods

We collected Passalidae in Guatemala and surrounding areas during the last 30 years. Scarabaeidae have been collected intensively during the last 18 years. The Universidad del Valle de Guatemala collection of Scarabaeoidea includes approximately six Cornell cabinets of mostly Guatemalan material, and most of this material collected by us and José Monzón. Collections were made in each endemic area, including more than 30 cloud forests and other habitats. Passalids were collected by opening logs with an axe and/or machete. Specimens of *Chrysina* and the *Phyllophaga* "schizorhina" group were collected primarily at light traps with additional data from the literature (Monzón 1995, 2006; Morón-Ríos and Morón 2001; Morón 1990, 2003; Morón and Riley 2005; Morón and Blas 2006). The most intensely collected area by light trap is the south coastal volcanic regions, which have fewer endemic species of *Phyllophaga* "schizorhina" group.

Eight general areas of endemism of Passalidae were delineated by Schuster *et al.* (2000) (Fig. 1) and used for all focal taxa. To determine relationships between these areas of endemism, we plotted distributions of species of Passalidae (Table 1), *Chrysina* (Table 2) and the *Phyllophaga* "schizorhina" group (Table 3) and determined areas of distributional coincidence. Total numbers of endemic species were determined for each area.

Tens of thousands of specimens were collected. Areas that are comparatively deficient in collecting include: east Guatemala (area 7c), north Honduras (area 8), and, for *Phyllophaga*, Trifinio (area 6) and Sierra de Santa Cruz (area 5b). No data are available for possible areas of endemism (above 1,000 m altitude) in the Maya Mountains of Belize, although one endemic frog is known from there (Campbell and Vannini 1989).

For passalids and *Chrysina* we compared the similarities of assemblages among areas using the similarity index of Dice (1945) ($2a/2a+b+c$, where a = number of shared species between sites b and c; b = number of species exclusive to site b, and; c = number of species exclusive to site c). The Dice coefficients were subjected to cluster analysis using the unweighted pair-group method with arithmetic averages using the SPSS package (SPSS 1999). Species common to all areas were not considered (e.g., *Oileus sargi* [Kaup] and *Chrysina quetzalcoatl* [Morón]).

We included complementary data of the dung beetle genera *Phanaeus*, *Copris*, and *Geotrupes* obtained from specimens deposited at the Universidad del Valle de Guatemala collection and from literature (Delgado and Kohlmann 2001; Edmonds 1994; Howden 1964, 1974, 1980, 1994).

Results and Discussion

Areas of Endemism

Most previous discussions of biotic areas in Nuclear Central America (areas of endemism) have been based on phenetic analyses of related taxa, especially reptiles and amphibians (*e.g.*, Johnson 1989; Stuart 1943; Campbell and Vannini 1989). Here we compare phenetically two groups (Passalidae and *Chrysina* assemblages) using cluster analysis. We complement this analysis with a phylogenetic study of *Proculus* (Schuster *et al.* 2003) and a simple comparison of *Phyllophaga* “schizorhina” group assemblages. The hypotheses presented here will undoubtedly be modified as new species are discovered, new range distributions are determined, and more analyses are done.

On the basis of passalid distributions, eight areas of endemism were defined between western Honduras and Chiapas, Mexico (Schuster *et al.* 2000) (Fig. 1). Cluster analysis of these areas of endemism for Passalidae (Fig. 2) corroborates the general pattern described by Schuster *et al.* (2000). Schuster *et al.* (2000) referred to area 7d as La Tigra, Honduras; actually, it is the area of Santa Barbara (west of Lake Yojoa), and La Tigra is newly designated as area 9. Santa Barbara is apparently an area of transition between southeastern (area 7a) and southwestern (area 9) Honduras, similar to what occurs in La Union, Zacapa, between eastern Guatemala-southwestern Honduras (area 7) and Sierra de las Minas (area 5a). Most of northern and eastern Honduras are unexplored for passalids and *Phyllophaga* “schizorhina” group. The passalid cluster analysis (Fig. 2) also suggests that areas 1 (northern Chiapas) and 3 (western Cuchumatanes) are closely related. However, we consider them distinct on the basis of unique endemic species in each area (see Table 1).

Cluster analysis for *Chrysina* (Fig. 3) agrees in general with conclusions based on passalids with three exceptions. First, Trifinio (area 6) is grouped with La Unión (area 7b) and Merendon (area 8), the latter not being as separate from other areas as in the Passalidae. Second, Miramundo-Tecuamburro Volcano (area 7c) is grouped with the coastal volcanoes (areas 2 and 4) instead of grouping with the rest of areas 7a and 7b (La Union and El Portillo). Greater vagility (flight) may explain these area relationships for *Chrysina*. The main collecting site for area 7c (east Guatemala) is Miramundo-Tecuamburro Volcano, much closer to area 4 (coastal volcanoes, specifically, Agua Volcano) than to the rest of area 7 (La Union and, specifically, El Portillo, Honduras) and, thus, more accessible to beetles that are able to fly. Third, El Portillo in southern Honduras is isolated from all groups and not connected to areas 7b and 7c (La Union, Miramundo-Tecuamburro).

Stuart (1943, 1950, 1964), Schmidt and Stuart (1941), Campbell and Vannini (1989), and others have described faunal biotic areas for Guatemala and northern Mesoamerica, mostly for reptiles. These are not strictly comparable to our endemic areas because they include dry biomes, whereas endemic passalids, *Chrysina*, and the *Phyllophaga* “schizorhina” group do not occur there. Endemism of these scarabaeoid groups differs somewhat from that of most reptiles, because these beetles occur primarily in cloud forests and high montane areas, similar to what occurs in some salamanders. Johnson (1989) mentioned three endemic areas for reptiles in Chiapas: the Central Plateau (corresponding to our area 1), the southeastern Sierra Madre Highland (our area 2) and the northwestern Sierra Madre Highland, an area in northwest Chiapas bordering Oaxaca separated from the southeastern Sierra Madre Highland by a deep valley. We know of no passalid collections from this third area, which apparently does include cloud forest.

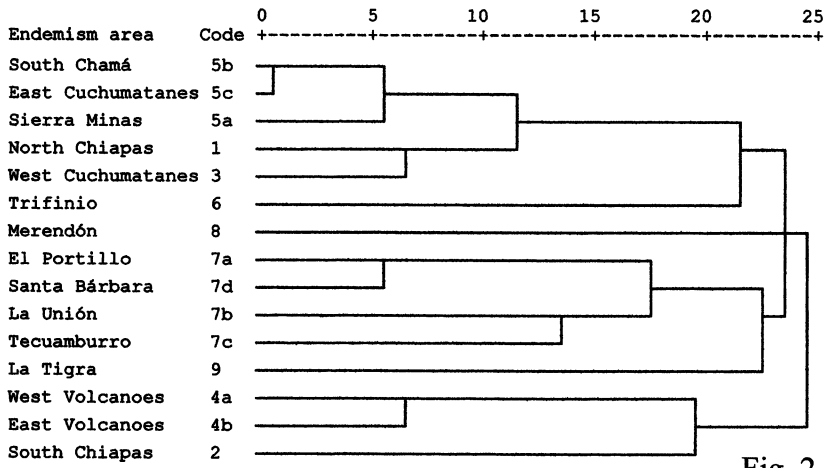


Fig. 2

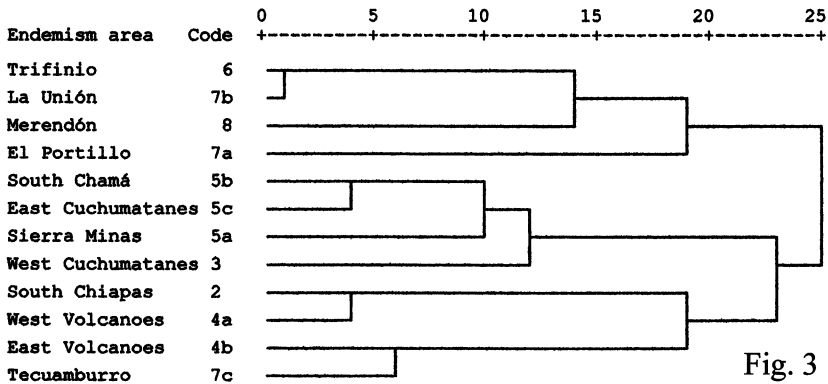


Fig. 3

Figs. 2-3. (2): Cluster analysis of *Passalidae* species in areas of endemism of Nuclear Central America. [Rescaled distance cluster combined, index is Dice, grouping is UPGMA.] (3): Cluster analysis of *Chrysina* species in areas of endemism of Nuclear Central America. [Rescaled distance cluster combined, index is Dice, grouping is UPGMA.]

Stuart (1943) and Campbell and Vannini (1989) concurred in defining the Cucumatanes area from their Quecchian area by the valley of the Rio Negro or Chixoy. This was the original idea for passalid area definition as well (Schuster 1992) until our recent exploration north of Uspantán indicated a passalid assemblage similar to that of the area further east. Therefore, we modified the border between areas 3 and 5 (east and west Cucumatanes), locating it somewhere between Nebaj and Macalajau. What geophysical or ecological barrier this represents or represented is unknown.

If we sum the total endemic species of the three taxa (*Passalidae*, *Chrysina*, and *Phyllophaga*) for each area of endemism, four areas stand out: area 5a (Sierra de las Minas) with 14 endemic species; area 8 (Merendón, including Sierra de Caral in Guatemala and Cusuco reserve in Honduras) with 12 endemic species; area 4a (west volcanoes, including Tacaná volcano shared between Guatemala and

Mexico) with 11 endemic species; area 3 (west Cuchumatanes) with 8 endemic species; and the under-collected area 1 (north Chiapas mountains) and area 2 (south Chiapas mountains) each with 6 endemic species. In terms of conservation, these results highlight the need for protected reserves, especially in area 4a (west volcanoes) and area 3 (west Cuchumatanes), regions that currently lack functional reserves.

Highland Biogeographic Scenarios

We proposed (Schuster and Cano 2005) the division of the highland cloud forest endemic areas into two groups: one to the north and one to the south of a barrier that correlates with the subhumid corridor of northern Central America (Stuart 1954). This dry corridor corresponds with a region from the Rio Motagua Valley to the Central Chiapas Depression. Six scarab taxa are associated with this division: Passalidae, *Chrysina*, *Phyllophaga*, *Copris*, *Geotrupes*, and *Phanaeus*.

Dendrograms for passalids and *Chrysina* (Figs. 2–3), as well as distribution data for *Phyllophaga* (Table 3), suggest a fundamental relationship among areas 1, 3, and 5, which are all Atlantic drainage areas (north Chiapas to the Sierra de las Minas) north of the subhumid corridor (see Fig. 5 in Schuster and Cano 2005). Additionally, the presence of *Chrysina purulensis* (Monzón and Warner) and *Proculus mniszewski* Kaup in the Mayan Mountains of Belize (Warner and Monzón 1993; Schuster *et al.* 2003) suggests a close relationship of the Mayan Mountains to area 5 (west Cuchumatanes to Sierra de las Minas). We know of no distributional data of the *Phyllophaga* “schizorhina” group (Table 3) from the Mayan Mountains. Nevertheless, though showing few species in common among areas, this group also suggests a close relationship among area 1 (north Chiapas), area 3 (Cuchumatanes), and area 5a (Sierra de las Minas) (*e.g.*, *P. izabalana* Morón, *P. javepacuana* Morón, *P. rugulosa* Blanchard, *P. submetallica* Bates, *P. mentalis* Saylor).

The *Phyllophaga* “schizorhina” data (Table 3) considers only Chiapan and Guatemalan species found above 800 m altitude. The data are in general concordance with those of Passalidae and *Chrysina* with the exception of *P. ginigra* Saylor¹ from Atlantic lowland forests (*e.g.*, Tikal, Petén, **New Country Record**). Nevertheless, certain differences are apparent for other groups and subgenera of *Phyllophaga* due to the fact that many *Phyllophaga* species are not limited to cloud forests. It is surprising that some areas (*e.g.*, 4a, west volcanoes), despite being well collected, have few species of the *Phyllophaga* “schizorhina” group, yet have many passalid and *Chrysina* species.

Further support for the linkage of areas 1, 3, and 5 is the distribution in each of these areas of *Copris matthewsi matthewsi* Delgado and Kohlmann (see Fig. 3 in Delgado and Kohlmann 2001), *Geotrupes guatemalensis unidentatus* Howden, and *Phanaeus amethystinus amethystinus* Harold. Also, the group that includes *Ogyges cakchiqueli* Schuster and Reyes-Castillo (*O. tzutuhili* Schuster and Reyes-Castillo, *O. kekchii* Schuster and Reyes-Castillo, *O. furcillatus* Schuster and Reyes-Castillo, *O. championi* [Bates], and *O. coxchicopi* Schuster *et al.*) is distributed in areas 1 (north Chiapas), 3, and 5a (Sierra de las Minas).

To the south of the subhumid corridor, southern Chiapas (area 2) and the Volcanic Area (area 4) are strongly associated endemic areas (Figs. 2–3). They share the passalids *Proculus goryi* (Melly) and *Pseudacanthus junctistriatus* Kuwert. The relationship between southern areas (area 2 [southern Chiapas], area 4 [volcanic chain], and area 7c [eastern volcanic chain]) is also supported by two

¹ Morón (2003) reported this species from tropical rain forests and subdeciduous tropical forests from 160–1,000 m elevation, from Ishuatán, Palenque and Ocozocuaula, Chiapas, México.

species recently described from Chiapas, *P. alvareztoroi* Morón and Blas and *P. acacoyahuana* Morón and Blas, and which we have found in Guatemala (on the southern slope of Volcan Atitlan and Cerro Miramundo near Pueblo Nuevo Viñas, respectively) (**New Country Records**). The endemic species of the *Phyllophaga* “schizorhina” group all occur in our areas of endemism (see Table 3).

The association of other southern regions is less clear based on cluster analyses of *Chrysina* and passalid beetles. Even so, further evidence of the linkage of the Volcanic Area area 4) to eastern Guatemala-southern Honduras (area 7) and Trifinio (area 6) is supported by the species group formed by *Ogyges laevis* (Kaup), *O. hondurensis* Schuster and Reyes-Castillo, and *O. politus* (Hincks). The dung beetle, *Copris matthewsi pacificus* Delgado and Kohlmann, links all these areas as do *Geotrupes onitidipes* Bates, *G. guatemalensis guatemalensis* Bates, and *Phanaeus amethystinus guatemalensis* Harold. Phylogenetic analysis of *Proculus* species (Schuster *et al.* 2003) suggests colonization of the volcanoes (area 4) from area 7 (eastern Guatemala-southern Honduras).

Areas 1, 3, and 5 (northern Chiapas through Sierra de las Minas, north of the subhumid corridor) are completely different with respect to the composition of passalid species compared with areas 2 and 4 (southern Chiapas and volcanic area, south of the subhumid corridor). Only in eastern Guatemala (from La Unión, Zacapa) and eastward through the Sierra de Merendon does some mixing of passalid species occur among areas (*e.g.*, *Proculus mniszewski* in areas 5a [Sierra de las Minas], 7b [La Unión], 8 [Sierra de Merendon]; *Phyllophaga mentalis* Saylor and *Popilius* n. sp. 2 in areas 5a [Sierra de las Minas] and 7b [La Unión]). Evidence for a relationship between areas 7b-8 (La Unión-Sierra de Merendon) and 3-5 (Cuchumatanes-Sierra de las Minas) includes the presence of the dung beetle, *Copris mubilosus* Kohlmann *et al.*, from Cerro Azul (area 8; Copán, Honduras, 1,400 m), La Unión, Zacapa, (area 7b), Purulhá, Baja Verapaz (area 5a) and Barillas, Huehuetenango (area 3) (Kohlmann *et al.* 2003). Also, species in the *Petrejoides* “reyesi” group, including *P. reyesi* Schuster (La Tigra, area 7d), *P. pokomchii* Schuster (Sierra de las Minas, area 5a), *P. salvadorae* Schuster (Trifinio, area 6), *P. guatemalae* Reyes-Castillo and Schuster (Cuchumatanes, area 3), and *P.* n. sp. (El Pital, El Salvador, 7a) are each distributed on different, isolated mountain ranges, mostly to the north of the corridor *except* in Honduras, El Salvador, and Trifinio. These mountains are old compared with the coastal volcanoes, most of which are probably late Pleistocene from the last 100,000 years (S. Bonis pers. comm. 1999). The coastal volcanoes (area 4) were not colonized by the *Petrejoides* “reyesi” group, thus indicating a possible pre-Wisconsinian colonization at their present locations by the ancestral species. This region of the lower Motagua Valley seems to have been a corridor for dispersal among these areas in the Pleistocene.

Passalids, *Chrysina* species, and the group of *Phyllophaga* species studied belong to Halffter’s Mesoamerican Distribution Pattern (Halffter 1978). A Nearctic element is represented by *Geotrupes* species, whose distribution extends south to El Trifinio (*G. guatemalensis tridentatus* Howden from Cerro Montecristo), Chalatenango in El Salvador (*G. onitidipes* Bates) (Howden 1964, 1974), and one unknown locality in Honduras (*G. felschei* Nonfried) (Howden 1994).

Lowland Biogeographic Scenarios

Concerning lowland, tropical wet forests, the Atlantic slope scarabaeoid fauna seems to be richer than the Pacific slope fauna. For example, three species of passalids of the Atlantic slope don’t occur on the Pacific slope (*Verres cavicollis*

Bates, *V. corticicola* [Truqui], and *Heliscus yucatanus* [Bates]). *Chrysina diversa* (Ohaus), from the Atlantic slope (Alta Verapaz), is absent from the Pacific.

Differences in biogeographic diversity are also observed in populations of *Passalus punctiger* Lepeletier and Serville on the Pacific and Atlantic slopes of Guatemala (Schuster 1983). Atlantic and Pacific Coast populations are isolated from each other in Guatemala. Length of individuals in the Pacific slope population average 39.8 mm (n=24), while those of the Atlantic slope average 34.7 mm (n=27). We are investigating possible DNA differences between these populations.

The origin of the scarabaeoid fauna of the tropical lowland forests appears to be from the south, with some species only reaching as far north as Izabal southeast of the Motagua valley (e.g., *Chrysina luteomarginata* [Ohaus], *Passalus jansonii* [Bates], *Phyllophaga solisiana* Morón). This is similar to other organisms such as the bushy-tailed olingo, *Bassaricyon gabbii* Allen (Ordoñez *et al.* 1999–2000).

Lacking are studies of scarabs endemic to dry areas, such as the Motagua valley and Nentón area. Nevertheless, the distribution of dung beetles (e.g., *Phanaeus demon* Laporte-Castelnau, *Ph. tridens pseudofurcosus* Balthasar, *Ph. eximius* Bates, *Canthon humectus* [Say], and *C. deyrollei* Harold, among others) suggests that the somewhat isolated valleys of the dry corridor of Stuart (1954) form a biogeographical unit.

Conclusions

With respect to the original question as to what can Scarabaeoidea contribute to the knowledge of the biogeography of Guatemala, analysis of cloud forest scarabaeoids has resulted in an understanding of areas of endemism for the region and knowledge concerning relationships of these areas. Scarabaeoids are perhaps the best known invertebrates with respect to taxonomy and distribution in the Nuclear Central American region. They have been used in the prioritization of areas for conservation to support the establishment of protected reserves such as the Sierra de las Minas Biosphere Reserve, recognized by UNESCO (Schuster 1988; Schuster *et al.* 2000). In Guatemala, Passalidae now are being used as a major component of Technical Studies for Declaration of Protected Areas of cloud forests for the Parque Nacional Cerro El Amay, Quiché Department (CONAP 2005a) and Reserva de Vida Silvestre Volcán Lacandón, Quetzaltenango Department (CONAP 2005b). Evaluation of the Area Protegida Trinacional Montecristo (Trifinio), shared between Guatemala, El Salvador, and Honduras, also included the study of passalid beetles (Komar *et al.* 2005). Knowledge of *Chrysina* and *Phyllophaga* species presented here should also be incorporated into decision-making for prioritization of conservation areas.

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Table 1. Continued.

Species of Passalidae	Areas and subareas of endemism in Nuclear Central America														
	1	2	3	4a	4b	5a	5b	5c	6	7a	7b	7c	7d	8	9
<i>Pse. n. sp. 2*</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Publius granulipennis</i> (Zang)*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spurius dichotomus</i> Zang	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1
<i>Vindex sculptilis</i> Bates	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0
<i>Vindex synelitris</i> Gravely*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 1*</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 2*</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 3*</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 4*</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 5*</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Vindex n. sp. 6*</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 7*</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 8*</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Vindex n. sp. 9*</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Xylopassaloides chortii</i> Schuster*	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>X. moxi</i> Schuster*	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>X. pereirae</i> R-C <i>et al.</i> *	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>X. pterocavis</i> R-C <i>et al.</i> *	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>X. schusteri</i> R-C <i>et al.</i>	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0
TOTAL SPECIES**	12	7	15	12	5	22	10	9	5	4	4	3	3	8	3
TOTAL ENDEMICS	2	5	6	7	0	9	0	0	4	0	0	2	0	7	1

Table 2. Species of *Chrysina* by areas of endemism for Guatemala. [*=Endemic species. See (Fig. 1) for areas of endemism.]

Species of <i>Chrysina</i>	Areas and subareas of endemism in Nuclear Central America												
	1	2	3	4a	4b	5a	5b	5c	6	7a	7b	7c	8
<i>Ch. alfredolau</i> (Hawks 1995)	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Ch. auropunctata</i> (Ohaus 1913)	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Ch. centralis</i> (Morón 1990)*	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Ch. cusuquensis</i> (Curoe 1994)*	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ch. diversa</i> (Ohaus 1912)	1	0	0	0	0	0	1	1	0	0	0	0	0
<i>Ch. ericsmithi</i> (Monzón & Cano 1999)*	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ch. guatemalensis</i> (Monzón <i>et al.</i> 1999)*	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Ch. halffieri</i> (Morón 1990)	1	0	1	0	0	0	0	0	0	0	0	0	0
<i>Ch. karschi</i> (Nonfried 1891)	0	0	0	0	0	0	0	0	1	0	1	0	1
<i>Ch. luteomarginata</i> (Ohaus 1913)	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ch. moroni</i> (Curoe & Beraud 1994)	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Ch. pastori</i> (Curoe 1994)*	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ch. pehlkei</i> (Ohaus 1930)	0	0	0	1	1	0	0	0	0	0	0	1	0
<i>Ch. prototelica</i> (Morón & Howden 1992)	0	0	0	0	1	1	0	0	0	0	0	1	0
<i>Ch. psittacina</i> (Sturm 1843)*	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Ch. purulhensis</i> (Monzón & Warner 1993)	0	0	1	0	0	1	1	1	0	0	0	0	0
<i>Ch. quetzalcoatli</i> (Morón 1990)	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Ch. quiche</i> (Morón 1990)	0	1	1	1	0	1	1	1	0	0	0	0	0
<i>Ch. rodriguezi</i> (Boucard 1878)	0	0	1	0	0	1	0	1	0	0	0	0	0
<i>Ch. schusteri</i> (Monzón <i>et al.</i> 1999)*	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Ch. spectabilis</i> (Ratcliffe <i>et al.</i> 1992)*	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ch. strasseni</i> (Ohaus 1924)	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Ch. tecunumani</i> (Cano & Morón 1994)*	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Ch. triumphalis</i> Morón 1990	0	1	1	1	0	0	0	0	0	0	0	0	0
<i>Ch. turckheimi</i> (Ohaus 1913)	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Ch. n. sp. 1</i>	0	0	1	0	0	1	0	1	0	0	0	0	0
<i>Ch. n. sp. 2</i>	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Ch. n. sp. 3*</i>	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Ch. n. sp. 4*</i>	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Ch. n. sp. 5</i>	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Ch. n. sp. 6*</i>	0	0	0	0	0	0	0	0	0	1	0	0	0
TOTAL SPECIES	3	7	11	10	6	8	4	7	2	2	3	3	8
TOTAL ENDEMICS	0	1	1	3	0	2	0	0	0	1	0	0	4

